Copyrighted Material

TUNA

PHYSIOLOGY, ECOLOGY, AND EVOLUTION

EDITED BY
BARBARA A. BLOCK
E. DONALD STEVENS

Copyrighted Material

Copyrighted Material

Front cover photograph: A close-up view of Bluefin Tuna (*Thunnus maccoyii*). Photo © Art Womack, used with permission.

Frontispiece: Yellowfin Tuna (*Thunnus albacares*) seen in Magdalena Bay, Baja California, Mexico. Photo © Richard Herrmann/Innerspace Visions, used with permission.

This book is printed on acid-free paper. ♾

Copyright © 2001 by ACADEMIC PRESS

All Rights Reserved.
No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system, without permission in writing from the publisher.

Requests for permission to make copies of any part of the work should be mailed to: Permissions Department, Harcourt Inc., 6277 Sea Harbor Drive, Orlando, Florida 32887-6777

Explicit permission from Academic Press is not required to reproduce a maximum of two figures or tables from an Academic Press chapter in another scientific or research publication provided that the material has not been credited to another source and that full credit to the Academic Press chapter is given.

Academic Press
A division of Harcourt, Inc.
525 B Street, Suite 1900, San Diego, California 92101-4495, USA
http://www.academicpress.com

Academic Press
Harcourt Place, 32 Jamestown Road, London NW1 7BY, UK
http://www.academicpress.com

Library of Congress Catalog Card Number: 201090604

International Standard Book Number: 0-12-350443-0

PRINTED IN THE UNITED STATES OF AMERICA
01 02 03 04 05 06 SB 9 8 7 6 5 4 3 2 1

Copyrighted Material

Volume 19, Pages 1-468 (2001)

◄ Previous vol/iss Next vol/iss ►

Tuna: Physiology, Ecology, and Evolution

Edited by: Barbara Block and E. Stevens
ISBN: 978-0-12-350443-2

Add to my Quick Links

Email Articles Open All Previews

articles **1 - 15**

1. **Contributors**
Pages ix-x
Preview Purchase PDF (66 K) |
Related Articles

2. **Preface**
Pages xi-xiii
Barbara A. Block, E. Donald Stevens
Preview Purchase PDF (207 K) |
Related Articles

3. **Systematics of the tunas and mackerels (Scombridae)**
Pages 1-33
Bruce B. Collette, Carol Reeb, Barbara A. Block
Preview Purchase PDF (2248 K) |
Related Articles

4. **Tuna metabolism and energetics**
Pages 35-78
Keith E. Korsmeyer, Heidi Dewar
Preview Purchase PDF (4460 K) |
Related Articles

5. **The cardiovascular system of tunas**
Pages 79-120
Richard W. Brill, Peter G. Bushnell
Preview Purchase PDF (4499 K) | Related Articles

6. **Anatomical and physiological specializations for endothermy**
Pages 121-165
Jeffrey B. Graham, Kathryn A. Dickson
Preview Purchase PDF (4573 K) | Related Articles

7. **Advances in acoustic, archival, and satellite tagging of tunas**
Pages 167-224
John Gunn, Barbara Block
Preview Purchase PDF (11483 K) | Related Articles

8. **Reproductive biology of tunas**
Pages 225-270
Kurt M. Schaefer
Preview Purchase PDF (9867 K) | Related Articles

9. **7. Mechanical design for swimming: muscle, tendon, and bone**
Pages 271-311
Mark W. Westneat, Stephen A. Wainwright
Preview Purchase PDF (29231 K) | Related Articles

10. **8. Swimming and muscle function**
Pages 313-344
John D. Altringham, Robert E. Shadwick
Preview Purchase PDF (4804 K) | Related Articles

11. **Tuna oceanography—an applied science**
Pages 345-389
Gary D. Sharp
Preview Purchase PDF (4320 K) | Related Articles

12. **10. Tunas in captivity**
Pages 391-412
Charles J. Farwell
Preview Purchase PDF (1831 K) | Related Articles

13. **11. Tuna conservation**
Pages 413-459
Carl Safina
Preview Purchase PDF (3379 K) | Related Articles

14. **Index**
Pages 461-466

Preview Purchase PDF (274 K) |
Related Articles

15. **Other volumes in the fish physiology series**
Pages 467-468
Preview Purchase PDF (67 K) |
Related Articles

CONTRIBUTORS

The numbers in parentheses indicate the pages on which the authors' contributions begin.

JOHN ALTRINGHAM *(313), School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom*

BARBARA BLOCK *(1, 167), Hopkins Marine Station, Stanford University, Pacific Grove, California 93950*

RICHARD BRILL *(79), National Marine Fisheries Service, Southwest Fisheries Science Center, Honolulu Laboratory, Honolulu, Hawaii 96822-2396*

PETER BUSHNELL *(79), Department of Biological Sciences, Indiana University South Bend, South Bend, Indiana 46634-7111*

BRUCE COLLETTE *(1), NMFS Systematics Lab, National Museum of Natural History, Washington, DC 20560-0153*

HEIDI DEWAR *(35), Pfleger Institute of Environmental Research, Oceanside, California 92054*

KATHRYN DICKSON *(121), Department of Biological Science, California State University Fullerton, Fullerton, California 92834*

CHARLES A. FARWELL *(391), Monterey Bay Aquarium, Monterey, California 93940*

JEFFREY GRAHAM *(121), Center for Marine Biotechnology and Biomedicine, Scripps Institute of Oceanography, University of California at San Diego, La Jolla, California 92093–02045*

JOHN S. GUNN *(167), CSIRO Marine Research, Hobart, Australia 7000*

KEITH KORSMEYER *(35), Hawaii Pacific University, Kaneohe, Hawaii 96744*

CAROL REEB *(1), Hopkins Marine Station, Stanford University, Pacific Grove, California 93950*

CARL SAFINA *(413), Living Oceans Program, National Audubon Society, Islip, New York 11751*

ROBERT SHADWICK *(313), Marine Biology Research Division, Scripps Institute of Oceanography, University of California at San Diego, La Jolla, California 92093*

KURT SCHAEFER *(225), Inter-American Tropical Tuna Commission, La Jolla, California 92093*

GARY SHARP *(345), Center for Climate/Ocean Resources Study, Monterey, California 93940*

STEPHEN WAINWRIGHT *(271), Department of Zoology, Duke University, Durham, North Carolina 27706*

MARK WESTNEAT *(271), Department of Zoology, Field Museum of Natural History, Chicago, Illinois 60605-2496*

PREFACE

Watching a tuna swim, you can't help but be impressed by its power, grace, and speed. If you've tried to catch a tuna on a fishing line, you have undoubtedly discovered its tremendous strength. Its superbly streamlined shape reflects its ceaseless activity. Even the scientific family name of the tunas, *Thunnus*, comes from the Greek verb thuno—meaning rush. Almost 40 years ago the real life of tunas was hinted at when a bluefin tuna tagged in the Bahamas was caught less than 50 days later off the coast of Norway, 6700 km distant (Mather, 1962). This migratory lifestyle and the extraordinary anatomical and physiological features that permit it have interested observers since Aristotle. Hunting, catching, and even the study of tunas have long been intertwined with ancient cultures and traditions (Maggio, 2000). Over the past two decades, tuna science has sparked new interest and the participation of a large number of very talented biologists using innovative techniques.

Tunas are, of course, very valuable and this has raised interest in the fish as a commodity. Although they constitute less than 5% of the world's commercial catch by weight, they contribute a much larger fraction by dollar value. Bluefin tunas are among the most valuable fish in the sea. Nearly every year since the mid-1970s, another fish has been 'awarded' a new highest-ever price, $10,000, $12,000 . . . to upward of $35,000. In January 2001 an individual fish sold for $175,000 in Tokyo. This value has created huge incentive for those trying to catch tunas for profit. It has also sparked concern and passion among those trying to prevent bluefin tuna from being fished to extinction.

This volume reflects the growing interests of two types of researchers that study tuna: one driven by the discovery of the extraordinary morphological and physiological features that make tuna unique, and the other by fisheries' concerns. Our book is an attempt to synthesize and integrate both basic and applied research within one volume. We examine the relationships of tunas, mackerels, and bonitos; their evolutionary history; the recent technological advances in our knowledge of their metabolism, cardiovascular physiology, and reproductive biology; and the physiological ecology and oceanography of tunas in the oceans.

The unique features of the circulatory systems and internalization of the slow-oxidative swimming muscles of the tunas prompted Kishinouye (1923) to

place tunas in their own order, the Plecostei, to separate them from all other teleosts. This suggestion was not generally accepted by systematists, but highlights the uniqueness that many early researchers noted. The chapter by Collette, Reeb, and Block shows us that the systematics of tunas and their relatives is controversial and requires further study.

Despite the practical challenges of working with tunas that limit rapid advances in studies of tuna physiology and morphology, this volume demonstrates that significant findings have emerged from the past two decades of laboratory and field research. Tunas have exceptional cardiac performance, high metabolic rates, and endothermic traits. Tunas utilize metabolic heat to warm the muscle, viscera, brain, and eyes, but the heart operates at ambient water temperatures. Just to supply oxygen to the tuna's endothermic swimming muscles requires an extraordinary metabolism and a unique cardiac system when compared to all other teleosts. Korsmeyer and Dewar summarize information on metabolism and aerobic capacity of tunas, and Brill and Bushnell focus on the cardiovascular and respiratory features required to acquire and deliver oxygen to the tissues. Graham and Dickson review the recent laboratory studies on the thermoregulation of tunas and examine morphological and physiological traits associated with endothermy in a phylogenetic context. Westneat and Wainwright use gross dissection of tunas and their relatives to provide information on the linkages between tendon, muscle, and bone that make tunas efficient swimmers. This chapter is complemented by a chapter on physiology of the swimmers muscles by Altringham and Shadwick. They apply modern techniques of muscle physiology of hydrodynamical analysis to tuna swimming and show the mechanical advantage of warm muscles. In addition, they provide an analysis of the characteristic swimming form of the group: thunniform swimming.

The chapter by Schaefer is a fascinating account of the reproductive lifestyle and its huge annual metabolic cost in tunas. All tunas are oviparous, multiple spawners and shed their gametes directly into the sea at locales where sea-surface temperatures are warm. For some species such as the giant bluefins, this brief period in warm waters may be the most physiologically demanding. The chapter by Sharp shows that considerable insight into tuna lifestyles has been achieved by looking when, where, and how commercial fishers seek and catch them. We learn that tuna are constrained to some extent by the availability of oxygen and appropriate water temperatures and that these constraints depend on time of day, season, stage of development, and reproductive status. The tuna lifestyle seems to have three phases: feeding, traveling, and reproduction. Technology has had the greatest impact in revealing details about the lifestyle of tunas. The major breakthrough is the development of devices that can record and archive data so that it is no longer essential to follow a fish with a ship. We knew tuna had a capacity for huge migrations, but little was known about the day-to-day life of a tuna. The chapter by Gunn and Block reveals much in this regard. Conventional tag data yielded

two data points (release and capture location). Modern tags can reveal depth, external and internal temperature every few minutes, and daily locations yielding tens of thousands of data points. Before there was a paucity; now we may be overwhelmed by the volume of data. Over 20,000 days of archival data have been collected in the past five years and knowledge of what tunas really do is becoming a reality.

By increasing knowledge about tunas we can hope to ensure their future on Earth. This book appears at a time when it is more vital than ever to begin to close the gap between what we know about tunas and what we need to know. Tunas are apex pelagic predators who are threatened by little except expansion of our own species. As Carl Safina eloquently writes in his chapter, "Can tunas bear the appetite of a world with 6 billion people?" Tunas are increasingly being retained in pens for growout, study, and display, as Farwell describes in his chapter, "Tunas in Captivity." Scientists and "ranchers" alike seek to raise tunas through their life cycle for knowledge as well as profit.

We express our sincerest thanks to the authors for their contributions and to the reviewers who enriched their content. The Block and Stevens labs helped throughout the process and we thank our students for their contributions. We dedicate our book to the two Franks: Carey and Mather. Frank Carey inspired many of us to think more about how and why tunas stay warm and pioneered the study of tunas in the wild. Frank Mather spent a lifetime trying to figure out the puzzle, which remains unsolved to this day, of the movements of the most noble fish in the sea, the Atlantic bluefin tuna. They shared their enthusiasm for tuna and the sea first with one another, and then just as enthusiastically with us. We hope this volume reflects their spirit and commitment to tuna biology and scientific excellence.

Barbara A. Block
E. Donald Stevens

Kishinouye, K. (1923). Contributions to the comparative study of the so-called scombroid fishes. *J. Coll. Agric. Imp. Univ. Tokyo* **8**, 293–475.

Maggio, T. (2001). *Mattanza*. The Ancient Sicilian Ritual of Bluefin Tuna Fishing. Penguin, New York.

Mather, F. (1962). Transatlantic migration of two large bluefin tuna. *J. Conseil Perm. Int. Exploration Mer.* **27**, 325–327.

1

SYSTEMATICS OF THE TUNAS AND MACKERELS (SCOMBRIDAE)

BRUCE B. COLLETTE
CAROL REEB
BARBARA A. BLOCK

I. Morphological Systematics
  A. Gasterochismatinae Lahille, 1903
  B. Subfamily Scombrinae Bonaparte, 1831
II. Molecular Systematics
  A. Are Billfishes Scombroid Fishes?
  B. Is Gasterochismatinae a Sister Group to the Scombrinae?
  C. Can Molecular Phylogenies Resolve the Thunnini and Sardini Tribes?
  D. Problems Caused by Partial Sequences and Homoplasy
  E. Are *Thunnus* Monophyletic?
  F. Has Mitochondrial Introgression Occurred between Bluefin and Albacore Tuna?
  G. Can Molecular Data Resolve the Relationships among Spanish Mackerels?
  H. Is *Scomber scombrus* Generically Different from *Scomber japonicus* and *Scomber australasicus*?
III. Conclusions

The Scombridae is a family of 15 genera and about 50 species of epipelagic marine fishes (see Table I). They possess many morphological and physiological adaptations that are of great interest to physiologists and evolutionary biologists. Mackerels, Spanish mackerels, bonitos, and tunas form the basis of important commercial and recreational fisheries throughout tropical and temperate waters of the world.

The currently accepted classification (Collette and Nauen, 1983; Collette *et al.*, 1984) of the mackerels and tunas (family Scombridae) within the suborder Scombroidei (Figure 1) is largely based on classical morphological studies of Kishinouye (1923), Godsil and co-workers (e.g., Godsil and Byers, 1944; Godsil, 1954), and Johnson (1986), and research by Collette with a series of co-workers

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

Table I
Synopsis of Scombrid Classification

Subfamily Gasterochismatinae Lahille, 1903
Gasterochisma Richardson, 1845
Gasterochisma melampus Richardson, 1845
Subfamily Scombrinae Bonaparte, 1831
Tribe Scombrini Bonaparte, 1831
Rastrelliger Jordan and Starks, 1908
Rastrelliger brachysoma (Bleeker, 1851)
Rastrelliger faughni Matsui, 1967
Rastrelliger kanagurta (Cuvier, 1816)
Scomber Linnaeus, 1758
Scomber australasicus Cuvier in Cuvier and Valenciennes, 1832
Scomber japonicus Houttuyn, 1782
Scomber colias Gmelin, 1789
Scomber scombrus Linnaeus, 1758
Tribe Scomberomorini Starks, 1910
Acanthocybium Gill, 1862
Acanthocybium solandri (Cuvier in Cuvier and Valenciennes, 1832)
Grammatorcynus Gill, 1862
Grammatorcynus bicarinatus (Quoy and Gaimard, 1825)
Grammatorcynus bilineatus (Rüppell, 1836)
Scomberomorus Lacepède, 1801
Scomberomorus brasilensis Collette, Russo, and Zavala-Camin, 1978
Scomberomorus cavalla (Cuvier, 1829)
Scomberomorus commerson (Lacepède, 1800)
Scomberomorus concolor (Lockington, 1879)
Scomberomorus guttatus (Bloch and Schneider, 1801)
Scomberomorus koreanus (Kishinouye, 1915)
Scomberomorus lineolatus (Cuvier in Cuvier and Valenciennes, 1831)
Scomberomorus maculatus (Mitchill, 1815)
Scomberomorus multiradiatus Munro, 1964
Scomberomorus munroi Collette and Russo, 1980
Scomberomorus niphonius (Cuvier in Cuvier and Valenciennes, 1832)
Scomberomorus plurilineatus Fourmanoir, 1966
Scomberomorus queenslandicus Munro, 1943
Scomberomorus regalis (Bloch, 1793)
Scomberomorus semifasciatus (Macleay, 1883)
Scomberomorus sierra Jordan and Starks in Jordan, 1895
Scomberomorus sinensis (Lacepède, 1800)
Scomberomorus tritor (Cuvier in Cuvier and Valenciennes, 1832)
Tribe Sardini Jordan and Evermann, 1896
Cybiosarda Whitley, 1935
Cybiosarda elegans (Whitley, 1935)
Gymnosarda Gill, 1862
Gymnosarda unicolor (Rüppell, 1836)
Orcynopsis Gill, 1862
Orcynopsis unicolor (E. Geoffroy St. Hilaire, 1817)

Sarda Cuvier, 1829
Sarda australis (Macleay, 1881)
Sarda chiliensis chiliensis (Cuvier in Cuvier and Valenciennes, 1832)
Sarda chiliensis lineolata Girard, 1859
Sarda orientalis (Temminck and Schlegel, 1844)
Sarda sarda (Bloch, 1793)
Tribe Thunnini Starks, 1910
Allothunnus Serventy, 1948
Allothunnus fallai Serventy, 1948
Auxis Cuvier, 1829
Auxis Cuvier, 1829
Auxis rochei rochei (Risso, 1810)
Auxis rochei eudorax Collette and Aadland, 1996
Auxis thazard thazard (Lacepède, 1800)
Auxis thazard brachydorax Collette and Aadland, 1996
Euthynnus Lütken, 1882
Euthynnus affinis (Cantor, 1849)
Euthynnus alletteratus (Rafinesque, 1810)
Euthynnus lineatus Kishinouye, 1920
Katsuwonus Kishinouye, 1923
Katsuwonus pelamis (Linnaeus, 1758)
Thunnus South, 1845
(*Thunnus* South, 1845)
Thunnus alalunga (Bonnaterre, 1788)
Thunnus maccoyii (Castlenau, 1872)
Thunnus obesus (Lowe, 1839)
Thunnus thynnus (Linnaeus, 1758)
Thunnus orientalis (Temminck and Schlegel, 1844)
(*Neothunnu* Kishinouye, 1923)
Thunnus albacares (Bonnaterre, 1788)
Thunnus atlanticus (Lesson, 1831)
Thunnus tonggol (Bleeker, 1851)

starting in the 1960s (e.g., Gibbs and Collette, 1967; Collette and Chao, 1975; Collette and Russo, 1985b; Carpenter *et al.,* 1995; Collette and Gillis, 1992; Collette and Aadland, 1996; Collette, 1999). Recently, a number of investigators have begun to test portions of this classification with molecular methods using both nuclear and mitochondrial DNA (mtDNA), raising some taxonomic questions and controversies (Bartlett and Davidson, 1991; Block *et al.,* 1993; Finnerty and Block, 1995; Chow and Kishino, 1995; Elliot and Ward, 1995; Alvarado Bremer *et al.,* 1996). This chapter presents a synopsis of scombrid systematics based on classical morphological characters followed by an examination of some of these hypothesized relationships using genetic data. In the future a combination of molecules and morphology should provide the best approximation of relationships among scombrids.

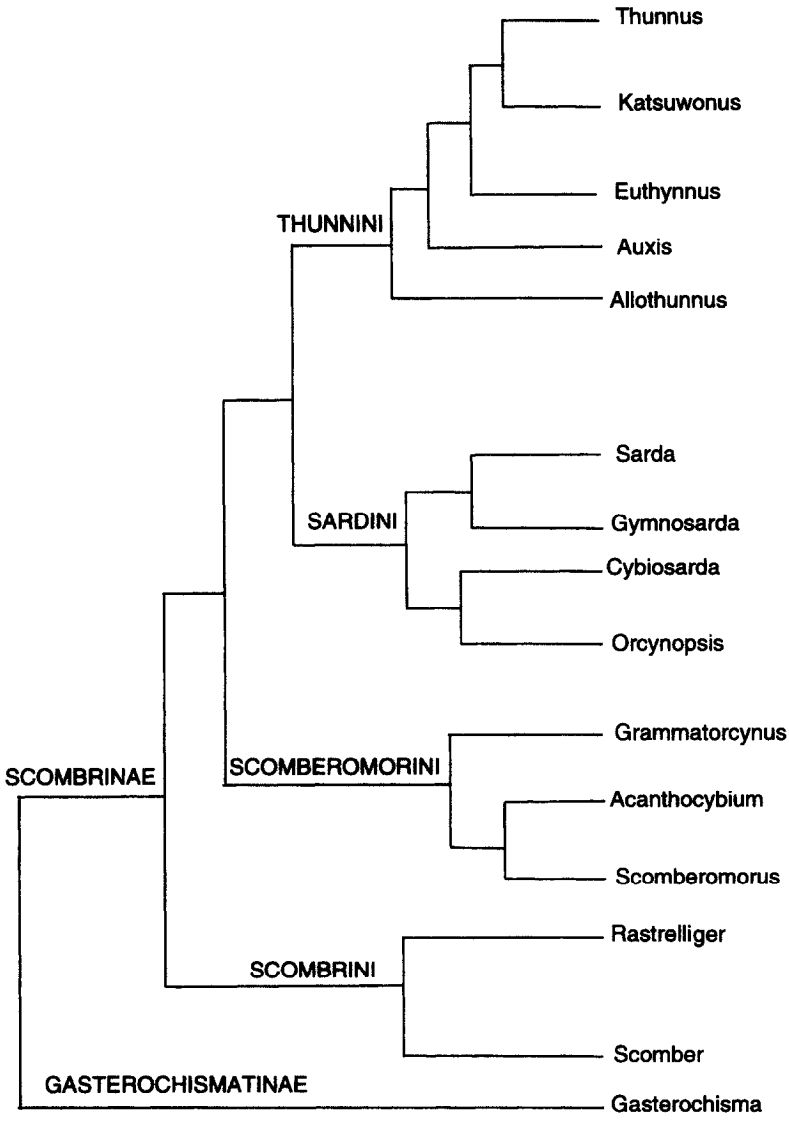


Fig. 1. Morphological tree of the family Scombridae (from Collette and Russo, 1985a), with permission.

I. MORPHOLOGICAL SYSTEMATICS

A. Gasterochismatinae Lahille, 1903

1. *Gasterochisma* Richardson, 1845

This distinctive monotypic genus is of a different and more primitive evolutionary lineage than the other scombrids. *Gasterochisma melampus* Richardson, 1845, appears different enough morphologically from other scombrids that it may well belong in a separate family. It has very large cycloid scales and two anterior projections of the swim bladder that extend into the back of the skull, close to the inner ear. The pelvic fins are huge in juveniles but become proportionally smaller as the fish increases in size. At all sizes the pelvic fins fit into a groove much as the first dorsal spines do in all scombrids. There is a thick layer of fat under the scales, perhaps an adaptation to the cold waters of its habitat around the world at low latitudes of the Southern Ocean. It has a brain heater derived from the lateral extraocular muscle, which is distinct in its muscular origin from the heater organ of the billfishes (Block, 1994). *Gasterochisma* lacks the median keel on the caudal peduncle and has only the pair of small keels on each side of the base of the caudal fin that are characteristic of all scombrids. *Gasterochisma* reaches a large size (over 1320 mm fork length). The number of vertebrae are 21 precaudal plus 23 caudal.

B. Subfamily Scombrinae Bonaparte, 1831

The subfamily Scombrinae is composed of two groups of two tribes. The more primitive mackerels (Scombrini) and Spanish mackerels (Scomberomorini) have a distinct notch in the hypural plate, lack any bony support for the median fleshy caudal peduncle keels, and do not have the penultimate vertebral centra greatly shortened.

1. Tribe Scombrini Bonaparte, 1831

Two genera of mackerels have been recognized, *Scomber* and *Rastrelliger*, each with three species (Matsui, 1967). Mackerels have small conical teeth and many gill rakers. They have the fewest vertebrae (31) in the family and only two small caudal peduncle keels, lacking the median keel found in higher scombrids. *Scomber* and *Rastrelliger* differ in a number of anatomical characters (Matsui, 1967). For *Scomber*, these characters include the following: teeth present on the vomer and palatines, last branchiostegal ray only slightly flattened, 12–28 interneural bones under first dorsal fin, first haemal spine somewhat flattened and bent backward (Matsui, 1967, Figure 4), first interhaemal bone anterior to haemal spine of 15th vertebra, and finally, vertebrae 31 and either 13 or 14 being precaudal while vertebrae 17 or 18 are caudal.

Matsui (1967) recognized three species of *Scomber*: *S. scombrus* Linnaeus, 1758; *S. australasicus* Cuvier, 1832; and *S. japonicus* Houttuyn, 1782, a polytypic worldwide antitropical species. The species differ in a series of characters summarized by Matsui (1967, Table 5). These characters include the sculpturing of the skull, number of precaudal vertebrae (13 in *S. scombrus*; 14 in the other two species), arrangement of palatine teeth, number of interneural bones under the first dorsal fin (12–15 in *S. japonicus,* 15–20 in *S. australasicus,* and 21–28 in *S. scombrus*), number of first dorsal spines, relative length of space between dorsal fins, presence of swim bladder (absent only in *S. scombrus*), and color pattern.

Scomber scombrus is restricted to the North Atlantic, with populations in both the western and the eastern North Atlantic. *Scomber australasicus* has been considered to be restricted to the Pacific Ocean and southeast Indian Ocean, with major populations in the northwestern Pacific—Japan, Taiwan, and Philippines—the southwestern Pacific, Australia, and New Zealand, plus a small population in the Revillagigedo Islands off the coast of Mexico in the eastern Pacific. However, more recently, it has been found to occur in the northern Indian Ocean and Red Sea (Baker and Collette, 1998).

Scomber japonicus has been considered to be the most widespread species in the genus, sympatric with *S. scombrus* in the North Atlantic and with *S. australasicus* in the northwestern Pacific. It is found, antitropically, in separate populations in all oceans. Most populations have been named as species or subspecies at some time in the past: *japonicus* Houttuyn, 1782, from Japan; *colias* Gmelin, 1789, from the eastern Atlantic; *grex* Mitchill, 1815, from the western Atlantic; *diego* Ayres, 1857, from the northeastern Pacific; *peruanus* Jordan and Hubbs, 1925, from the southeastern Pacific; and *marplatensis* Lopez, 1935, from Argentina. Recent molecular evidence (see Section II) combined with morphological data convinced Collette (1999) to recognize the Atlantic *S. colias* as a distinct species, separate from the Indo-Pacific *S. japonicus.*

Because both *S. japonicus* and *S. australasicus* possess swim bladders, the generic name *Pneumatophorus* Jordan and Gilbert, 1883, meaning swim-bladder bearer, has been used to distinguish them from *S. scombrus,* which lacks this organ. However, more recent authors (Fraser-Brunner, 1950; Collette and Gibbs, 1963; Matsui, 1967; Collette, 1979) have considered *Pneumatophorus* a synonym of *Scomber.* In addition to having lost its swim bladder, *S. scombrus* differs from *S. japonicus* and *S. australasicus* in several other morphological characters: *S. scombrus* has 13 + 18 vertebrae instead of 14 + 17, has the first haemal spine anterior to the first interhaemal bone, has more heavily ossified bones (Matsui, 1967, Table 5), and has a very different otolith morphology from the other two *Scomber* taxa (Fitch and Craig, 1964). This suggests that the earlier division of *Scomber* into two genera, one containing *S. scombrus* and the other containing *S. japonicus* and *S. australasicus,* is a hypothesis that can be tested with molecular data.

Rastrelliger Jordan and Starks, 1908, was described as differing from *Scomber* in having larger scales, more numerous and more elongate gill rakers, and a more compressed body. However, description of a third species in the genus made these differences less definite, and it became necessary to rely on anatomical characters to distinguish the genera. Matsui (1967, Table 4) summarized the diagnostic characters of *Rastrelliger,* which include a toothless vomer and palatines, last branchiostegal ray flattened and forming a wide plate (Matsui, 1967, Figure 3), rudimentary anal spine, 11 interneural bones under the first dorsal fin, first interhaemal bone anterior to the haemal spine of the 14th vertebra, and first haemal spine flattened and hooklike. The number of vertebrae are 13 precaudal plus 18 caudal.

There are three species of *Rastrelliger* according to Matsui (1967)—*R. faughni* Matsui, 1967, from Taiwan, the Philippine Islands, and Indonesia; *R. brachysoma* Bleeker, 1851, in the same general area of the western Pacific as *R. faughni* but extending east to Fiji; and *R. kanagurta* Cuvier, 1817, which is widespread throughout the Indo-West Pacific from Taiwan, the Philippines, Samoa, and Australia, east throughout the Indian Ocean to Madagascar and the Red Sea. At least one individual has gone through the Suez Canal into the eastern Mediterranean Sea (Collette, 1970). Matsui (1967, Table 2) summarized characters distinguishing the three species: number of gill rakers, length of the intestine (about equal to the length of the fish in *R. faughni,* 1.3–1.7 times longer in *R. kanagurta,* and 3–3.4 times longer in *R. brachysoma*), number of bristles on the longest gill raker, and body depth.

2. Tribe Scomberomorini Starks, 1910

This is the most speciose tribe in the family, containing 21 of the 50 species. Most of these are the 18 species of *Scomberomorus,* the Spanish mackerels and seerfishes; the other 3 species belong to the monotypic genus *Acanthocybium* and to *Grammatorcynus.* Scomberomorini have large compressed teeth which are serrate in some species. As in higher scombrids, there is a well-developed median keel on the caudal peduncle, but there is no bony support as is present in the Sardini and Thunnini.

a. Grammatorcynus Gill, 1862. This Indo-West Pacific genus differs from *Scomberomorus* in having two lateral lines, a pineal window, a single interpelvic process, fewer vertebrae, a well-developed swim bladder, and larger scales. It has the same number of vertebrae as do the Scombrini (31), usually 13 precaudal plus 18 caudal. Possession of an extra, ventral lateral line is unique in the family. Johnson (1986, Figure 1) placed *Grammatorcynus* in the middle of his cladogram, sister to Sardini, Thunnini, Scomberomorini, and the billfishes. Here, the genus is considered to be the plesiomorphic sister group of *Scomberomorus* + *Acanthocybium.* Long thought to be monotypic, the genus contains two species (Collette

and Gillis, 1992). The double-lined mackerel *G. bilineatus* Rüppell, 1836, is widespread in the tropical Indo-West Pacific, particularly near coral reefs from the Marshalls and Carolines, Philippine Islands, Australia, and the East Indies, west to the Red Sea. The shark mackerel, *G. bicarinatus* Quoy and Gaimard, 1825, has a smaller eye, fewer gill-rakers, and several osteological differences. It is restricted to the northern three-quarters of Australia and the Gulf of Papua.

b. Scomberomorus Lacepède, 1801. As many as seven subgenera of *Scomberomorus* were recognized by Munro (1943), exclusive of *Lepidocybium,* which belongs to the Gempylidae, and *Cybiosarda,* which is a member of the Sardini. Fraser-Brunner divided the genus into only two subgenera, *Cybium* with two species (*cavalla* and *commerson*) and *Scomberomorus* with seven species. Mago Leccia (1958) also noted the close relationships of *S. cavalla* and *S. commerson.* Fraser-Brunner placed a number of valid species in synonymy, and new species have been described since then. *Scomberomorus* differs from the other two genera in the tribe, *Acanthocybium* and *Grammatorcynus,* by lacking a swim bladder. *Scomberomorus* also lacks the extra lateral line present in *Grammatorcynus* and the elongate snout characteristic of *Acanthocybium.*

There are 18 species in the genus (Collette and Russo, 1985b): 1 species in the Gulf of Guinea and Mediterranean Sea (*S. tritor* Cuvier, 1832); 4 in the western Atlantic (*cavalla* Cuvier, 1829; *regalis* Bloch, 1793; *maculatus* Mitchill, 1815; and *brasiliensis* Collette, Russo, and Zavala-Camin, 1978); and 2 in the eastern Pacific (*concolor* Lockington, 1879, and *sierra* Jordan and Starks, 1895). The remaining species are Indo-West Pacific: *guttatus* Bloch and Schneider, 1801; *koreanus* Kishinouye, 1915; *lineolatus* Cuvier, 1832; *plurilineatus* Fourmanoir, 1966; *commerson* Lacepède, 1800; *sinensis* Lacepède, 1800; *semifasciatus* Macleay, 1883; *queenslandicus* Munro, 1943; *niphonius* Cuvier, 1832; *munroi* Collette and Russo, 1980, from Australia and New Guinea; and *multiradiatus* Munro, 1964. This last species has the most restricted range of any member of the family; it is known only from off the mouth of the Fly River in Papua New Guinea.

Meristic characters of value at the specific level in *Scomberomorus* include numbers of gill rakers, dorsal spines, dorsal and anal fin rays, vertebrae, and intestinal folds (Collette and Russo, 1985b). Dips in the lateral line and the locations of these dips distinguish *S. cavalla, S. commerson,* and *S. sinensis.* Fine branches extend off the anterior part of the lateral line in *S. guttatus* and *S. koreanus.* A number of morphometric characters are useful in separating species—head length, body depth, pelvic fin length, heights of second dorsal and anal fins, width of the median caudal peduncle keel, etc. Adult color pattern is also important in this genus; there are barred species (*cavalla, commerson,* and *semifasciatus*), species with variously interrupted horizontal lines (*regalis, lineolatus,* and *plurilineatus*), species with spots of varying sizes and numbers (*maculatus, sierra, tritor, guttatus, koreanus, niphonius, queenslandicus* and *sinensis*), and species with es-

sentially no markings at all (*concolor* and *multiradiatus*). The number of gill rakers ranges from 1–4 in *S. multiradiatus* to 21–27 in *S. concolor.* Vertebrae range from as low as (19 to 20) + (20 to 22) = 39 to 42 in *S. sinensis* to as high as (20 to 21) + (35 to 36) = 55 to 56 in *S. multiradiatus.*

One well-defined monophyletic group of species within the genus is the *regalis* group (Collette and Russo, 1985b). This group is defined by the presence of nasal denticles—teeth in the nose. Characters of the anterior arterial system, pelvic girdle, and skull define groups within the *regalis* group. The phylogeny constructed from morphological characters can be compared with the distributions of the species. Collette (1999, Figure 10) shows a cladogram inferred from species distributions which is identical to that based on morphology (Collette, 1999, Figure 9). Both trees show *S. regalis* and *S. brasiliensis* being most closely related, with *S. sierra* as the sister taxon to this pair, followed by *S. concolor. Scomberomorus tritor* was the most plesiomorphic species.

Host–parasite relationships of parasitic copepods were utilized to provide an independent assessment of relationships of Spanish mackerels of the *S. regalis* species group (Collette and Russo, 1985a). Clustering of the hosts based on hypothesized parasite relationships resulted in a slightly different tree, with the two eastern Pacific species, *concolor* and *sierra,* showing closer relationships than in the morphology-based tree. The differences between the tree based on morphology and one derived from host–parasite relationships suggest that a discrepancy exists, and this can be examined further using molecular data.

c. Acanthocybium Gill, 1862. This monotypic genus appears to be a specialized offshoot of *Scomberomorus* and does not merit placement in its own subfamily or tribe as has been advocated by previous authors such as Starks (1910). The wahoo, *A. solandri* Cuvier, 1831, is a large species (reaching over 1500 mm SL) and has a well-developed swim bladder. It is a high seas epipelagic species found around the world in tropical and subtropical waters. It is closest to the *Cybium* group of *Scomberomorus* (*S. cavalla* and *S. commerson*) according to Conrad (1938), Mago Leccia (1958), and Collette and Russo (1985b). Johnson (1986) presented an alternative hypothesis of scombroid relationships in which the wahoo was placed between Spanish mackerels and billfishes. The wahoo has lost all its gill rakers, the gill filament blades are interconnected by an extensive latticework of cartilaginous bridges invested with tooth plates, the number of vertebrae has increased to over 60, and its snout and jaws are elongate and beaklike. However, in both hypotheses, numerous reversals and independent acquisitions must have occurred no matter where billfishes are placed (Carpenter *et al.,* 1995).

3. Tribe Sardini Jordan and Evermann, 1896

The bonitos are a grade of seven species placed in four genera (Collette and Chao, 1975; Collette, 1999). They differ from the more primitive mackerels and

Spanish mackerels in lacking a notch in the hypural plate and in having a bony keel to support the median fleshy keel on the caudal peduncle. From the tunas, they differ in having the bony keel only partially developed, in lacking any countercurrent heat exchange system, and in lacking a pair of dorsally projecting cartilaginous ridges on the upper surface of the tongue. Sardini lack the prominent paired frontoparietal foramina characteristic of all Thunnini except *Auxis*. Sardini differ from Thunnini in lacking prominent prootic pits on the ventral surface of the cranium and complete centralization of the slow-oxidative muscle. Sardini lack any known synapomorphies, so from a cladistic point of view the group should be combined with Thunnini. There are some practical advantages of keeping bonitos separate from tunas so the tribes are maintained here. Collette and Chao (1975, Table 14) have summarized characters distinguishing genera of Sardini.

a. Orcynopsis Gill, 1862. The monotypic genera *Orcynopsis* and *Cybiosarda* share several characters that distinguish them from *Sarda* and *Gymnosarda*: low and poorly developed bony caudal peduncle keels versus well-developed keels divided into anterior and posterior sections on each preural vertebra; the right lobe of the liver being longest versus the right and left lobes much longer than the middle lobe; and the spleen small and concealed under the liver in ventral view versus large and prominent in ventral view. *Orcynopsis, Cybiosarda,* and *Gymnosarda* have two patches of tongue teeth, but the patches are attached to the glossohyal bone in the former two genera and are on separate plates that fit over the bone in *Gymnosarda. Orcynopsis* differs from *Cybiosarda* most obviously by lacking the bold pattern of stripes and blotches of the latter. *Orcynopsis* has fewer fin rays, ribs, and vertebrae than *Cybiosarda. Orcynopsis* is a short-bodied and short-headed bonito. *Orcynopsis unicolor* Geoffrey St. Hilaire, 1817, is an eastern Atlantic endemic whose range is centered in the Mediterranean Sea but extends south to Dakar, Senegal, and north to Oslo, Norway (Collette and Chao, 1975, Figure 69).

b. Cybiosarda Whitley, 1935. As noted above, the monotypic genera *Cybiosarda* and *Orcynopsis* share a suite of characters that differentiate them from *Sarda* and *Gymnosarda. Cybiosarda* is the most conspicuously marked scombrid, with a prominent pattern of black spots over a deep blue background above the lateral line, dark stripes on the light venter reminiscent of the skipjack *Katsuwonus,* a high first dorsal fin that is jet black anteriorly and pure white posteriorly, and yellow dorsal and anal fins. *Cybiosarda* has more fin rays, ribs, and vertebrae than *Orcynopsis. Cybiosarda elegans* (Whitley, 1935) is virtually an Australian endemic found along the northern three-quarters of the continent from Perth, Western Australia, to Sydney, New South Wales (Collette and Chao, 1975, Figure 69), and also along the south coast of Papua New Guinea.

c. Sarda Cuvier, 1829. The four species of *Sarda* all have several dorsal stripes, ranging from horizontal to oblique in orientation. *Sarda* and *Gymnosarda* share a number of characters that distinguish them from *Orcynopsis* and *Cybiosarda*: the bony caudal keels are well developed as in Thunnini but are divided into anterior and posterior sections on each vertebra; the spleen is large and prominent in ventral view versus small and concealed; and the right and left lobes of the liver are longer than the middle lobe versus the right lobe being the longest. *Sarda* resembles *Allothunnus* and differs from other genera of bonitos in having the intestine run straight from the stomach to the anus (instead of having two additional loops) and having two intermuscular bones per side attached to the rear of the skull (*Gymnosarda* has none, and the other three genera have one per side).

Collette and Chao (1975) recognized four species of *Sarda: S. australis* Macleay, 1881, is restricted to the east coast of Australia plus Norfolk Island; *S. chiliensis* inhabits the eastern Pacific, where it is divisible into two subspecies, *S. c. chiliensis* Cuvier, 1832, from Peru and Chile, and *S. c. lineolata* Girard, 1859, from Alaska to Baja California; *S. orientalis* Temminck and Schlegel, 1844, is widespread in the Indo-Pacific from South Africa and the Red Sea, east to Japan, China, the Philippine Islands, and the Hawaiian Islands, and across into the eastern Pacific from Baja California to Peru; and *S. sarda* Bloch, 1793, is found throughout tropical and temperate waters of the Atlantic Ocean, including the Gulf of Mexico and the Mediterranean and Black seas (Collette and Chao, 1975, Figure 70).

A summary of the 26 most important characters used in distinguishing species of *Sarda* has been presented by Collette and Chao (1975, Table 17). Meristic characters include numbers of nasal lamellae, upper and lower jaw teeth, gill rakers, ribs, vertebrae, dorsal fin spines, anal fin rays, dorsal and anal finlets, and pectoral fin rays. There are a number of osteological differences in various bones. Morphometric differences have also been summarized (Collette and Chao, 1975, Table 18).

d. Gymnosarda Gill, 1862. The monotypic genus *Gymnosarda* differs from other bonitos in having a well-developed swim bladder, in lacking intermuscular bones on the rear of the skull, and in having more lamellae in the olfactory rosette (48–56 vs. 21–39 in the other Sardini). *Gymnosarda* is the only bonito with 19 precaudal and 19 caudal vertebrae. It has a differently shaped head—larger eyes, wider interorbital distance, shorter postorbital distance, and more elongate opercular bones. As noted above, *Gymnosarda* and *Sarda* share several characters that distinguish them from *Orcynopsis* and *Cybiosarda. Gymnosarda* differs from *Sarda* in lacking scales on the body posterior to the corselet, having a pair of tooth plates on the tongue, lacking the stripes characteristic of *Sarda,* and having a loop in the intestine. *Gymnosarda unicolor* (Rüppell 1836), the dogtooth tuna, is a coral reef species of the tropical Indo-West Pacific (Collette and Chao, 1975, Fig-

ure 69). Its large eyes and teeth, numerous olfactory lamellae, and well-developed swim bladder suggest that it may be more of a lurking predator on larger fishes than are other bonitos.

4. Tribe Thunnini Starks, 1910

Four genera of tunas were included in Thunnini by Collette (1979), but later *Allothunnus* was added as the most primitive member of the tribe. The four genera are unique among bony fishes in having a countercurrent heat exchanger system of retia mirabilia in the circulatory system. A similar system has evolved independently in lamnid sharks (Carey *et al.,* 1971). The rete mirabilia provide the vascular mechanism for conserving metabolic heat in the muscle, viscera, and brain of tunas and lamnid sharks. This permits the fish to maintain body tissue temperatures warmer than the surrounding water. The three more primitive genera (*Auxis, Euthynnus,* and *Katsuwonus*) and the three members of the subgenus *Neothunnus* (*Thunnus albacares, Thunnus tonggol,* and *Thunnus atlanticus*) have central as well as lateral heat exchangers; the cold-water members of the subgenus *Thunnus* (bluefins, bigeye, and albacore) have no central heat exchanger and have evolved a well-developed lateral heat exchanger (Carey *et al.,* 1971; Graham, 1973, 1975). In addition, the cold-water *Thunnus* have visceral and cranial retia mirabilia. Thunnini are the only scombrids with a pair of dorsally projecting ridges on the upper surface of the tongue. The bony keels on the caudal peduncle vertebrae are completely developed rather than only partially developed as in the Sardini. Thunnini, except *Allothunnus* and *Auxis,* have a prominent pair of frontoparietal foramina on the dorsal surface of the skull. All Thunnini have well-developed prootic pits on the ventral surface of the skull.

a. Allothunnus Serventy, 1948. The monotypic *Allothunnus* differs from all other scombrids in its very high number of gill rakers. *Allothunnus* differs from all other scombrids in having the prootic bones remarkably extended laterally as wings that frame the posterior margin of the orbit. *Allothunnus* resembles other Thunnini and differs from Sardini in having a prootic pit in the ventral surface of the skull. The pineal window is large and oval in *Allothunnus,* and elongate and slit-shaped in the Thunnini and Sardini. The liver has three subequal lobes as in the bluefin species group of *Thunnus.* Recent studies on the morphology of *Allothunnus* by Graham and Dickson (2000) confirm its position as the most primitive member of the Thunnini because it has a highly modified central circulation (heat-exchanging aorta, postcardinal vein, and associated branch vessels) similar to the central heat-exchanging retia of tunas, and enlarged haemal arches and anterior, internal placement of red muscles as in tunas. *Allothunnus fallai* Serventy, 1948, the slender tuna, is found around the world in the Southern Ocean south of 35° S (Collette and Chao, 1975, Figure 69), with two highly unusual records from the North Pacific, one from the Los Angeles–Long Beach harbor complex (Fitch and

Craig, 1964) and the second from the North Pacific subarctic gyre at 44°N, 151°W (Schaefer and Childers, 1999).

b. Auxis Cuvier, 1829. After *Allothunnus, Auxis* is the next most primitive genus of the Thunnini. It lacks the prominent frontoparietal foramina found in the three genera of higher tunas, *Euthynnus, Katsuwonus,* and *Thunnus.* Dorsal and ventral branches of the cutaneous artery originate separately in *Auxis* (Godsil, 1954); a common cutaneous artery divides into dorsal and ventral branches lateral to the aorta in the other three genera. The ventral branch is very poorly developed—less so than in the three more advanced genera. In *Auxis* the dorsal cutaneous artery lies ventral to the corresponding vein, versus dorsal in *Euthynnus* (Godsil, 1954). The vertebral column differs from all other scombrids in having a long pedicel or epihaemal process which forces the dorsal aorta to run much further ventrally from the vertebral column (1.5–2 times the centrum depth) than in other tunas. *Auxis* shows no suturing of the first vertebra to the skull as is present in higher Thunnini. *Auxis* has a single huge interpelvic process which is about equal to the pelvic fins in length. *Auxis* resemble *Scomber* in having a long distance between the dorsal fins. The liver is similar to that in *Euthynnus* in having a very long right lobe running the length of the body cavity. Prominent branches of the hepatic vein are present on the ventral surface of the liver lobes in both genera. *Auxis* differs from *Euthynnus* in having a greatly reduced left liver lobe; the left and middle lobes are of about equal length in *Euthynnus.* The swim bladder is absent and the body is naked posterior to the corselet, as in *Euthynnus* and *Katsuwonus.* There are a total of 39 vertebrae as in *Thunnus* and some species of *Euthynnus*—20 precaudal plus 19 caudal. Gill rakers range from 37 to 47 in number.

There are two species of frigate tunas (Collette and Aadland, 1996): the narrow-corseleted *A. thazard* (Lacepède, 1800) and the wide-corseleted *A. rochei* (Risso, 1810). In both species an extension of the corselet follows the lateral line posteriorly. In *A. thazard* the extension is only 1–5 scales wide beneath the second dorsal fin; in *A. rochei* it is 6 scales or more. This difference is correlated with a difference in number of gill rakers, 37–43 (mean about 40) in *A. thazard* and 40–47 (mean about 45) in *A. rochei.* Both species are widely distributed in tropical and subtropical waters of the Indo-Pacific. The two species were clearly distinguished in the Pacific by Kishinouye (1923), Wade (1949), and Matsumoto (1960), under a variety of names. Occurrence of both species in the Atlantic was not confirmed until recently (Richards and Randall, 1967; Collette and Aadland, 1996). Frigate tunas are the smallest of the tunas, *A. rochei* reaching 500 mm FL and *A. thazard* at least 580 mm FL. Eastern Pacific populations of both species differ morphologically from populations in the rest of the world, leading Collette and Aadland (1996) to describe them as subspecies. The eastern Pacific *A. thazard brachydorax* Collette and Aadland, 1996, has more gill rakers than the widespread

A. t. thazard, usually 43–48 versus 38–42, and also differs in several morphometric characters. The eastern Pacific *A. rochei eudorax* Collette and Aadland, 1996, has an even wider corselet than that of *A. r. rochei*—usually more than 20 scales wide compared with 6–19 scales.

c. Euthynnus Lütken in Jordan and Gilbert, 1882. *Euthynnus* is closely related to both the more primitive *Auxis* and the more advanced *Katsuwonus.* Some researchers (Fraser-Brunner, 1950; Collette and Gibbs, 1963) placed *Katsuwonus* in synonymy with *Euthynnus,* but this obscures the relationships of *Euthynnus* sensu stricto with *Auxis* and of *Katsuwonus* with *Thunnus. Euthynnus* differs from *Auxis* in having a common trunk for the dorsal and ventral branches of the cutaneous artery. It is less advanced than *Katsuwonus* because the ventral branch of the cutaneous artery is short and dendritic (Godsil, 1954), and much less developed than the dorsal branch. In *Euthynnus* the dorsal cutaneous artery lies dorsal to the corresponding vein, and not ventral as in *Auxis.* The trelliswork on the vertebral column moves the aorta ventrally a distance greater than the depth of the centrum—less than in *Auxis* and more than in *Katsuwonus. Euthynnus* is similar to *Auxis* and *Katsuwonus* in lacking a swim bladder and in having the body naked posterior to the corselet. *Euthynnus* resembles *Auxis* in having the right lobe of the liver extending the length of the body cavity and in having prominent hepatic veins on the ventral surface of the liver. It differs from *Auxis* in having a much longer left lobe that is about equal in length to the middle lobe. *Katsuwonus* has a much shorter and narrower right lobe and lacks hepatic veins on the ventral surface of the liver. *Euthynnus* resembles *Katsuwonus* in having the upper half of the first vertebra sutured to the skull—more than in *Auxis* but less than in *Thunnus.* The number of vertebrae is 37–39, fewer than in *Katsuwonus* (41).

There are three allopatric species of *Euthynnus*: *E. alletteratus* Rafinesque, 1810, in the Atlantic; *E. affinis* Cantor, 1849, throughout the Indo-West Pacific; and *E. lineatus* Kishinouye, 1920, in the eastern Pacific. There is a valid record of *E. affinis* from the eastern Pacific (Godsil, 1954, 139) and two of *E. lineatus* from the Hawaiian Islands (Matsumoto and Kang, 1967; Matsumoto, 1976). Godsil (1954, Table 17) summarized the characters that differentiate the species (with *E. affinis* as *E. yaito*): vomerine teeth (absent only in *E. alletteratus*); gill rakers (29–33 in *E. affinis,* 33–39 in *E. lineatus,* and 37–40 in *E. alletteratus*); vertebrae (37 in *E. lineatus* and 39 in the other two species); vertebral protuberances (absent in *E. affinis,* incipient on 33rd and 34th vertebrae in *E. alletteratus,* and four large lobes on the 31st and 32nd vertebrae in *E. lineatus*); and location of caudal keels (on 31st and 32nd vertebrae in *E. lineatus,* and 33rd and 34th in the other two species). Species of *Euthynnus* characteristically, but not invariably, have a variable number of black blotches on the sides between the pectoral and pelvic fins. Gill rakers range from 29 to 40 in number, many fewer than in *Katsuwonus* (53–63).

d. Katsuwonus Kishinouye, 1923. This monotypic genus is most closely related to *Euthynnus* and *Thunnus*. It is more advanced than *Euthynnus* in having the dorsal and ventral branches of the cutaneous artery about equally developed instead of having the ventral branch short and dendritic (Godsil, 1954). Trelliswork on the vertebral column moves the aorta ventrally a distance slightly less than the depth of a centrum—less than in *Auxis* and *Euthynnus*, and more than in *Thunnus*. The liver resembles that of the yellowfin group of *Thunnus* more than that of *Euthynnus* and *Auxis*, because the right lobe does not extend the length of the body cavity and hepatic veins are absent from the ventral surface of the liver. *Katsuwonus* resembles *Auxis* and *Euthynnus* and differs from *Thunnus* in having the body naked posterior to the corselet. *Katsuwonus* has more vertebrae than *Thunnus* (41 compared to 39). *Katsuwonus* resembles *Euthynnus* in having only the upper half of the first vertebra sutured to the skull compared to completely sutured in *Thunnus*. As in *Auxis* and *Euthynnus*, no swim bladder is present and the intestine is straight, without folds. *Katsuwonus pelamis* Linnaeus, 1758, the skipjack, is a moderate-sized species of tuna reaching about a meter in length and a weight of 18 kg (rarely as high as 23 kg). It has a striking pattern of dark longitudinal stripes on the ventral half of the body. It has many gill rakers, with 53–63 on the first arch. It is cosmopolitan in tropical and subtropical seas.

e. Thunnus South, 1845. This, the most advanced genus of Scombridae, contains eight species. *Thunnus* is more specialized than other genera of Thunnini in having more pectoral fin rays (30–36 vs. 23–27) and in having the first vertebra completely sutured to the skull. *Thunnus* has fewer vertebrae than *Katsuwonus* (39 vs. 41). Posterior to the corselet, the body is covered with small scales, compared to being naked in the other genera of Thunnini. A swim bladder is present in all the species except *T. tonggol*. The intestine has an additional loop in it that is not present in the other four genera. While vertebral trelliswork is present in *Euthynnus* and *Katsuwonus*, it is reduced (yellowfin species group) or absent (bluefin group) in *Thunnus*.

A number of workers (e.g., Kishinouye, 1923; Godsil and Byers, 1944) divided *Thunnus* into several genera, reaching an extreme of six genera for the seven species then recognized. Gibbs and Collette (1967) placed the nominal genera *Parathunnus* (for bigeye), *Neothunnus* and *Semathunnus* (for yellowfin), *Germo* (for albacore), and *Kishinoella* (for longtail) in the synonymy of *Thunnus* (based on bluefin). They argued strongly against subdividing *Thunnus* into genera because reliance on different characters led to very different groups of species. They did show that there were two groups of species with the bigeye tuna, *T. obesus*, intermediate between the groups. Le Gall *et al.* (1976) performed a multivariate analysis on the data presented by Gibbs and Collette and confirmed their findings that there are two groups of species, with *T. obesus* intermediate. Le Gall *et al.* (1976) concluded that it was useful to recognize three subgenera: *Thunnus*

for the bluefin group, *Neothunnus* for the yellowfin group, and *Parathunnus* for *T. obesus.*

Collette (1979, 1999) divided the genus into two subgenera, *Thunnus* for the cold-water clade—bluefins, southern bluefin, and albacore—and *Neothunnus* for the tropical tunas—yellowfin, blackfin, and longtail. This classification was based largely on morphological differences in adaptations for endothermy such as liver morphology, vascularization, position of the cutaneous artery, and size of ventrolateral vertebral foramina. Species of *Neothunnus* possess both central and lateral heat exchangers, although the lateral retia mirabilia are relatively small. Members of *Thunnus* have their lateral retia highly developed, but the central heat exchanger has been lost or reduced, and this group also has additional retia which function to elevate the temperature of their viscera, eyes, and brains. The major differences between the two subgenera are associated with this loss of the central heat exchanger in the bluefin group (Carey *et al.,* 1971; Graham, 1975). With an understanding of the adaptive significance of the differences in heat exchangers between the two subgenera, *T. obesus* seems best placed in the subgenus *Thunnus.*

f. Subgenus *Neothunnus* Kishinouye, 1923. This subgenus contains the three tropical species of *Thunnus* which have central heat exchangers, as do the three less advanced genera of Thunnini. Gibbs and Collette (1967, 99) found that these three species were similar to each other in 15–16 of 18 characters. No striations are present on the ventral surface of the liver and no vascular retia mirabilia are present on the dorsal surface. The postcardinal vein is present as in more primitive Thunnini. Several structural modifications in the vertebral column permit the passage of more or larger blood vessels through the haemal arch, as Graham (1975) has pointed out: the prezygapophyses arise more ventrad on the haemal arch, the postzygapophyses are longer, and the interior foramina are larger (Gibbs and Collette, 1967, Figures 10–13).

The three species in the subgenus *Neothunnus* are the blackfin tuna, *Thunnus atlanticus* (Lesson, 1831), of the western Atlantic (Martha's Vineyard, MA, to Rio de Janeiro); the longtail tuna, *T. tonggol* (Bleeker, 1851), of the Indo-West Pacific (Japan to Australia, and west through the Indo-Australian Archipelago to Somalia and the Red Sea); and the yellowfin tuna, *T. albacares* (Bonnaterre, 1788), a pantropical species (Scoles and Graves, 1998). *Thunnus atlanticus* differs from other species of *Thunnus* in having 19 + 20 vertebrae instead of 18 + 21. Both *T. atlanticus* and *T. tonggol* have few gill rakers (19–25 and 19–28, respectively). *Thunnus tonggol* differs from other *Thunnus* in lacking a swim bladder. Other differences are treated in detail by Gibbs and Collette (1967).

g. Subgenus *Thunnus* South, 1845. This subgenus contains the five larger species of tunas which have been able to invade cooler waters due to their possession

of effective lateral heat exchangers. Gibbs and Collette (1967, 99) showed that three species of this group resembled each other in 14–16 of 18 characters. Striations caused by blood vessels are present on the ventral surface of the liver and vascular cones are associated with the dorsal surface of the liver, indicating presence of a visceral heat exchanger. The three lobes of the liver are roughly equal in length compared to the subgenus *Neothunnus*, where the right lobe is significantly longer than the other lobes. The postcardinal vein has been lost in some members but not all (present but reduced in size in *T. obesus*). The vertebral column shows no special modifications that would facilitate passage of more or larger blood vessels through the haemal arch; the prezygapophyses arise on the centra, the postzygapophyses are short, and the interior foramina are small.

Based on morphology, four species clearly belong to this subgenus: the Atlantic and Pacific bluefin tunas *T. thynnus* (Linnaeus, 1758), and *T. orientalis* (Temminck and Schlegel, 1844); the southern bluefin tuna *T. maccoyii* (Castelnau, 1872); and the albacore *T. alalunga* (Bonnaterre, 1788). The fifth species, the bigeye tuna *T. obesus* (Lowe, 1839), is intermediate between the subgenera, sharing 12 characters with *T. maccoyii* and 10 with *T. albacares* (Gibbs and Collette, 1967, 99). The bigeye tuna matches with the subgenus *Thunnus* in the important liver and vertebral characters; however, it is similar to *Neothunnus* with respect to the position where the cutaneous artery originates from the aorta and where it divides into dorsal and ventral branches. Because it has lost the central heat exchanger, it is placed in the subgenus *Thunnus*, although it is morphologically the most different of the five species in the subgenus.

Characters that distinguish species of the subgenus *Thunnus* and the distributions of the species are treated in detail by Gibbs and Collette (1967). All five species are widespread. Bluefin tunas extend into temperate waters of the North Atlantic (*T. thynnus*) and North Pacific (*T. orientalis*). The southern bluefin, *T. maccoyii*, has a distribution pattern similar to that of *Gasterochisma* and *Allothunnus* in the Southern Ocean. *Thunnus alalunga* is found from 42°N to 32°S in the Atlantic, 10°N to 30°S in the Indian Ocean, and 50°N to 45°S in the Pacific; however, most of the fisheries for it are concentrated in temperate waters. *Thunnus obesus* has much the same latitudinal distribution as the yellowfin *T. albacares*, but it usually is found in deeper and cooler waters than the yellowfin.

Of the subgenus *Thunnus*, *T. alalunga* has much longer pectoral fins than do the other species; *T. thynnus*, *T. orientalis*, and *T. maccoyii* have very short pectorals. *Thunnus thynnus*, *T. orientalis*, and *T. maccoyii* have more gill rakers (31–43) than do *T. alalunga* and *T. obesus* (23–31). *Thunnus alalunga* has the spleen on the right side of the viscera; the other species of the subgenus (and genus) have the spleen on the left. Hence, *T. alalunga* is somewhat different from the other species in the subgenus. This idea, along with others dealing with the number of unique lineages of the genus *Thunnus*, is addressed in Section II.

II. MOLECULAR SYSTEMATICS

Scombroids are among the best-known fishes anatomically (Carpenter *et al.*, 1995) and this group should present the systematist with the opportunity to produce well-corroborated phylogenies using the varied types of phylogenetic techniques currently available. However, despite extensive morphological efforts to construct phylogenies of the scombroids, this has not been the case. Cladistic phylogenies have been unstable, have generated conflicting hypotheses of scombroid relationships among various workers in the field, and have yielded multiple most-parsimonious trees (Carpenter *et al.*, 1995). Systematic relationships are often not clearly resolved and the choice of accepted trees often rests on the selection of outgroup species and the choice of phenotypic characters used to group taxa. As molecular genetic techniques have become more common in systematics, the opportunity has arisen to test some of the hypotheses proposed in the scombroid literature using characters known to be heritable. It was hoped these techniques would resolve key issues in scombroid systematics. Unfortunately, these methods have often fallen short of expectations.

The use of molecular data in fishery biology and systematics has recently led to notable progress. For example, mitochondrial DNA has been most useful for identifying all eight species of the genus *Thunnus* (Bartlett and Davidson, 1991; Finnerty and Block, 1995; Chow and Kishino, 1995; Alvarado-Bremer *et al.*, 1996). Genetic recognition of species in this genus has been extremely valuable to the study of early life stages because larval forms are challenging to identify morphologically (Collette *et al.*, 1984). Physiological traits, such as endothermy in scombroid fishes, have been mapped onto molecular phylogenies to examine the patterns of evolution along specific lineages (Block *et al.*, 1993; Finnerty and Block, 1995). Estimates of genetic divergence among populations can be used to visualize patterns of gene flow and corridors of migration in highly migratory species, like the swordfish (Reeb *et al.*, 2000), which can be useful for fishery management. While results of molecular studies have verified, rejected, or failed to resolve phylogenies, more often than not the data have provided both morphological and molecular systematists alike with a new perspective and alternative hypotheses to test, thus propelling the field forward.

Molecular fishery biology is still a young field and new ideas await discovery. In the meantime, scombroid genetics and molecular systematics are made difficult by the propensity of this group to undergo rapid bursts of speciation over time (Finnerty and Block, 1995), or for hybridization to confuse the phylogenetic history (e.g., Chow and Kishino, 1995; Banford *et al.*, 1999). Such phenomena are not unusual in evolution and scombroids are no exception. Many groups, including mammals, have experienced rapid bursts of speciation (e.g., bears; Waits *et al.*, 1999) and hybridization (e.g., European house mice; Sage *et al.*, 1993), which

were first revealed by molecular data and eventually understood. In this section we demonstrate six hypotheses established by morphological data and tested using molecular techniques. Molecular systematics of scombroids has been challenging, especially in resolving relationships among older lineages. We believe that the biggest challenge faced by systematists in resolving the deeper scombrid lineages with molecular data is to overcome the problems associated with the use of short DNA sequences for phylogenetic analysis and the frequent occurrence of reversion mutation (homoplasy).

A. Are Billfishes Scombroid Fishes?

There has been a debate in the morphological literature as to the exact relationships among billfishes, tunas, and other scombroids (Collette *et al.*, 1984; Johnson, 1986; Carpenter *et al.*, 1995). Parsimony analysis of both nucleotide and amino acid sequences generated from 590 base pairs (bp) of the cytochrome *b* gene and a 628-bp segment of the lactate dehydrogenase b locus places the wahoo, *Acanthocybium solandri,* within a monophyletic Scombridae, Gempylidae, Trichiuridae clade, while billfishes are consistently placed as a sister group to this clade (Block *et al.*, 1993; Finnerty and Block, 1994, 1995). Parsimony analysis of the mitochondrial ATPase 6 gene (using both nucleotide and amino acid sequences) confirms monophyly of the billfishes (Alvarado Bremer, 1994). Thus, molecular data provide a clear phylogenetic signal supporting monophyly of billfishes and is in support of the morphological placement of wahoo in Scomberomorini (Collette and Russo, 1985b). Billfishes are genetically distinct from other scombroids and possibly belong in a separate suborder (Finnerty and Block, 1995). The apparent similarity in billfish morphology to that of Scombridae noted earlier is likely equivocal largely because many of the cladistic characters that unite billfish with the Scombridae appear to be convergent or reversals (Carpenter *et al.*, 1995; Finnerty and Block, 1995) causing homoplasy in the morphological tree.

B. Is Gasterochismatinae a Sister Group to the Scombrinae?

The currently accepted phylogeny of Collette and Russo (1985a) shown in Figure 1 places the subfamily Gasterochismatinae at the base of the Scombridae. As discussed above, Block *et al.* (1993) and Finnerty and Block (1995) used DNA sequences of cytochrome *b* to construct a phylogeny of billfishes, mackerels, and tunas in which *Gasterochisma melampus* was included. Their tree provided the first molecular evidence that *Gasterochisma* may not form a sister relationship to the Scombrinae. Figure 2 shows the phylogenetic relationships among scombroid fishes derived from a 515-bp sequence of cytochrome *b* (from Block *et al.*, 1993)

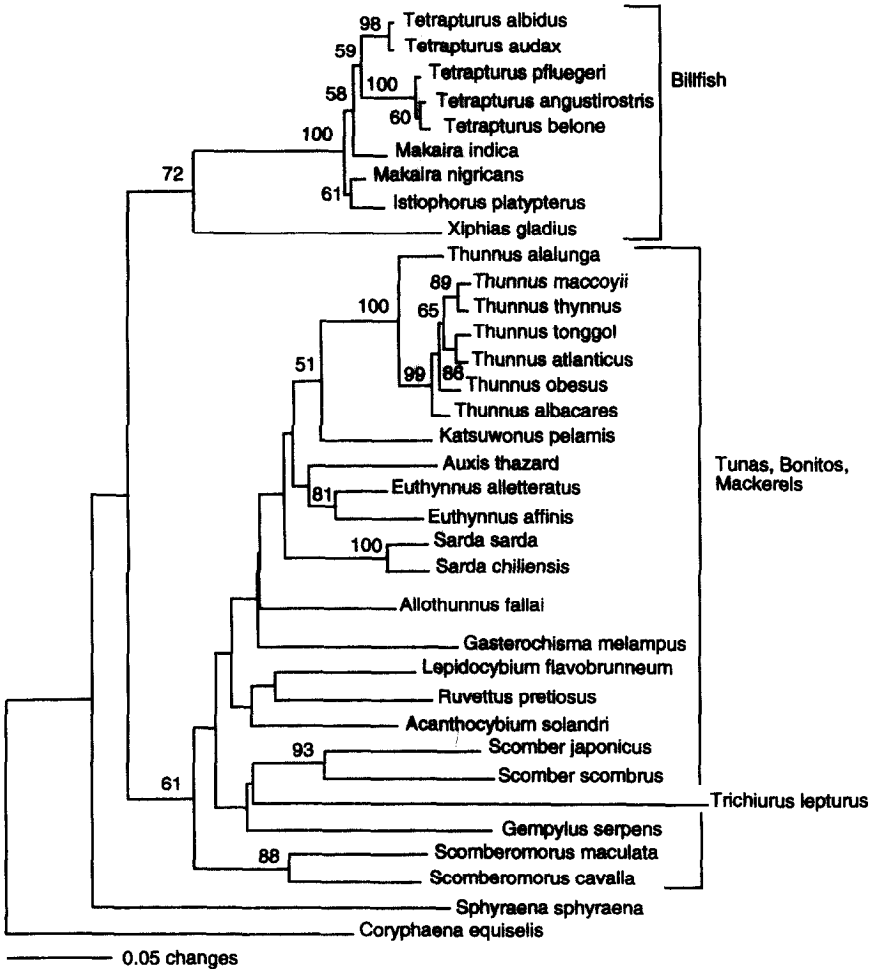


Fig. 2. Cytochrome *b* phylogeny for selected tunas, bonitos, mackerels, and billfish from data from Block *et al.* (1993), Finnerty and Block (1995), Chow (unpublished), and Reeb and Block (unpublished). Neighbor-joining tree drawn with 515 bp using maximum likelihood distance. Values on the nodes of branches are the percentage of bootstrap values out of 1000 replicates. Only values greater than 50% are shown. Transition : transversion ratio is 10. Outgroup is *Coryphaena equiselis*.

along with two sequences from Chow for *Thunnus tonggol* and *Thunnus atlanticus* (unpublished; GenBank accession numbers *T. atlanticus* AF239963 and *T. tonggol* AF239964). We have recently sequenced 515 bp of cytochrome *b* from *Allothunnus fallai* for inclusion in this analysis.

The tree in Figure 2 is a neighbor-joining tree using maximum likelihood dis-

tance and rooted with *Coryphaena equiselis*. The same placement of *Gasterochisma* is obtained when any one of the billfish species is used as an outgroup (data not shown). The position of *Gasterochisma* could only be supported as a polytomy after bootstrap analysis that includes Scombridae, Trichiuridae, and Gempylidae, but excludes billfishes. This lack of resolution of the relationships is significant as it clearly highlights a major dilemma in scombroid molecular systematics. The cytochrome *b* gene is highly saturated and homoplasy obscures the relationships at the nodes of the tree where the Scombridae underwent diversification into its major taxonomic lineages. As noted below, transitions in the silent nucleotide sites of the cytochrome *b* gene are saturated in comparisons of older scombroid taxa. Thus, resolution of the deeper nodes where the Scombridae underwent diversification is unclear. The exception to this is the divergence between billfish and the rest of the scombroids. In this case, there are a number of amino acids that change in addition to silent mutations, providing additional characters to construct the tree (Finnerty and Block, 1995). One way to overcome the saturation problem of the cytochrome *b* gene in the analysis of relationships among tunas, bonitos, and mackerels is to sequence a more slowly evolving gene such as the 16S ribosomal gene (rDNA) in mitochondria.

In Figure 3 the phylogenetic tree is constructed from a partial sequence (475 bp) of 16S ribosomal DNA using maximum likelihood distance and the neighbor-joining algorithm. *Thunnus* and *Tetrapturus* sequences were obtained from Reeb (1995), while the remainder were sequenced for this analysis (Reeb and Block, unpublished). Striped marlin was used as the outgroup. This phylogeny again places *Gasterochisma* within the Scombrinae, only this time it clusters with the tuna–bonito clade with a bootstrap value of 71%. From both the 16S and cytochrome *b* trees it is clear that *Gasterochisma* does not form a sister relationship outside the Scombrinae, but rather falls within the family. However, Figure 1 places Gasterochismatinae as sister taxon to Scombrinae (Collette and Russo, 1985a), thus rooting the phylogeny. The position of *Gasterochisma* as a sister taxon to the Scombrinae has been somewhat controversial as some morphological studies have used alternative characters and interpretations and placed it within the Scombridae (e.g., Carpenter *et al.*, 1995).

C. Can Molecular Phylogenies Resolve the Thunnini and Sardini Tribes?

In Figure 1, *Allothunnus* has been placed as the most primitive member of the tribe Thunnini, while *Katsuwonus* is considered the sister group to the genus *Thunnus* (Collette and Russo, 1985a; Collette, 1999). Allozymes (Elliott and Ward, 1995) and cytochrome *b* gene studies (Block *et al.*, 1993; Finnerty and Block, 1995) indicate that there is strong molecular support for monophyly of *Thunnus*, but less for the relationships of *Euthynnus*, *Katsuwonus*, and *Auxis* to one another and to *Thunnus*. In the phylogenies shown in Figures 2 and 3, *Allo-*

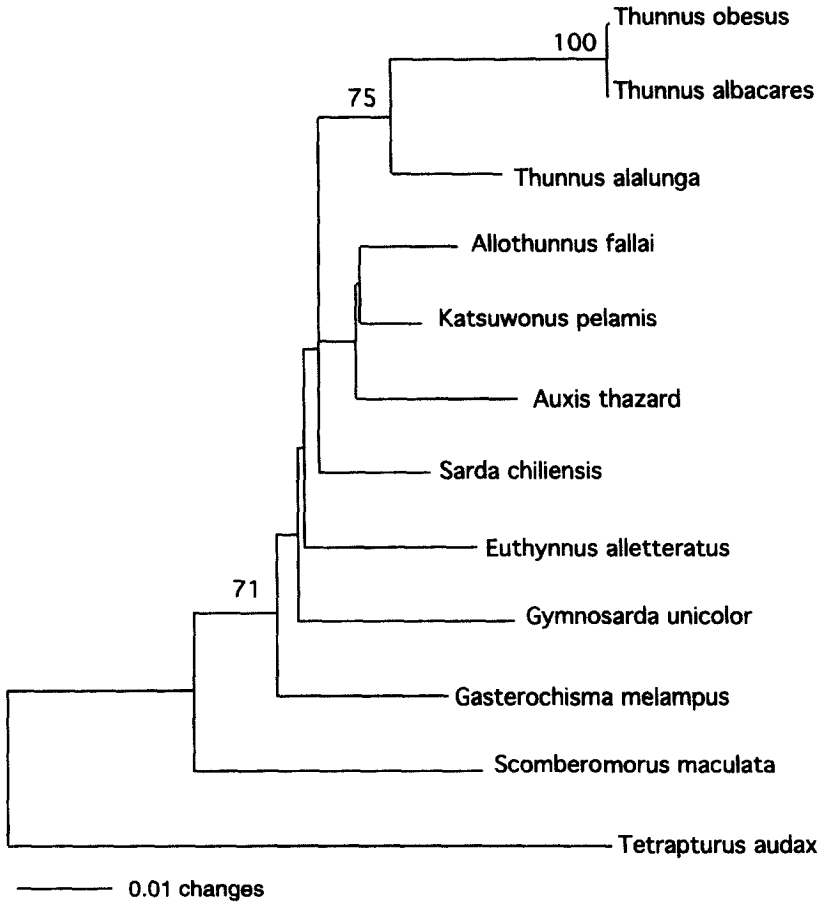


Fig. 3. The 16S phylogeny of selected tunas, bonitos, and mackerels from Reeb (1995) and Reeb and Block (unpublished). Neighbor-joining tree drawn from 475 bp using maximum likelihood distance. Transition:transversion ratio is 2. Values on the nodes of branches are the percentage of bootstrap values out of 1000 replicates. Only values greater than 50% are shown. Outgroup is *Tetrapturus audax*.

thunnus has been added, and neither the cytochrome *b* nor the 16s rDNA trees are able to support the relationships proposed by morphology as bootstrap values fall well below 50%. Furthermore, there is little support for the separation of Thunnini from Sardini as even the 16s phylogeny shows a polytomy among the members of the two tribes. It should be noted that while several morphological characters can distinguish Thunnini as a good monophyletic group, the Sardini do not possess such characters. Thus, the morphological data are in agreement with the mo-

lecular data suggesting that there is minimal support for the recognition of two phylogenetically distinct tribes.

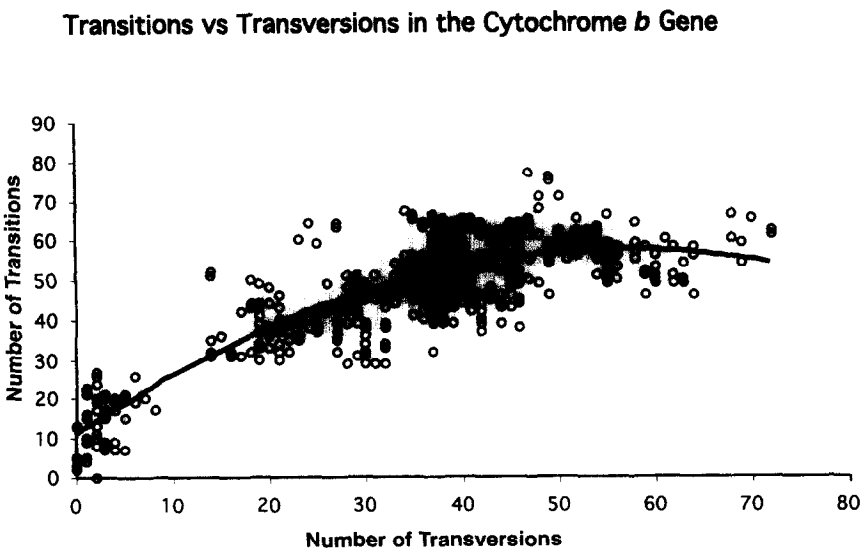
D. Problems Caused by Partial Sequences and Homoplasy

Partial sequences of the cytochrome *b* gene of the maternally inherited mitochondrial DNA (mtDNA) are used routinely in systematic studies to resolve relationships at the species level. However, analysis of short DNA sequences (<750 bp) has been shown to cause errors in estimates of evolutionary relatedness among taxa due to a large variance in substitution rate (Martin *et al.*, 1990). Hence, longer sequences are preferable, especially when the sequence is of a protein-coding gene where not all sites are free to vary. Another complication is the use of a molecular marker that evolves too quickly. This can lead to the loss of phylogenetic information through back mutation or reversals (Irwin *et al.*, 1991; Meyer, 1994).

Evidence for homoplasy is apparent in the cytochrome *b* data of scombroids both in unresolved trees and in saturation curves. Figure 4 is a plot of transitions (purine–purine or pyrimidine–pyrimidine substitutions) against transversions (purine–pyrimidine substitutions) for the cytochrome *b* and 16S sequences in Figures 2 and 3. In Figure 4a, transitions appear to be saturated relative to transversions in cytochrome *b*. It is not unusual for saturation to be reached quickly with transitions as these substitutions occur more frequently than transversions (Irwin *et al.*, 1991). However, in this case, the ratio of transitions to transversions is roughly equal, especially for comparisons between the deeper nodes in the scombrids such as *Euthynnus, Katsuwonus, Auxis,* and *Allothunnus.* In this situation, increased homoplasy in transitions can mask the phylogenetic signal of transversions, thus distorting the relationships among taxa in the deeper nodes of the tree. Finnerty and Block (1995, Figure 4) made an attempt to recover the true tree by weighting transitions and transversions based on their frequency of occurrence. However, the deeper nodes of the tree remained unresolved. Finnerty and Block (1995) also constructed a phylogeny using only amino acid sequences in an attempt to examine the deeper nodes. Because most of the mutations among scombrid taxa occur at the noncoding or silent third positions of codons, very few amino acid changes are evident and again, the deeper nodes of the tree remained unresolved.

Figure 4b is a saturation plot for the more slowly evolving 16S ribosomal gene of mtDNA using taxa comprising the phylogeny in Figure 3 constructed from a partial sequence (475 bp) of 16s ribosomal DNA (rDNA). This plot shows no evidence of saturation. However, the relationships among many of the scombroid taxa in Figure 3 remain poorly resolved. Although both the cytochrome *b* and 16S data are limited in information, they do provide interesting insight into the evolution of the Scombridae that will emerge repeatedly as future research examines the systematic hierarchy of these fish.

A



B

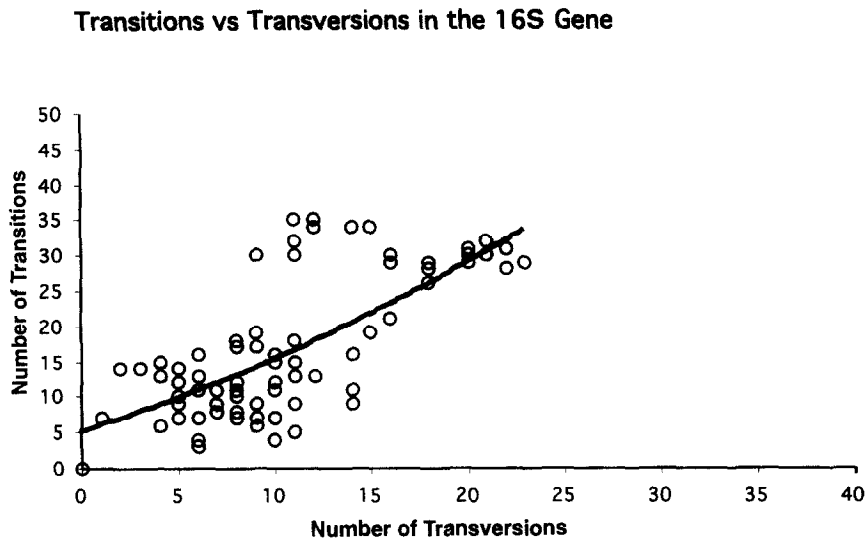


Fig. 4. Plot of the number of transitions versus transversions for (a) cytochrome *b* and (b) 16S for the Scombridae taxa in Figures 2 and 3, respectively.

The lack of resolution in the molecular trees based on molecules might stem from the possibility that the Scombridae have undergone recurrent bouts of rapid speciation. It is clear that the moderately evolving cytochrome *b* gene evolves too quickly to retain its phylogenetic information before homoplasy becomes a problem among the deeper nodes. However, the slowly evolving 16S sequences are unable to mutate fast enough to distinguish each lineage as it arose; hence all lineages appear to coalesce to the same ancestral node, not to a series of bifurcating sister taxa as the morphological hypotheses would predict. One exception is the monophyletic *Thunnus* lineage. Because this genus is recently derived, it can be distinguished from the other Scombridae with the faster evolving cytochrome *b* sequence (discussed below). The results in Figures 2 and 3 strongly suggest that the major lineages of Scombridae evolved during periods of rapid speciation, making it difficult for characters that evolve slowly to accumulate enough synapomorphies. Meanwhile, faster evolving characters appear to undergo reversions over time. Thus the molecular data explain why reconstructing the systematic relationships within this family using either molecules or morphology remains a challenge for systematists. One way to better support the hypothesis that rapid speciation has occurred is to analyze much longer sequences from many different genes. This approach has been used to show that bears have undergone bouts of rapid speciation events (Waits *et al.*, 1999).

E. Are *Thunnus* Monophyletic?

Molecular data sets have shown robust support for the monophyly of the genus *Thunnus* (Elliott and Ward, 1995; Finnerty and Block, 1995; Chow and Kishino, 1995; Alvarado Bremer *et al.*, 1996), which is consistent with morphological hypotheses. As noted earlier in this chapter, Collette (1979) proposed that *Thunnus* should be divided into two subgenera comprising the tropical *Neothunnus* (*T. albacares, T. tonggol,* and *T. atlanticus*) and the more cold-tolerant *Thunnus* (*T. thynnus, T. maccoyii, T. alalunga,* and *T. obesus*). In a series of studies involving both mitochondrial and nuclear genes (Sharp and Pirages, 1979; Chow and Inoue, 1993; Finnerty and Block, 1995; Elliott and Ward, 1995; Ward, 1995), the results have not been concordant with the morphology. For instance, in four molecular studies the albacore, *T. alalunga,* was found to be the most divergent member of the genus. This leaves *Neothunnus* and the remaining *Thunnus* taxa as a separate group, thereby rejecting the morphological hypothesis that the subgenus *Thunnus* is monophyletic. The issue of whether *Neothunnus* is monophyletic was not completely addressed in these early studies as neither the longtail (*T. tonggol*) nor the blackfin (*T. atlanticus*) were available for analysis.

The study of Chow and Kishino (1995, Figure 4) was the first to include all eight *Thunnus* species in a molecular phylogeny. Analysis of a short (292 bp), highly conserved fragment of cytochrome *b* and a 400-bp fragment of the mito-

chondrial ATPase gene produced a phylogenetic clustering of the species of the subgenus *Neothunnus.* However, the node of the *Neothunnus* clade was not supported by bootstrap analysis (values < 50%) in Chow and Kishino's study. Alvarado Bremer *et al.* (1996, Figure 4) sequenced 450 bp of the rapidly evolving, noncoding d-loop region of the mitochondrial DNA, and a maximum-parsimony analysis was able to support *Neothunnus* as a monophyletic group with a bootstrap value of 79%. Importantly, in this analysis, the subgenus *Thunnus* was not shown to be monophyletic as *Neothunnus* fell within the *Thunnus* subgenus. Interestingly, both studies showed that the bigeye (*T. obesus*) clustered weakly with the tropical *Neothunnus* and not its hypothesized *Thunnus* relatives, thereby complicating the generic subdivision based on warm- and cold-water preferences. As noted earlier, the bigeye tuna appears to be intermediate between *Neothunnus* and *Thunnus* based on morphological characters (Gibbs and Collette, 1967, 99; Le Gall *et al.,* 1976).

F. Has Mitochondrial Introgression Occurred between Bluefin and Albacore Tuna?

Two mitochondrial studies of the *Thunnus* genus discussed above show a surprisingly close relationship between albacore (*T. alalunga*) and Pacific bluefin (*T. orientalis*), while the Atlantic bluefin (*T. thynnus*) and southern bluefin (*T. maccoyii*) group together as their vernacular names imply. Chow and Kishino (1995) explain the sequence similarity between albacore and Pacific bluefin by interspecific transfer of mtDNA, with albacore mtDNA introduced by hybridization replacing most of the original mitochondrial lineages in the Pacific bluefin. If this explanation is correct, it is a case of horizontal rather than vertical evolution and should not be a factor in deciding taxonomic status of Pacific bluefin.

Gibbs and Collette (1967) felt that the morphological differences between southern bluefin on the one hand (first ventrally directed parapophysis on the 9th vertebrae, yellow caudal keels) and Atlantic and Pacific bluefins on the other (first ventrally directed parapophysis on the 10th vertebrae, dark caudal keels) were strong enough to support species status of the southern bluefin. However, they argued that the slight differences between Atlantic and Pacific bluefins (shape of the dorsal wall of the body cavity in large specimens and numbers of gill rakers) justified recognition of these two only as subspecies, *T. thynnus thynnus* and *T. thynnus orientalis,* respectively. Ward *et al.* (1994), Chow and Kishino (1995), and Alvarado Bremer *et al.* (1996) have provided molecular data supporting the division of bluefin into three taxonomic groups. In light of this newer molecular data along with the morphological distinctions, although slight, between Atlantic and Pacific bluefins, Collette (1999) now advocates separation of these bluefins into Atlantic, *T. thynnus,* and Pacific, *T. orientalis,* species.

G. Can Molecular Data Resolve the Relationships among Spanish Mackerels?

Collette (1999) noted a discrepancy in the phylogenies of Spanish mackerels when morphology or species distributions were used to construct the tree versus when host–parasite relationships were used. In an effort to determine which tree better approximates phylogeny, Banford *et al.* (1999) reexamined the relationships of the *regalis* group using both nuclear and mitochondrial DNA with the Indo-Pacific *Scomberomorus guttatus* as the outgroup. The *regalis* group is monophyletic and the Gulf of Guinea species, *Scomberomorus tritor,* is confirmed as the most plesiomorphic sister species to the five American species. The Atlantic Spanish mackerel, *Scomberomorus maculatus,* could not be distinguished from *Scomberomorus regalis* on the basis of their mtDNA sequences due to mitochondrial introgression. The nuclear-encoded aldolase sequence strongly supported the distinctiveness of *S. maculatus* and *S. regalis,* and the basal position of *S. maculatus* within the New World species. The two eastern Pacific species, *concolor* and *sierra,* appear closely related to each other, similar more to the hypothesis generated from the parasite data than to that from the morphological data.

H. Is *Scomber scombrus* Generically Different from *Scomber japonicus* and *Scomber australasicus*?

Scoles *et al.* (1998, Figure 5) used 418 bp of cytochrome *b* sequence and a parsimony algorithm to generate a consensus tree rooted with *Rastrelliger kanagurta* to show that *S. japonicus* and *S. australasicus* cluster together and away from *S. scombrus.* Agreement of morphological and molecular data led Collette (1999) to support division of *Scomber* into two genera or subgenera.

The genetic data also reveal an interesting problem. The tree in Scoles *et al.* (1998, Figure 5) shows that *S. japonicus* and *S. australasicus* do not form separate monophyletic clades. This conflicts with what was observed in an earlier study of nuclear allozymes that showed fixed differences between a limited sample of the two species (Kijima *et al.,* 1986). Instead, the mtDNA tree shows three major lineages, *S. japonicus, S. australasicus,* and one containing individuals of both species. This suggests the possibility of hybridization after the speciation of *S. japonicus* and *S. australasicus* (Scoles *et al.,* 1998). Biparentally inherited nuclear genes in the hybrid might retain a bit of the phylogenetic history of both paternal and maternal ancestries while the maternally inherited mtDNA would not. It may be that unidirectional backcrossing to males has homogenized the nuclear genome over time to resemble one species.

Scoles (1994) undertook a preliminary study of 10 allozyme loci for 10 individuals from the two divergent *S. australasicus* lineages. No differences were

noted between the nuclear genes in these two lineages. Thus it appears that the mtDNA of one species has introgressed into the other, while the nuclear genome regained its original state presumably through backcrossing. However, more intensive analysis of nuclear genes could recover bits of genetic evidence proving hybridization, particularly in the clade of individuals containing a mixture of mtDNA lineages. Additional nuclear markers applied to both *S. australasicus* and *S. japonicus* might better resolve this question.

Scoles *et al.* (1998) noted a divergence between Pacific and Atlantic populations of *S. japonicus*. Restriction enzyme analysis of mtDNA molecules from 246 *S. japonicus* and *S. australasicus* (Scoles *et al.*, 1998, Figure 3) showed a division of Pacific and Atlantic *S. japonicus* within the clade containing both species. The geographic sorting of the two *japonicus* lineages by ocean basin suggests that these might represent separate species. There is some weak morphological evidence for this as Pacific populations are unmarked or only slightly marked on the belly compared to the strong markings present in the Atlantic populations (Matsui, 1967, Table 7). In addition, the mandibular and premaxillary teeth are only lightly crenulated in Pacific populations versus strongly crenulated in Atlantic populations. Given this evidence, Collette (1999) decided to recognize the Atlantic populations as a separate species, *Scomber colias*.

III. CONCLUSIONS

This chapter demonstrates the value of examining both morphological and molecular data in constructing hypotheses about the evolution of scombrid fishes. Each data set provides directions as well as areas of focus for the other. Scombrid fishes have a rich history and morphological systematists have identified numerous morphological and physiological characters. However, they still have not unraveled the evolutionary history. More data are required in some cases to tease apart the true relationships (e.g., *Gasterochisma*). However, in several cases the evolutionary history of the group was clarified by examining the molecular data. For example, the morphological controversy surrounding the placement of *Acanthocybium* was put to rest. In another case, molecular data showed that the subgenus *Thunnus* was not monophyletic since bigeye (*T. obesus*) clustered weakly with the tropical *Neothunnus* and not its hypothesized *Thunnus* relatives. The morphological data likewise indicated that the bigeye tuna appeared to be intermediate between *Neothunnus* and *Thunnus*. On occasion molecular data have provided reason for reexamining morphological hypotheses. For example, all the molecular data indicate the albacore is the most divergent lineage of *Thunnus*. Few have examined the evolution of the *Thunnus* lineage in this light (Block *et al.*, 1997). Future investigations should seek to clarify which is the most primitive

member of the genus as it has tremendous bearing on theories of the evolution of endothermy of tunas.

The evolutionary history of the Scombridae is among the most interesting to examine in bony fish. Endothermy, along with the unique form of swimming known as "thunniform," arose with numerous physiological and morphological characters that have evolved only in this lineage. Until we fully understand the evolutionary relationships we will not be able to comprehend the direction of character evolution for either complex trait. We advocate examining both types of data and trying to understand differences between trees based on molecules and morphology. Combining data into "total evidence" trees where morphology and molecules are put into a single data matrix to draw a tree might provide new directions. Or the use of alternative molecular markers and analysis may finally clarify some of the deeper nodes in the tree where apparent rapid speciation events may be confusing the tree topology. Some molecular markers, particularly those that identify insertion or deletion events of multiple nucleotides along a segment of DNA or those that analyze DNA structure beyond the typical primary sequence structure, have proven useful in the systematics of other difficult taxa. These markers include secondary structures of ribosomal genes (Reeb, 1995; Billoud *et al.*, 2000) and repetitive sequences scattered in the genome such as short interspersed nuclear elements (e.g., Shedlock and Okada, 2000). To date, no one has used these approaches for scombroid phylogeny.

One of the most fascinating evolutionary questions surrounding the scombrid fishes centers upon understanding how and why endothermy evolved. Whether this occurred in warm or cold seas remains an open question. The inability of molecular data to unequivocally resolve the position of *Allothunnus* does not negate the importance of the recent discoveries of countercurrent heat exchangers (Graham and Dickson, 2000). Both data sets agree that *Allothunnus* is a part of the Thunnini–Sardini continuum. The exact placement of this fish within the continuum based on molecular data requires further investigation. *Allothunnus* shares several derived features with the Thunnini which would corroborate its morphological placement as sister taxa to more derived tuna lineages. The existence of this fish in cool southern oceans would suggest that the endothermic condition and the concomitant benefits of muscle tissue warming began in a cold-water temperate fish. Supporting this hypothesis would be the independent evolution within the scombrid fish of the heater organs in the cold-water *Gasterochisma.* Complications in the hypothesis arise when examining *Auxis, Euthynnus, Katsuwonus,* and *Thunnus* due to the lack of agreement on the exact evolutionary relationships within the genus *Thunnus.* Future efforts should be directed at finding additional characters, either genetic, morphological, or physiological (e.g., some *Thunnus* such as the yellowfin have countercurrent blood supply within the cecum tissue), for analysis. Once the systematics is clarified, a greater understanding of evolutionary change among these unusual, widespread, commercially exploited species will be obtained.

ACKNOWLEDGMENTS

Helpful comments on drafts of the manuscript for this chapter were provided by Drs. Kent Carpenter, G. David Johnson, and Michael Vecchione. We thank Seinen Chow for access to unpublished data.

REFERENCES

Alvarado Bremer, J. R. (1994). Assessment of morphological and genetic variation of the swordfish (*Xiphias gladius* L.): Evolutionary implications of allometric growth and of the patterns of nucleotide substitution in the mitochondrial genome. Ph.D. dissertation, University of Toronto, Toronto.

Alvarado Bremer, J. R., Naseri, I. I., and Ely, B. (1996). Orthodox and unorthodox phylogenetic relationships among tunas revealed by the nucleotide sequence analysis of the mitochondrial DNA control region. *J. Fish Biol.* **50,** 540–554.

Baker, E. A., and Collette, B. B. (1998). Mackerel from the northern Indian Ocean and the Red Sea are *Scomber australasicus,* not *Scomber japonicus. Ichthyol. Res.* **45,** 29–33.

Banford, H. M., Bermingham, E., Collette, B. B., and McCafferty, S. S. (1999). Phylogenetic systematics of the *Scomberomorus regalis* (Teleostei: Scombridae) species group: Molecules, morphology and biogeography of Spanish mackerels. *Copeia* **1999,** 596–613.

Bartlett, S. E., and Davidson, W. S. (1991). Identification of *Thunnus* tuna species by the polymerase chain reaction and direct sequence analysis of their mitochondrial cytochrome *b* genes. *Can. J. Fish. Aquat. Sci.* **48,** 309–317.

Billoud, B., Guerrucci, M., Masselot, M., and Deutsch, J. S. (2000). Cirripede phylogeny using a novel approach: Molecular morphometrics. *Mol. Biol. Evol.* **17,** 1435–1445.

Block, B. A. (1994). Thermogenesis in muscle. *Annu. Rev. Physiol.* **56,** 535–577.

Block, B. A., Finnerty, J. R., Stewart, A. F. R., and Kidd, J. (1993). Evolution of endothermy in fish: Mapping physiological traits on a molecular phylogeny. *Science* **260,** 210–214.

Block, B. A., Keen, J. E., Castillo, B., Dewar, H., Freund, E. V., Marcinek, D. J., Brill, R. W., and Farwell, C. (1997). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Mar. Biol.* **130,** 119–132.

Carey, F. G., Teal, J. M., Kanwisher, J. W., Lawson, K. D., and Beckett, K. S. (1971). Warm-bodied fish. *Am. Zool.* **11,** 135–143.

Carpenter, K. E., Collette, B. B., and Russo, J. L. (1995). Unstable and stable classifications of scombroid fishes. *Bull. Mar. Sci.* **56,** 379–405.

Chow, S., and Inoue, S. (1993). Intra- and interspecific restriction fragment length polymorphism in mitochondrial genes of *Thunnus* tuna species. *Bull. Natl. Inst. Far Seas Fish.* **30,** 207–225.

Chow, S., and Kishino, H. (1995). Phylogenetic relationships between tuna species of the genus *Thunnus* (Scombridae: Teleostei): Inconsistent implications from morphology, nuclear and mitochondrial genomes. *J. Mol. Evol.* **41,** 741–748.

Collette, B. B. (1970). *Rastrelliger kanagurta,* another Red Sea immigrant into the Mediterranean Sea, with a key to the Mediterranean species of Scombridae. *Bull. Sea Fish. Res. Sta., Haifa* **54,** 3–6.

Collette, B. B. (1979). Adaptations and systematics of the mackerels and tunas. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 7–39. Academic Press, New York.

Collette, B. B. (1999). Mackerels, molecules, and morphology. Proc. 5th Indo-Pacific Fish. Conf., Nouméa, 1997, Soc. Fr. Ichtyol., pp.149–164.

Collette, B. B., and Aadland, C. R. (1996). Revision of the frigate tunas (Scombridae, *Auxis*), with descriptions of two new subspecies from the eastern Pacific. *Fish. Bull. U.S.* **94,** 423–441.

Collette, B. B., and Chao, L. N. (1975). Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). *Fish. Bull. U.S.* **73,** 516–625.

Collette, B. B., and Gibbs, R. H., Jr. (1963). A preliminary review of the fishes of the family Scombridae. *FAO Fish. Rep.* **6,** 23–32.

Collette, B. B., and Gillis, G. B. (1992). Morphology, systematics, and biology of the double-lined mackerels (*Grammatorcynus,* Scombridae). *Fish. Bull. U.S.* **90,** 13–53.

Collette, B. B., and Nauen, C. E. (1983). FAO species catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. *FAO Fish. Synop.* **125,** 1–137.

Collette, B. B., and Russo, J. L. (1985a). Interrelationships of the Spanish mackerels (Pisces: Scombridae: *Scomberomorus*) and their copepod parasites. *Cladistics* **1,**141–158.

Collette, B. B., and Russo, J. L. (1985b). Morphology, systematics, and biology of the Spanish mackerels (*Scomberomorus,* Scombridae). *Fish. Bull. U.S.* **82,** 545–692.

Collette, B. B., Potthoff, T., Richards, W. J., Ueyanagi, S., Russo, J. L., and Nishikawa, Y. (1984). Scombroidei: Development and relationships. *In* "Ontogeny and Systematics of Fishes" (Moser, H. G., *et al.,* Eds.), No. 1, pp. 591–620. Am. Soc. Ichthyol. Herp. Spec. Publ.

Conrad, G. M. (1938). The osteology and relationships of the wahoo (*Acanthocybium solandri*), a scombrid fish. *Am. Mus. Nat. Hist. Novitates* **1000,** 1–32.

Elliott, N. G., and Ward, R. D. (1995). Genetic relationships of eight species of Pacific tunas (Teleostei, Scombridae) inferred from allozyme analysis. *Mar. Freshw. Res.* **46,** 1021–1032.

Finnerty, J. R., and Block, B. A. (1994). Accounting for endothermy in fishes: Response. *Science* **265,** 1250–1251.

Finnerty, J. R., and Block, B. A. (1995). Evolution of cytochrome *b* in the Scombroidei (Teleostei): Molecular insights into billfish (Istiophoridae and Xiphiidae) relationships. *Fish. Bull. U.S.* **93,** 78–96.

Fitch, J. E., and Craig, W. L. (1964). First records for the bigeye thresher (*Alopias superciliosus*) and slender tuna (*Allothunnus fallai*) from California, with notes on eastern Pacific scombrid otoliths. *Calif. Fish Game* **50,** 195–206.

Fraser-Brunner, A. (1950). The fishes of the family Scombridae. *Ann. Mag. Nat. Hist., Ser. 12,* **3,** 131–163.

Gibbs, R. H., Jr., and Collette, B. B. (1967). Comparative anatomy and systematics of the tunas, genus *Thunnus*. *U.S. Fish. Wildl. Serv., Fish. Bull.* **66,** 65–130.

Godsil, H. C. (1954). A descriptive study of certain tuna-like fishes. *Calif. Div. Fish Game, Fish Bull.* **97,** 1–188.

Godsil, H. C., and Byers, R. D. (1944). A systematic study of the Pacific tunas. *Calif. Div. Fish Game, Fish Bull.* **60,** 1–131.

Graham, J. B. (1973). Heat exchange in the black skipjack and the blood-gas relationship of warm-bodied fishes. *Proc. Natl. Acad. Sci.* **70,** 1964–1967.

Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares,* and skipjack tuna, *Katsuwonus pelamis,* and the adaptive significance of elevated body temperatures in scombrid fishes. *Fish. Bull. U.S.* **73,** 219–229.

Graham, J. B., and Dickson, K. A. (2000). The evolution of thunniform locomotion and heat conservation in scombrid fishes: New insights based on the morphology of *Allothunnus fallai*. *Zool. J. Linnean Soc.* **129,** 419–466.

Irwin, D. M., Kocher, T. D., and Wilson, A. C. (1991). Evolution of the cytochrome *b* gene of mammals. *J. Mol. Evol.* **32,** 128–144.

Johnson, G. D. (1986). Scombroid phylogeny: An alternative hypothesis. *Bull. Mar. Sci.* **39,** 1–41.

Kijima, A., Taniguchi, N., and Ochiai, A. (1986). Genetic divergence and morphological difference between the spotted and common mackerel. *Jpn. J. Ichthyol.* **33,** 152–161.

Kishinouye, K. (1923). Contributions to the comparative study of the so-called scombroid fishes. *J. Coll. Agr. Imp. Univ. Tokyo* **8,** 293–475.

Le Gall, J. Y., Laurec, A., and Chardy, P. (1976). Mise en évidence des relations phénotypiques et phylogénétiques à l'intérieur du genre *Thunnus* par une analyse multicritère. *Bull. Mus. Nat. Hist. Nat., Ser. 3,* **339,** 1349–1368.

Mago Leccia, F. (1958). The comparative osteology of the scombroid fishes of the genus *Scomberomorus* from Florida. *Bull. Mar. Sci. Gulf. Carib.* **8,** 299–341.

Martin, A. P., Kessing, B. D., and Palumbi, S. R. (1990). Accuracy of estimating genetic distance between species from short sequences of mitochondrial DNA. *Mol. Biol. Evol.* **7,** 485–488.

Matsui, T. (1967). Review of the mackerel genera *Scomber* and *Rastrelliger* with description of a new species of *Rastrelliger. Copeia* **1967,** 71–83.

Matsumoto, W. M. (1960). Notes on the Hawaiian frigate mackerel of the genus *Auxis. Pacific Sci.* **14,** 173–177.

Matsumoto, W. M. (1976). Second record of black skipjack, *Euthynnus lineatus,* from the Hawaiian Islands. *Fish. Bull. U.S.* **74,** 207.

Matsumoto, W. M., and Kang, T. (1967). The first record of black skipjack, *Euthynnus lineatus,* from the Hawaiian Islands. *Copeia* **1967,** 837–838.

Meyer, A. (1994). Shortcomings of the cytochrome *b* gene as a molecular marker. *Trends Ecol. Evol.* **9,** 278–280.

Munro, I. S. R. (1943). Revision of Australian species of *Scomberomorus. Mem. Queensland Mus.* **12,** 65–95.

Reeb, C. A. 1995. Molecular insights into the evolution of a circumtropical fish (*Coryphaena hippurus*) and an Indo-Pacific group of mollusks (*Cellana*). Ph.D. dissertation, J. A. Burns School of Medicine, University of Hawaii, Manoa.

Reeb, C. A., Arcangeli, L., and Block, B. A. (2000). Structure and migration corridors in Pacific populations of the swordfish, *Xiphius gladius,* as inferred through analysis of mitochondrial DNA. *Mar. Biol.* **136,** 1123–1131.

Richards, W. J., and Randall, J. E. (1967). First Atlantic records of the narrow-corseleted frigate mackerel, *Auxis thazard. Copeia* **1967,** 245–247.

Sage, R. D., Atchley, W. R., and Capanna, E. (1993). House mice as models in systematic biology. *Syst. Biol.* **42,** 523–561.

Schaefer, K. M., and Childers, J. (1999). Northernmost occurrence of the slender tuna, *Allothunnus fallai,* in the Pacific Ocean. *Calif. Fish Game* **85,** 121–123.

Scoles, D. R. (1994). Global phylogeography of yellowfin tuna, *Thunnus albacares,* and mackerels of the genus *Scomber.* Ph.D. dissertation, School of Marine Science, College of William and Mary, Williamsburg, VA.

Scoles, D. R., and Graves, J. E. (1993). Genetic analysis of the population structure of yellowfin tuna, *Thunnus albacares,* from the Pacific Ocean. *Fish. Bull. U.S.* **91,** 690–698.

Scoles, D. R., Collette, B. B., and Graves, J. E. (1998). Global phylogeography of mackerels of the genus *Scomber. Fish. Bull. U.S.* **96,** 823–842.

Sharp, G. D., and Pirages, S. W. (1979). The distribution of red and white swimming muscles, their biochemistry, and the biochemical phylogeny of selected scombroid fishes. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 41–78. Academic Press, New York.

Shedlock, A. M., and Okada, M. C. (2000). SINE insertions: Powerful tools for molecular systematics. *Bioessays* **22,** 148–160.

Wade, C. B. (1949). Notes on the Philippine frigate mackerels, family Thunnidae, genus *Auxis. U.S. Fish Wildl. Serv., Fish. Bull.* **51,** 229–240.

Waits, L. P., Sullivan, J., O'Brien, S. J., and Ward, R. H. (1999). Rapid radiation events in the family Ursidae indicated by likelihood phylogenetic estimation from multiple fragments of mtDNA. *Mol. Phylogenet. Evol.* **5,** 567–575.

Ward, R. D. (1995). Population genetic of tunas. *J. Fish Biol.* **47,** 259–280.

Ward, R. D., Elliott, N. G., Grewe, P. M., and Smolenski, A. J. (1994). Allozyme and mitochondrial DNA variation in yellowfin tuna (*Thunnus albacares*) from the Pacific Ocean. *Mar. Biol.* **118,** 531–539.

2

TUNA METABOLISM AND ENERGETICS

KEITH E. KORSMEYER
HEIDI DEWAR

I. Introduction
II. History of Tuna Metabolic Studies
III. Metabolic Rates
  A. Standard and Routine Metabolic Rate
  B. Maximum Metabolic Rate
  C. Scaling of Metabolic Rate
  D. Temperature Effects on Metabolic Rate
  E. Hypoxia Effects on Metabolic Rate
  F. Metabolic Rate and Swimming Velocity
IV. Oxygen Uptake and Delivery
V. Metabolic Capacity of Tissues
  A. Red Muscle
  B. White Muscle
  C. Other Tissues
VI. Multiple Metabolic Demands
  A. Specific Dynamic Action (R_F)
  B. Growth and Reproduction ($R_{G\&R}$)
  C. Oxygen Debt Recovery (R_D)
  D. Modeling Multiple Metabolic Costs
VII. Discussion and Conclusions
  A. How Does the Metabolic Rate of Tunas Compare with Other Fishes?
  B. What Are the Adaptations Related to Supporting the Energetic Demands of Swimming and Other Metabolic Processes?
  C. How Do Tuna Energetics Relate to Their Swimming Performance?
  D. What Metabolic Processes Account for the Total Energetic Costs in Tunas?
  E. Finally, How Does the Metabolism of Tunas Relate to Their Pelagic Existence and the Evolution of Regional Endothermy?
VIII. The Future

Reports of the tuna's extreme swimming capabilities and endothermy have resulted in considerable interest in their metabolism. Progress in tuna energetics has been linked to the development of methods and facilities for their study as

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

well as the newly available data for closely related species and other active teleosts. Metabolic measurements indicate that, although standard metabolic rate (SMR) is elevated in tunas compared with many species, similar SMR and routine metabolic rates are observed in other active fish. The elevated SMR is associated with an increase in aerobic scope, which reduces potential energetic limitations on physiological functions. Consequently, tuna can meet their basal metabolic demands (SMR and locomotion) without compromising recovery from oxygen debt, digestion, growth, or reproduction. Contrary to previous reports, tunas appear to be no more efficient swimmers than other teleosts, at least during steady, sustained swimming in a swim tunnel. High metabolic rates require that all steps in the path from the gills to the mitochondria facilitate high levels of oxygen and metabolite flux. While some differences exist between tunas and other active fishes at the gills, cardiovascular system, and tissue, the most marked difference, other than endothermy, is that the total aerobic capacity of the white muscle tissue mass is greater than that of the red muscle. The white muscle's aerobic capacity facilitates rapid recovery from oxygen debt incurred during burst swimming. Studies comparing the tuna with ectothermic scombrids suggest that endothermy may have evolved following an increase in aerobic poise.

I. INTRODUCTION

Tunas, with their sleek bodies, warm muscles, and powerful swimming, are the focus of considerable interest, particularly in the areas of metabolism and energetics. How do these predatory fish grow so rapidly and swim so quickly, apparently expending large amounts of energy, while living in a pelagic ocean environment which is generally depauperate of prey (Blackburn, 1968)? Tunas, like other animals, use chemical energy acquired from prey to perform the various functions of life. The amount of energy acquired must exceed the amount expended by daily activities to permit growth and reproduction. Based on optimal foraging theory, natural selection should operate to maximize the ratio of energy income to energy expenditure (Webb, 1975; Townsend and Winfield, 1985). The more efficient individuals, at a given energy intake, will have more energy to invest in growth and reproduction, and therefore have a higher fitness. How do tunas fit into this scheme? This question not only has implications for energetics but may also provide insight into the evolution of endothermy.

Much of the research on tunas over the last 30 years has focused on measuring metabolic rates, in attempt to quantify swimming costs, and to ascertain the consequence of endothermy on metabolic function (Stevens, 1972; Brill, 1979, 1987; Gooding *et al.*, 1981; Graham *et al.*, 1989; Boggs and Kitchell, 1991; Dewar and Graham, 1994). Measured metabolic rates of tunas exceed those of other well-studied fishes (e.g., salmonids) by approximately threefold. These observations have

led to investigations into the adaptations enabling high rates of oxygen uptake, delivery, and utilization as well as how energy is partitioned (Muir and Hughes, 1969; Brill and Bushnell, 1991; Mathieu-Costello *et al.*, 1992; Moyes *et al.*, 1992; Dickson, 1995; Freund 1999). The purpose of the present review is to highlight the advances in tuna energetics, and draw some conclusions about the possible implications for the questions raised above. Specifically, how does the metabolic rate of tunas compare with other fishes? What are the adaptations related to supporting the energetic demands of swimming and other metabolic processes? How do tuna energetics relate to their swimming performance? What metabolic processes account for the total energetic costs in tunas? Finally, how does the metabolism of tunas relate to their pelagic existence and the evolution of regional endothermy?

A great deal of new information has been gained since the last major review of tuna physiology (see *The Physiological Ecology of Tunas,* Academic Press, 1978). Much of our recently gained knowledge of tuna biology has benefited from greater emphasis on appropriate phylogenetic comparisons. Only by using the comparative approach can we sort out those features of tunas which are the result of adaptation to the pelagic environment or the acquisition of endothermy, and which are due to evolutionary constraints (Block and Finnerty, 1994). Historically, tunas have been distinguished by comparison with salmonids (Gooding *et al.*, 1981; Dewar and Graham, 1994), which provide the largest experimental data base in fish biology. Salmonids, however, are both distantly related to tunas (by approximately 100 million years of evolution; Carroll, 1988) and have a markedly different ecology (as anadromous or freshwater fishes from temperate and polar regions, whereas most of the physiological data on tunas come from studies of tropical species). Recent efforts have provided data on close relatives within the family Scombridae, which includes the mackerels (tribe Scombrini), seerfishes (tribe Scomberomorini), bonitos (tribe Sardini), and tunas (tribe Thunnini), and other large, warm-water pelagic fish, such as the dolphinfish (family Coryphaenidae; Benetti *et al.*, 1995; Dickson, 1995, 1996; Freund, 1999). Comparisons with the ectothermic scombrids, such as the mackerel and bonito, are of particular importance in examining the interplay between endothermy and energetics.

II. HISTORY OF TUNA METABOLIC STUDIES

To understand the current state of the field of tuna energetics it is useful to examine the historical developments that have driven its progress. Tuna research on metabolic rates has lagged far behind that of salmonids, which was relatively advanced by the early 1970s (Brett, 1964, 1965; Beamish, 1970; Brett and Glass, 1973; Webb, 1971; summarized in Webb, 1975). Efforts to study tunas have been hampered by the inherent difficulties in handling these large, active, pelagic fish. As a result, progress in the field has been tied to the advancement of new tech-

niques. Of critical importance has been the ability to maintain animals in captivity. Most research on live tunas (primarily the skipjack tuna *Katsuwonus pelamis,* yellowfin tuna *Thunnus albacares,* and kawakawa *Euthynnus affinis*) has been conducted on small fish (0.5 to 5 kg) at the National Marine Fisheries Service, Kewalo Research Facility, in Honolulu, Hawaii (Brill, 1992; Nakamura, 1972). More recently, the Tuna Research and Conservation Center in Monterey, California (Altringham and Block, 1997; Dewar *et al.,* 1999), has provided access to larger fish and also expanded the species held to bluefin tuna (*Thunnus thynnus*). Another important step was the development of a large recirculating water tunnel, which allowed physiological studies where swimming speed and environmental conditions could be controlled (Graham and Laurs, 1982; Graham *et al.,* 1989). Given the focus on locomotory abilities, quantifying physiological variables as a function of swimming speed was critical.

Over the last 30 years, researchers have used a variety of techniques in attempting to quantify the metabolic rates of tuna. Efforts began with measurements of the oxygen consumption of minced slow- and fast-twitch muscle tissue taken from skipjack and bigeye tuna (*Thunnus obesus;* Gordon, 1968). Interestingly, tissue metabolism changed little with temperature (Q_{10}, the factor by which the rate changes with a 10°C increase in temperature, of 1–1.2) and values for skipjack tuna aerobic, slow-twitch muscle (hereafter termed red muscle) were similar to mammalian muscle at 30 and 35°C. The applicability of these measures to *in vivo* contracting muscle is not clear. Stevens (1972) was the first to estimate whole-body metabolic rates by measuring the fraction of oxygen removed from water passed over the gills of an anesthetized tuna. Results from this study suggested that the metabolic rate of tuna (692 mg O_2 kg^{-1} h^{-1}) was at least four times higher than that of rainbow trout (*Oncorhynchus mykiss*). Brill (1979, 1987) obtained a more direct measure of metabolic rate by recording whole-animal rates of oxygen consumption from immobilized tropical tunas. These results (detailed below) provided estimates of the minimal metabolic demands, as well as effects of body size and temperature, and confirmed the assertion that metabolic rates in tuna were elevated.

The first measurements of oxygen consumption by swimming tuna were made by Gooding *et al.* (1981) on small groups of captive or recently captured skipjack tuna. The fish swam in an annular tank respirometer where swimming speed was estimated by averaging lap times for the group, providing the first estimate of velocity effects. These results were complicated by the determination of group averages rather than values for individual fish and the inability to precisely determine velocity. Also, the use of recently caught fish may overestimate metabolic rates due to anaerobic debt incurred during capture (Dewar and Graham, 1994) and digestive processes in postprandial fish. Using a different approach, Boggs (1984; Boggs and Kitchell, 1991) estimated metabolic demands by measuring reductions in caloric density of body tissues during fasting in captive groups of tuna. Despite the limitation of each technique and their differences, estimates of metabolic rates by Boggs were similar to those of Gooding *et al.* (1981).

Continued advancement in tuna energetics required the ability to monitor and control swimming speed and temperature while oxygen consumption was recorded. This was made possible by the development of a large recirculating water tunnel by Jeffrey Graham at Scripps Institution of Oceanography (Graham *et al.*, 1989, 1990; Graham and Laurs, 1982). The water tunnel was first used in a number of trips to sea to study albacore tuna (*Thunnus alalunga;* Graham and Laurs, 1982; Graham *et al.*, 1989), providing the first metabolic measurements made at controlled velocities. Graham then moved the water tunnel to the Kewalo Research Facility in Hawaii in the early 1990s, where captive-acclimated fish could be studied while swimming for up to 31 hours. Dewar and Graham (1994) were able to examine the influence of temperature, size, and swimming speed on the metabolic rate of yellowfin, kawakawa, and skipjack tunas.

While much has been done to define the metabolic parameters of a few tuna species, our ability to interpret these data has been limited by the lack of appropriate comparisons. In recent years, however, a number of researchers have been focusing on comparable measures for ectothermic scombrids, as well as other active tropical fish species (Benetti *et al.*, 1995; Dickson, 1995; Freund, 1999; Sepulveda and Dickson, 2000). Freund (1999), using the methods of Gooding *et al.* (1981), measured the routine metabolic rates the bonito, in comparison with skipjack and yellowfin. Sepulveda and Dickson (2000) have compared the metabolic rates of similarly sized tuna and mackerel swimming in a water tunnel. These phylogenetically correct comparisons improve our ability to determine the functional significance of the tuna's adaptations.

III. METABOLIC RATES

A number of different metabolic levels, or states, have been identified which facilitate comparisons among different studies and species. Standard metabolic rate (SMR) is defined as the resting and fasting metabolism at a given temperature. This is theoretically the minimal metabolic rate of the animal. The aerobic metabolism during low levels of spontaneous activity is termed the routine metabolic rate (RMR) and may cover a wide range of values depending on conditions. Finally, we can identify the maximal rate of aerobic metabolism (MMR).[1] The difference between MMR and SMR indicates the animal's aerobic metabolic scope available to power activities (Fry, 1971). The above metabolic designations do not

[1] We have chosen to use this MMR designation rather than the more traditional "active metabolic rate," or AMR, for several reasons. Active metabolic rate has been used to identify the maximal aerobic metabolic rate achieved during intense, but steady, swimming (Fry, 1971; Brett and Groves, 1979), but it has also been used to identify metabolic rates associated with swimming at *any* velocity (Videler, 1993). More importantly, it assumes that the maximal aerobic metabolic rate of the fish occurs as a result of locomotor activity alone. Although this may be the case for many fish, it does not hold true for all (Goolish, 1991), and may not hold true for tunas (Korsmeyer *et al.*, 1996a).

take into account activities powered by anaerobic metabolism. Anaerobic energy production may occur in addition to any aerobic metabolic rate and can temporarily exceed the MMR (by up to 10 times), resulting in the build up of an oxygen debt which must be repaid later (Brett, 1972).

Most studies on tunas have used oxygen consumption (respirometry) as an indirect measure of metabolic rate (Stevens, 1972; Gooding *et al.*, 1981; Brill 1979, 1987; Graham and Laurs, 1982; Graham *et al.*, 1989; Dewar and Graham 1994). While ideally one would use direct calorimetry (heat production), oxygen consumption is relatively easy to measure and can provide information on rapid changes (on the order of minutes) in metabolic demands, and errors associated with the difference in energy released by oxidation of different metabolic substrates is minimal (Randall *et al.*, 1997). Respirometry is limited, however, in that it cannot detect anaerobic contributions to metabolism. Also, comparisons between studies are sometimes complicated by the different metabolic states measured as well as the influence of stress, feeding, body mass, and temperature. Despite these problems, sufficient data are available to make some general conclusions about how tunas compare with other fishes.

A. Standard and Routine Metabolic Rate

Tunas must swim continually to maintain ventilatory water flow and generate sufficient lift to prevent sinking and thus never achieve the "resting state" which defines SMR (Magnuson, 1978). Estimates of SMR, however, are valuable as a basis for comparison with other species and for determining how resources are partitioned. For fish which swim continually, SMR is estimated using two methods: oxygen consumption ($\dot{M}O_2$) of immobilized specimens (by neuromuscular or spinal block), and extrapolation of $\dot{M}O_2$ and swimming velocity relationships back to zero swimming speed (Brill, 1979, 1987; Gooding *et al.*, 1981; Graham *et al.*, 1989; Dewar and Graham, 1994). Both methods have been validated in other fish species and provide similar results (Brett, 1964; Bushnell *et al.*, 1984; Brill, 1987; Dewar and Graham, 1994).

Standard metabolic rate data for tunas, with comparisons to other fish species, are summarized in Figure 1. The nontuna species chosen for comparison are considered to be active swimmers which generally have higher SMRs than more sluggish, or bottom-dwelling, species (Brett, 1965; Brett and Groves, 1979). The SMRs for tunas are 2 to 10 times greater than those for most active fishes shown in Figure 1, even when differences in temperature are taken into account. However, SMRs of some active pelagic fishes, such as dolphinfishes (*Coryphaena hippurus*), are similar to those of tunas (Figure 1; Benetti *et al.*, 1995). Like the tunas, dolphinfish are obligate ram ventilators, have large gill surface areas, and have high growth and reproductive rates (Palko *et al.*, 1982; Benetti *et al.*, 1995; Brill, 1996). Another active pelagic fish, the yellowtail (*Seriola quinqueradiata*, family

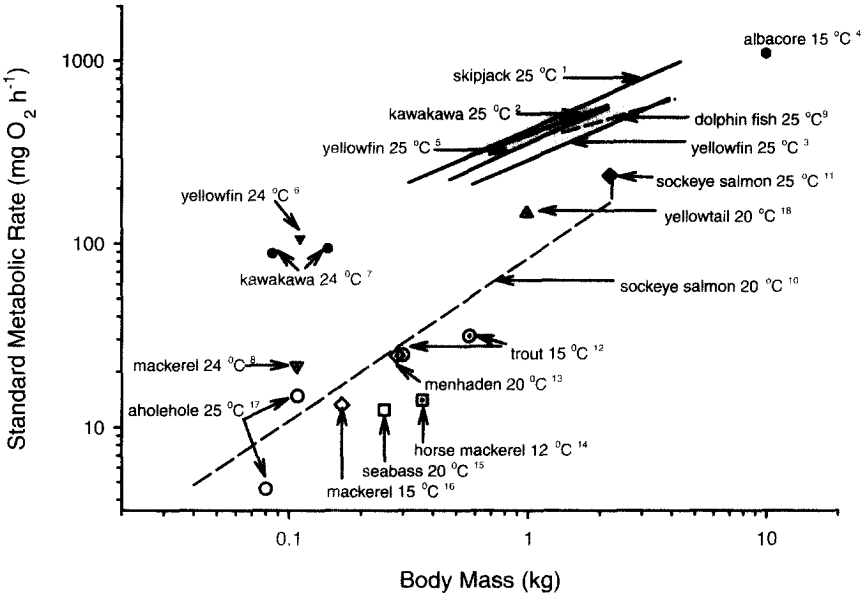


Fig. 1. Standard metabolic rate (mg O_2 h^{-1}) as a function of body mass (M, kg) for tunas (solid symbols, solid lines) compared with other active fishes (open symbols, dashed lines). [1]*Katsuwonus pelamis;* SMR = 412.0 $M^{0.563}$ (Brill, 1979). [2]*Euthynnus affinis;* SMR = 392.5 $M^{0.496}$ (Brill, 1987). [3]*Thunnus albacares;* SMR = 286.8 $M^{0.573}$ (Brill, 1987). [4]*Thunnus alalunga* (Graham *et al.*, 1989). [5]*Thunnus albacares* (Dewar and Graham, 1994). [6]*Thunnus albacares,* [7]*Euthynnus affinis,* and [8]*Scomber japonicus* calculated from data in Sepulveda and Dickson (2000) by extrapolating the logarithm of oxygen consumption as a function of velocity to zero velocity. [9]*Coryphaena hippurus* (Benitti *et al.*, 1995). [10]*Oncorhynchus nerka* (Brett and Glass, 1973). [11]*Oncorhynchus nerka* from Brett and Glass (1973) corrected to a temperature of 25°C assuming Q_{10} = 2. [12]*Oncorhynchus mykiss* (Bushnell *et al.*, 1984; Brill, 1987). [13]*Brevoortia tyrannus* (Macy *et al.*, 1999). [14]*Trachurus trachurus* (Wardle *et al.*, 1996). [15]*Dicentrarchus labrax* (Herskin and Steffensen, 1998). [16]*Scomber japonicus* (Steffensen and Shadwick, unpublished data). [17]*Kuhlia sandvicensis* (Brill, 1987). [18]*Seriola quinqueradiata* (Yamamoto *et al.*, 1981).

Carangidae), has an SMR intermediate between those of tunas and other fishes (Figure 1; Yamamoto *et al.*, 1981). Correcting for temperature differences, the tunas have SMRs that are only 1.4 to 2.0 times that of the yellowtail. Within the family Scombridae, SMR values are available only for the Pacific mackerel (*Scomber japonicus*). Similarly sized yellowfin and kawakawa, at the same temperature, have SMRs that are about 4 times greater than that of the mackerel (Figure 1; Sepulveda and Dickson, 2000).

Unlike the mackerel, another scombrid, the eastern Pacific bonito (*Sarda chiliensis*), appears to have similar metabolic rates as the tunas'. RMRs of the bonito

and skipjack tuna were recently compared while the fish swam in an annular respirometer (Freund, 1999). The $\dot{M}O_2$ values of skipjack (540 ± 63 mg O_2 kg^{-1} h^{-1}) and bonito (427 ± 63 mg O_2 kg^{-1} h^{-1}), which had similar masses (~1.4 kg) and average swimming velocities [0.5 lengths (L) s^{-1}, measured by recording lap times], were not significantly different.

The picture that is emerging is that while tunas have higher metabolic rates than many active fishes, including mackerel, so do some other pelagic species (e.g., dolphinfish and bonito). Therefore, fishes can have a high metabolic rate without the elevated tissue temperatures associated with endothermy.

B. Maximum Metabolic Rate

Maximum metabolic rate has not been measured directly in tunas, ectothermic scombrids, or other tropical pelagic fishes. A few very high $\dot{M}O_2$ values have been measured for tropical tunas (23–25°C), but whether these represent a maximum is not known. The mean $\dot{M}O_2$ measured for groups of skipjack tuna within the first two hours after capture at sea was 1300 mg O_2 kg^{-1} h^{-1} (1.8–2.2 kg body mass; Gooding *et al.*, 1981). Individual measurements ranged from 900 mg O_2 kg^{-1} h^{-1} to the highest $\dot{M}O_2$ ever recorded for fish of this size, 2500 mg O_2 kg^{-1} h^{-1}. These fish were swimming at high speeds (~3.5 L s^{-1}), were likely recovering from anaerobic activity, and may have been digesting food. A similarly high $\dot{M}O_2$ was recorded for one skipjack just after it was placed in a swimming respirometer (2200 mg O_2 kg^{-1} h^{-1}, ~1.7 kg; Dewar and Graham, 1994). The highest recorded $\dot{M}O_2$ for yellowfin in a swimming respirometer was 1290 mg O_2 kg^{-1} h^{-1} (~2 kg; Dewar and Graham, 1994). While these values may be less than the MMR, they do provide an estimate for its lower limit.

With the lack of any clear data, models have been developed to predict MMRs for tunas. Expanding on a model by Dizon (1977), Bushnell and Brill (1991; Brill, 1996) calculated maximum rates of oxygen extraction from the ventilatory water flow in yellowfin and skipjack tunas as a function of swimming speed. Maximum oxygen uptake for a body mass of 1.4 kg was predicted to be 2500 mg O_2 kg^{-1} h^{-1} for yellowfin and 2700 mg O_2 kg^{-1} h^{-1} for skipjack (Bushnell and Brill, 1991). For 2.0-kg fish, the MMR is predicted to be 1600 and 1800 mg O_2 kg^{-1} h^{-1} for yellowfin and skipjack, respectively (Brill, 1996). These model values of MMRs are considerably higher than the upper limit of $\dot{M}O_2$ reported for a number of other fishes (~1000 mg O_2 kg^{-1} h^{-1}; Brett, 1972).

One impetus for documenting MMRs is to calculate the aerobic scope, which would indicate the level of aerobic activity that can be sustained. Based on the values discussed above, a 2-kg skipjack (SMR ~ 300 mg O_2 kg^{-1} h^{-1}; Brill, 1979) should have an aerobic scope of between 1500 and 2200 mg O_2 kg^{-1} h^{-1}. This is considerably higher than that for a comparably sized sockeye salmon at approximately 700 mg O_2 kg^{-1} h^{-1} (20°C; Brett and Glass, 1973). Interestingly, the esti-

mated ratio of MMR to SMR for tunas (6–10) is similar to that of both other active fish species and terrestrial vertebrates (Brett and Groves, 1979; Bennett and Ruben, 1979; Else and Hulbert, 1981, 1985). It seems that the high SMRs of tunas are associated with a very high aerobic scope. Actual measurements of MMR in tunas and other pelagic fishes are needed to verify this.

C. Scaling of Metabolic Rate

SMR data for tunas over a significant size range (Figure 1) allow for estimation of the effect of body size on metabolic rate. Because of the difficulty of working with large fish, however, data are only available for relatively small body masses (0.1 to 10 kg). Given that yellowfin and bluefin tuna can grow as large as 180 and 680 kg, respectively (Collette and Nauen, 1983), extreme caution should be used in extrapolating these data much beyond 10 kg body mass.

The effect of body size can be described by the allometric equation relating metabolic rate and body mass (M),

$$SMR = aM^b,$$

where a (intercept) and b (slope) are constants. Brill (1979, 1987) calculated mass exponents (b) of 0.50 for kawakawa (0.5–2.2 kg), 0.57 for yellowfin (0.6–3.9 kg), and 0.56 for skipjack (0.3–4.7 kg), based on $\dot{M}O_2$ in spinally blocked fish. Dewar and Graham (1994) reported similar results (b = 0.60, 0.5–2.2 kg) for SMRs determined by extrapolating the yellowfin $\dot{M}O_2$ as a function of velocity to zero velocity. The SMRs of much smaller (~0.1-kg yellowfin and kawakawa) and larger tuna (~10-kg albacore) fit very well with the predicted $\dot{M}O_2$ based on these mass exponents (Figure 1; Graham *et al.*, 1989; Sepulveda and Dickson, 2000). A few earlier studies reported scaling of greater than unity for tunas [b = 1.18, mass range 0.6–3.8 kg (Gooding *et al.*, 1981); b = 1.19, mass range 8.5–12 kg (Graham and Laurs, 1982)]. However, these estimates likely result from basing comparisons on RMRs (i.e., the $\dot{M}O_2$ of swimming fish) rather than SMRs.

Tunas appear to have lower scaling exponents (0.5 to 0.6) compared with other fishes (range 0.65 to 0.9, average ~0.80; Jobling, 1994; Clarke and Johnston, 1999) and most animals (average ~0.75; Randall *et al.*, 1997). This difference indicates that mass-specific SMR in tunas decreases relatively rapidly as body mass increases (Brill, 1987). Given that the basis for SMR is poorly established, the reasons for this are difficult to interpret. Interestingly, Graham *et al.* (1983) found that the exponents for the scaling of red muscle mass with body mass were less than 1 in tunas (0.66–0.96), and greater than 1 in other scombrids (1.23–1.72). In other words, the relative amount of red muscle mass as a proportion of total mass decreases in larger tunas. If maintenance of the highly metabolically active red muscle contributes to SMR, this may partially explain the lower scaling exponent. It has been suggested that osmoregulatory costs are a large component

of SMR (Brill, 1987). Thus, one might expect the scaling relationship of gill surface area, the site of most osmoregulatory exchange, and SMR to be closely matched. However, the scaling relationship determined for total gill area in tunas is 0.85, which is similar to other fishes (Muir and Hughes, 1969; Hughes, 1984). Others have suggested that total gill area likely limits maximal rates of oxygen uptake, and therefore it should scale with MMR, rather than SMR (Hughes, 1984). This difference in gill area and SMR scaling suggests that larger tunas may have a greater aerobic scope than smaller tunas (Brill, 1987). Clearly additional measures, such as osmoregulatory costs, mitochondrial characteristics, and the maintenance of the different tissues and organ systems, need to be examined over a range of sizes. This information will be especially critical if we hope to make inferences about the SMR of larger tunas.

D. Temperature Effects on Metabolic Rate

Tunas regularly experience large (~10°C) changes in temperature as a result of both vertical and horizontal movements in the ocean (Holland *et al.*, 1990; Brill *et al.*, 1999; Gunn and Block, this volume). Acute temperature effects have been examined in tunas for both SMR and swimming $\dot{M}O_2$, and indicate a similar response in tunas, most teleosts, and terrestrial ectotherms ($Q_{10} = 2-3$; Bennett and Ruben, 1979; Brett, 1964; Brett and Glass, 1973; Brill, 1987; Dewar and Graham, 1994; Clarke and Johnston, 1999). Brill (1987) measured the change in SMR with temperature of tuna paralyzed with a neuromuscular blocking agent. The Q_{10}'s calculated over the range of 20 to 25°C were 2.44 for skipjack, 3.16 for kawakawa, and 2.31 for yellowfin. Examination of temperature effects on swimming tuna is complicated by their ability to elevate and control muscle temperature (Carey *et al.*, 1971; Dewar *et al.*, 1994). At a given ambient temperature, muscle temperature may differ depending on thermal history and swimming speed (and therefore muscle heat production). Dewar and Graham (1994) measured a Q_{10} of 1.67 for swimming yellowfin by changing temperature (18–30°C) while maintaining a constant speed. The lower Q_{10} in swimming tunas, compared with nonswimming subjects, could have been a result of their ability to increase excess muscle temperatures in cooler water. However, despite regional endothermy, tuna metabolic rates are still directly related to ambient temperature, which may limit tuna distributions and swimming performance (Brill, 1994; Korsmeyer *et al.*, 1996b; Brill *et al.*, 1999).

E. Hypoxia Effects on Metabolic Rate

In many areas, tunas may come into contact with waters of low oxygen content, which, like temperature, potentially limits their movements and distributions (Brill, 1994). Skipjack, yellowfin, and bigeye respond behaviorally (increases in

swimming speed) and/or physiologically (increases in ventilation volume and decreases in heart rate) to moderate hypoxia between ambient oxygen partial pressures (PO_2's) of 17.3 and 12.0 kPa (about 80 to 60% saturation; Dizon, 1977; Gooding *et al.*, 1981; Bushnell *et al.*, 1990; Bushnell and Brill, 1991, 1992; Korsmeyer, 1996; Korsmeyer *et al.*, 1996b). Bushnell and Brill (1992) determined that a PO_2 of 12.0 kPa limited oxygen delivery by the cardiorespiratory system in spinally blocked skipjack. This is caused by a hypoxia-induced decline in heart rate (bradycardia) which lowers cardiac output (see Brill and Bushnell, this volume). Yellowfin were more hypoxia tolerant, with limitation occurring at 6.7 kPa O_2, although Dizon (1977) found they could survive severe hypoxia (4.0 kPa) for greater than 200 min. Experiments by Graham *et al.* (1989) showed that the swimming $\dot{M}O_2$ of albacore (0.5–1.4 L s^{-1}) exposed to moderate hypoxia (between 6.7 and 13.2 kPa O_2, 15°C) was lower than rates in normoxia, suggesting an inability to maintain oxygen delivery within this range.

As tunas are ram ventilators, they may depend on increasing swimming speed in hypoxia in order to maintain oxygen supply to the gills. An increased swimming speed has been seen in both skipjack and yellowfin in response to hypoxia (Dizon, 1977; Gooding *et al.*, 1981; Bushnell and Brill, 1991). However, increases in swimming velocity will increase oxygen demand, and it is thus a somewhat paradoxical response to hypoxia. It may be that the velocity increase is an attempt to leave the area of hypoxia rather than compensation for these conditions (Dizon, 1977; Bushnell and Brill, 1991).

F. Metabolic Rate and Swimming Velocity

Much of the attention on tunas has resulted from their reported high-speed swimming abilities. Tunas traverse large distances during oceanic migrations and are clearly capable of rapid accelerations in short-duration swimming bursts (Mather, 1962; Magnuson, 1978; Walters and Fierstine, 1964; Fierstine and Walters, 1968). All tunas elevate the temperature of their swimming musculature with a presumed increase in muscle performance (see Altringham, this volume). Also, much of their external morphology would appear to increase swimming efficiency through reductions in drag, and consequently costs of locomotion (Webb, 1975; Magnuson, 1978; Dewar and Graham, 1994). To define the energetic implications of the these adaptations requires that the relationship between $\dot{M}O_2$ and velocity (U) be defined.

The relationships between $\dot{M}O_2$ and U measured for a number of tunas are shown in Figure 2. Among respirometry studies, the logarithm of $\dot{M}O_2$ is proportional to velocity, and the rate of increase is similar for yellowfin (Dewar and Graham, 1994), skipjack (Gooding *et al.*, 1981), and albacore tunas (Graham *et al.*, 1989). The lower mass-specific $\dot{M}O_2$ of albacore is expected given their greater mass (8.5–12 kg) and the lower water temperature (~15°C) than in the

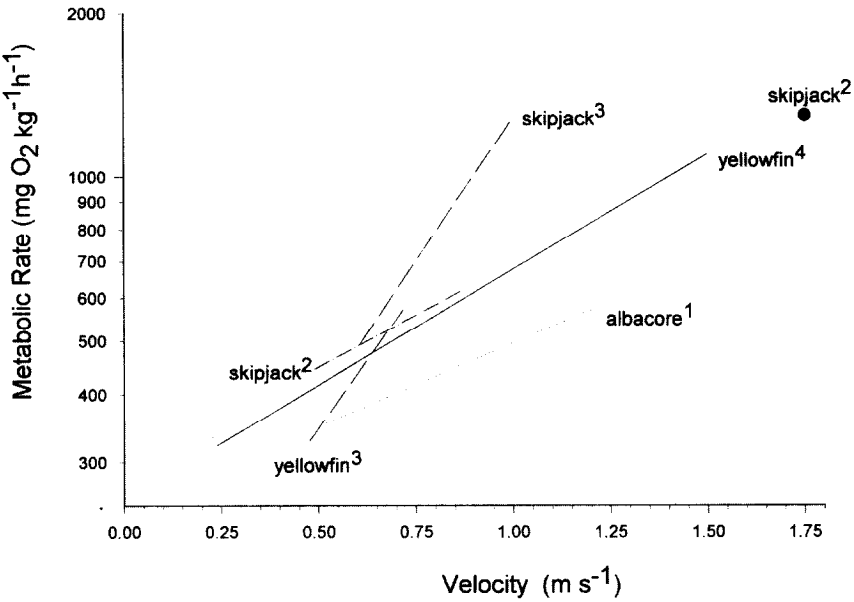


Fig. 2. Metabolic rate ($\dot{M}O_2$, mg O_2 $kg^{-1}h^{-1}$) as a function of swimming speed (U, m s^{-1}) for skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) at 25°C, and albacore (*Thunnus alalunga*) at 15°C. [1]Graham *et al.* (1989), [2]Gooding *et al.* (1981), [3]Boggs (1984), and [4]Dewar and Graham (1994). Estimates of metabolic rate were determined using respirometry[1,2,4] and by measuring reductions in caloric density of body tissues during fasting.[3] Semilog equations for each data set are albacore,[1] $\log \dot{M}O_2 = 0.30U + 2.39$; skipjack,[2] $\log \dot{M}O_2 = 0.38U + 2.46$; skipjack,[3] $\log \dot{M}O_2 = 1.06U + 2.05$; yellowfin,[3] $\log \dot{M}O_2 = 0.99U + 2.04$; and yellowfin,[4] $\log \dot{M}O_2 = 0.42U + 2.42$.

other studies (~2 kg and 25°C). Boggs' (1984) data based on changes in tissue caloric density during starvation differ from respirometry studies (Figure 2). Boggs' study measured lower metabolic rates at low speeds for yellowfin, and higher values at high speeds for both skipjack and yellowfin. This difference may be in part due to an overestimate at slower speeds in the swimming respirometer studies due to stress. However, in Boggs' study of velocity effects, the relation to metabolic rate may be confounded by the concurrent declines in swimming speed and body mass as starvation proceeded, as well as acclimation to captivity.

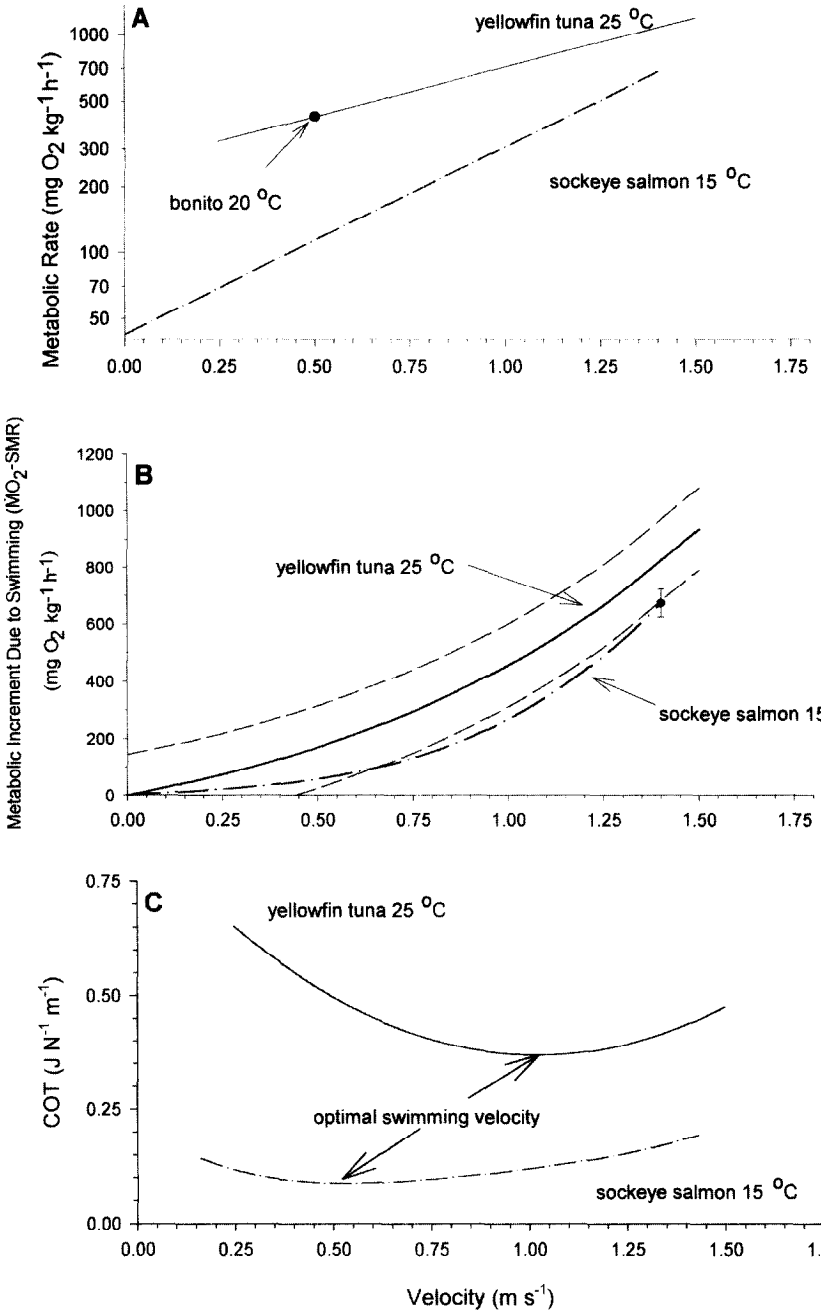
The relationship between $\dot{M}O_2$ and velocity, in comparison to similar studies with nontunas, allows us to determine if regional endothermy in tunas, and the features that result in thunniform swimming, results in greater swimming efficiency. Previous studies have reported that tuna are more efficient swimmers than salmonids, based on the lower slopes of the linear relationship between logarithm-transformed $\dot{M}O_2$ and velocity (Figure 3A; Gooding *et al.*, 1981; Graham *et al.*,

1989; Dewar and Graham, 1994). This relationship, however, is strongly dependent on the intercept with zero velocity, or SMR. Increases in SMR alone will result in a lower slope of the log-linear relationship. Removing SMR from $\dot{M}O_2$ during swimming is a measure of the metabolic increment due to locomotory costs. Comparison of this incremental swimming cost for yellowfin tuna and similarly sized (~50 cm) sockeye salmon is shown in Figure 3B. The differences between the tuna and the salmon are within the variability of the measurements, indicating that there is no significant difference in swimming costs.

A recent study on the swimming costs of small (~0.1 kg) tunas (kawakawa and yellowfin) in comparison with an ectothermic scombrid (Pacific mackerel) provide further evidence that tuna have swimming efficiencies similar to other active species (Figure 4; Sepulveda and Dickson, 2000). The two tunas have similar rates of increase in $\dot{M}O_2$ with U as the mackerel (although SMRs are much higher, as discussed above). However, we cannot make any conclusions about the influence of endothermy on swimming efficiency based on this study. The elevation in muscle temperatures (tuna, +1.5°C; mackerel, +0.4°C) may have been too low for its effects to be manifested. As tuna increase in size their thermal excess increases (Dickson, 1994), and external morphology also diverges from that of the ectothermic scombrids (Magnuson, 1978). Consequently, similar studies comparing larger ecto- and endothermic scombrids are needed. However, at present, there is no conclusive evidence that the energetic cost of swimming in tunas is less than that in other fishes, contrary to previous suggestions.

In addition to determining SMR and locomotor costs, measurement of $\dot{M}O_2$ as a function of velocity allows calculation of the cost of transport (COT). COT is the total amount of energy expended per unit weight per unit distance ($J\,N^{-1}\,m^{-1}$) at a given velocity and can be calculated from $\dot{M}O_2$ using a conversion factor of 14.1 J per milligram of O_2 (Tucker, 1975; Videler and Nolet, 1990; Videler, 1993). A plot of COT versus velocity produces a U-shaped curve (Figure 3C). Where COT reaches a minimum is defined as the optimal swimming velocity (U_{opt}). The higher COT below U_{opt} is a consequence of the relatively large contribution of SMR to total $\dot{M}O_2$ at low speeds. As a result, U_{opt} will be higher with increases in SMR.

The cost of transport (COT) and optimal swimming speed (U_{opt}) are frequently used to characterize swimming performance. Videler (1993) compiled values of COT at U_{opt} (minimum gross cost of transport, or GCOT) for a number of fishes (most at 15°C) and other submerged swimmers. Examination of values across a range of sizes indicates a decrease in U_{opt} with increasing mass (Figure 5A). Comparing values for similar-sized fish, the U_{opt} in tunas is high. For example, the U_{opt} for a 50-cm yellowfin tuna is ~2 $L\,s^{-1}$, compared to ~1 $L\,s^{-1}$ for a similarly sized sockeye salmon (Figures 3C and 5A; Dewar and Graham, 1994). This reflects the elevated SMR observed in tunas, which increases COT at low speeds. U_{opt} is considered a good predictor for routine swimming speeds in fishes (Videler, 1993),


A
yellowfin tuna 25 °C
bonito 20 °C
sockeye salmon 15 °C
Metabolic Rate (mg O2 kg-1 h-1)
1000
700
500
300
200
100
70
50
0.00
0.25
0.50
0.75
1.00
1.25
1.50
1.75
B
yellowfin tuna 25 °C
sockeye salmon 15 °C
Metabolic Increment Due to Swimming (MO2-SMR)
(mg O2 kg-1 h-1)
1200
1000
800
600
400
200
0
C
yellowfin tuna 25 °C
optimal swimming velocity
sockeye salmon 15 °C
COT (J N-1 m-1)
0.75
0.50
0.25
0.00
Velocity (m s-1)

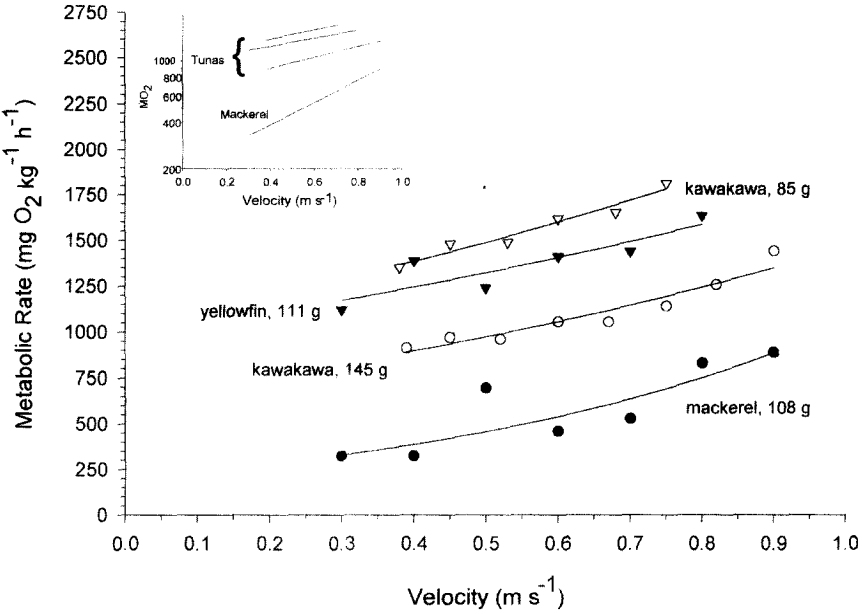
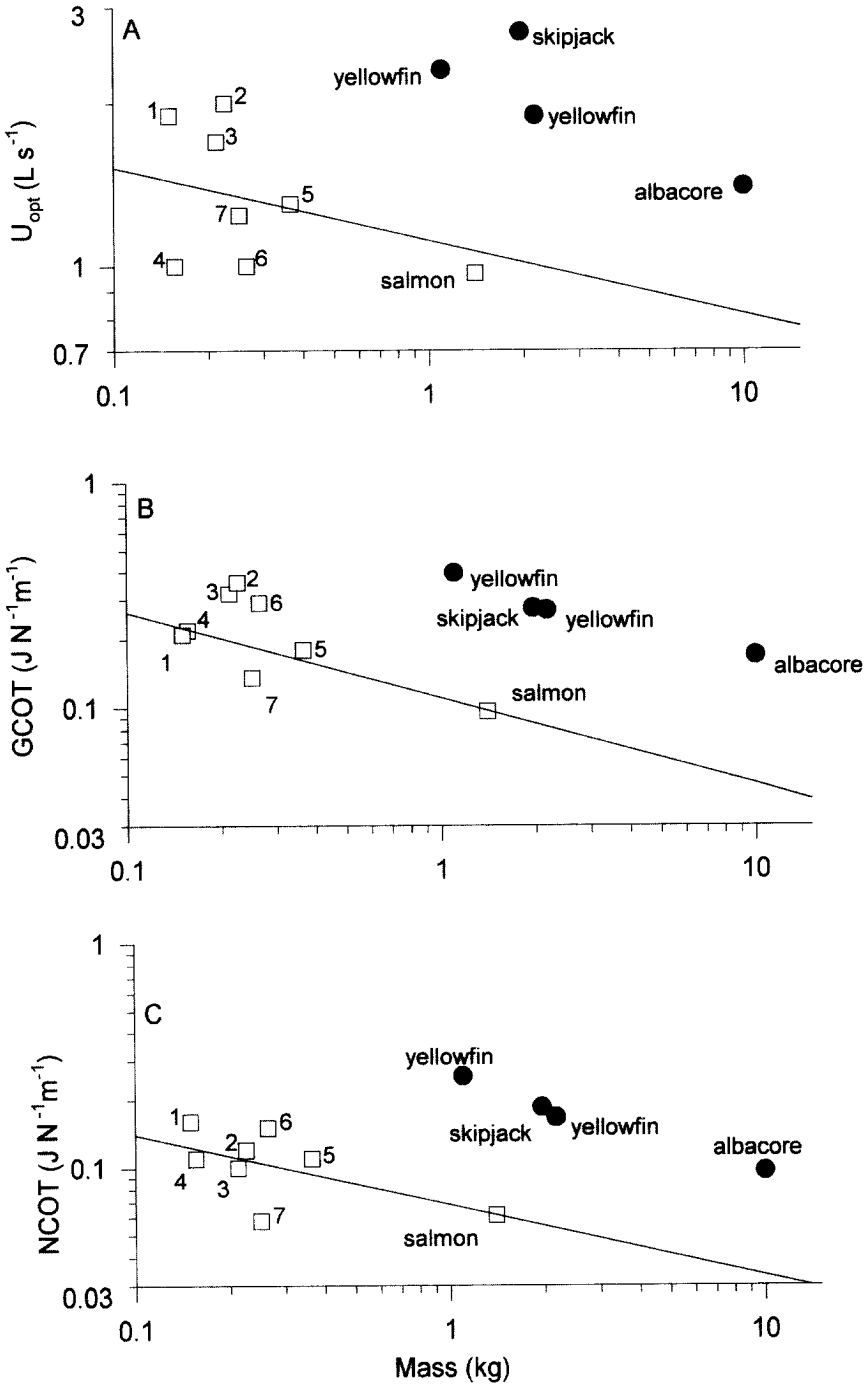


Fig. 4. Oxygen consumption ($\dot{M}O_2$mg O_2 kg^{-1} h^{-1}) versus swimming velocity (U, m s^{-1}) up to the critical swimming speed in four similarly sized scombrid fishes: yellowfin tuna (*Thunnus albacares*), a large and small kawakawa (*Euthynnus affinis*), and the Pacific mackerel (*Scomber japonicus;* Sepulveda and Dickson, 2000). The lines are exponential curves fitted to the data. Note that the Y-scale is linear rather than logarithmic. This is to make the actual increase in swimming costs above SMR apparent (see text). The inset shows the same data plotted on a semilog plot, illustrating the differences in slope that this presentation creates. The increase in $\dot{M}O_2$ during swimming does not differ significantly among species. However, at all speeds, metabolic rate is greater in the tunas than in the Pacific mackerel, indicating that total cost and standard metabolic rate (estimated from the Y-intercept) are greater in tunas. Semilog equations for each fish are, for mackerel, log $\dot{M}O_2$ = 0.154U + 2.30; large kawakawa, log $\dot{M}O_2$ = 0.0770U + 2.81; yellowfin, log $\dot{M}O_2$ = 0.0530U + 2.99; and small kawakawa, log $\dot{M}O_2$ = 0.0566U + 3.02.

Fig. 3. (A) Metabolic rates ($\dot{M}O_2$; mg O_2 $kg^{-1}h^{-1}$) as a function of swimming speed (U, m s^{-1}) for a yellowfin tuna (*Thunnus albacares*) of 2.2 kg, 51 cm (log $\dot{M}O_2$ = 0.42U + 2.4; Dewar and Graham, 1994) and for a sockeye salmon (*Oncorhynchus nerka*) of 1.4 kg, 54 cm (log $\dot{M}O_2$ = 0.86U+ 1.6; Brett, 1965). Data for salmon at 15°C are used because swimming performance was greatest at this temperature. One value is shown for the Pacific bonito *Sarda chiliensis* at its spontaneous swimming velocity (Freund, 1999). (B) Metabolic increment associated with swimming ($\dot{M}O_2$ minus standard metabolic rate) as a function of swimming speed (m s^{-1}) for tuna and salmon as in A. For the tuna, 95% confidence limits for the line's elevation and intercept are shown. The only available error estimates for the salmon occur at zero and the maximum velocity. For the salmon, values between the minimum and the maximum velocity represent the lowest $\dot{M}O_2$ recorded at a given speed. (C) Cost of transport (COT; J N^{-1} m^{-1}) as a function of velocity (m s^{-1}) for the tuna and salmon as in A and B. The optimal swimming velocity, where COT reaches a minimum, is indicated for both species.


A
B
C
skipjack
yellowfin
yellowfin
albacore
salmon
1
2
3
4
5
6
7
U_{opt} (L s^{-1})
GCOT (J N^{-1}m^{-1})
NCOT (J N^{-1}m^{-1})
Mass (kg)
3
1
0.7
0.1
10
0.03

including tunas (Dewar and Graham, 1994), suggesting that fish usually swim at speeds at which transport costs are at a minimum.

Similar to U_{opt}, GCOT decreases with increases in body mass in fishes (Videler, 1993). A larger animal needs fewer strides to cover the same absolute distance. Body size effects can be removed by multiplying GCOT by body length; this is the gross cost of transport per unit weight over one body length at U_{opt} (GCOT $\times$ L, in J N^{-1}; Videler, 1993). Compared with other fishes, GCOT for tunas is greater (Figure 5B). GCOT $\times$ L in tunas (mean = 0.15 J N^{-1}, from values plotted in Figure 5 multiplied by length) is about twice that of other fishes ($\sim$0.07 J N^{-1}; Videler, 1993). However, this value for tunas is half that for other submerged swimmers (GCOT $\times$ L $\approx$ 0.30 J N^{-1} for invertebrates, penguins, and marine mammals; Videler, 1993). The elevation in GCOT in tunas relative to other fishes is due in part to a higher U_{opt} and SMR. Removal of SMR from GCOT produces the net cost of transport (NCOT). Even with this correction, NCOT in tunas is greater than that of other fishes (Figure 5C). These comparisons at U_{opt} suggest that swimming in tunas is actually more costly than in other fishes. However, the tuna's high SMR results in a higher U_{opt}, and we would expect net swimming costs to be greater at a higher swimming velocity given the exponential increase in $\dot{M}O_2$ with increasing U.

IV. OXYGEN UPTAKE AND DELIVERY

The high metabolic rates of tunas have resulted in many investigations of the tuna's cardiorespiratory system, in search of specializations that permit rapid oxygen delivery to the tissues. This is not to imply that the only function of these systems is to supply oxygen, as they are also essential for metabolic substrate delivery and waste removal (Heisler, 1989; Weber, 1992). However, one of the most immediate requirements for high rates of aerobic metabolism is adequate O_2 delivery (Priede, 1985).

Tunas are obligate ram ventilators, relying on the forward motion of swim-

Fig. 5. (A) Optimal swimming velocity (U_{opt}) in lengths per second (L s^{-1}), (B) gross cost of swimming at U_{opt} (GCOT), and (C) net cost of swimming at U_{opt} (NCOT) related to body mass for tunas (●), other fishes (□), and general regressions for fishes (—) as determined by Videler (1993). Values calculated using methods of Videler and Nolet (1990) and Videler (1993). Yellowfin tuna (*Thunnus albacares*) data from Dewar and Graham (1994), skipjack tuna (*Katsuwonus pelamis*) from Gooding *et al.* (1981), albacore tuna (*Thunnus alalunga*) from Graham *et al.* (1989), and sockeye salmon (*Oncorhynchus nerka*) from Brett (1965). [1]Largemouth bass (*Micropterus salmoides*), [2]bluefish (*Pomatomus saltatrix*), [3]striped bass (*Morone saxatilis*), [4]haddock (*Melanogrammus aeglefinus*), [5]lake whitefish (*Coregonus clupeaformis*), and [6]rainbow trout (*Oncorhynchus mykiss*) values from Table 2 in Videler and Nolet (1990). [7]Seabass (*Dicentrarchus labrax*) from Herskin and Steffensen (1998).

ming to force water through the gill (Brown and Muir, 1970). Measured ventilation volumes in tunas are high, ranging from 3 to 6 liters kg^{-1} min^{-1} (Bushnell and Jones, 1994) compared with 0.2 to 0.5 liters kg^{-1} min^{-1} in rainbow trout (Kiceniuk and Jones, 1977; Davis and Cameron, 1971). Oxygen extraction from this high rate of water flow is enabled by a large gill surface area and thin gill epithelium (Hughes, 1984; Brill and Bushnell, this volume). The large, thin gills of tunas are protected in the face of a high ventilatory water flow by additional supporting tissue that fuses lamellae on adjacent filaments; this strengthens the gill sieve and may aid gas transfer by reducing water velocity through the lamellar channels (Muir and Kendall, 1968).

Delivery of oxygen from the gills to the tissues is dependent on the oxygen-carrying capacity of the blood and rates of blood flow. Although arterial oxygen contents in tunas are not extraordinary, their large hearts can generate high blood pressures and cardiac outputs (see Brill and Bushnell, this volume). During moderate exercise in yellowfin tuna, oxygen delivery is increased through near-equal contributions of an increased cardiac output (due entirely to heart rate) and oxygen extraction from the blood (arterial–venous oxygen content difference; Korsmeyer *et al.*, 1997). The uptake of oxygen at the tissue will depend on the capillary area for exchange and the oxygen gradient established between the capillary and the mitochondria. Most of the information available for oxygen delivery is for the myotomal muscle.

The majority of tissue in a fish, approximately 60% (Bone 1978a; Graham *et al.*, 1983; Freund, 1999), is the swimming musculature, of which fish have two primary types (Bone, 1978a; Johnston, 1981). Red (slow-twitch, oxidative) fibers are typically located in a superficial lateral wedge between the epaxial and hypaxial regions of white (fast-twitch, glycolytic) fibers. The red muscle is specialized for sustained, aerobic swimming contractions, while the white muscle has a high anaerobic capacity for powerful, short-duration bursts of activity. In tunas, the red muscle position is more internalized compared to ectothermic teleosts, extending from the superficial lateral region in toward the backbone. The lateral wedge in tunas may contain red, white, or pink (intermediate, or fast, oxidative-glycolytic) fibers, depending on the species (Dickson, 1996; Freund, 1999). The internalized position of the red muscle in tunas is associated with vascular countercurrent heat exchangers (*retia mirabilia*) which trap metabolic heat produced during muscle contractions, allowing tuna to elevate red muscle temperature above ambient (Carey and Teal, 1969; see Graham and Dickson, this volume).

Capillary density in skipjack tuna red muscle (2880 mm^{-2}; Mathieu-Costello *et al.*, 1992) is higher than values reported for many fishes (118–2672 mm^{-2}; Egginton and Johnston, 1983), but less than that in the anchovy (*Engraulis encrasicolus*, 6000 mm^{-2}; Johnston, 1982). The mean number of capillaries around each red muscle fiber in skipjack (4.75–4.97; Bone, 1978b; Mathieu-Costello *et al.*, 1992) is about 70% greater than that in the mackerels (*Scomber* spp., 2.8–

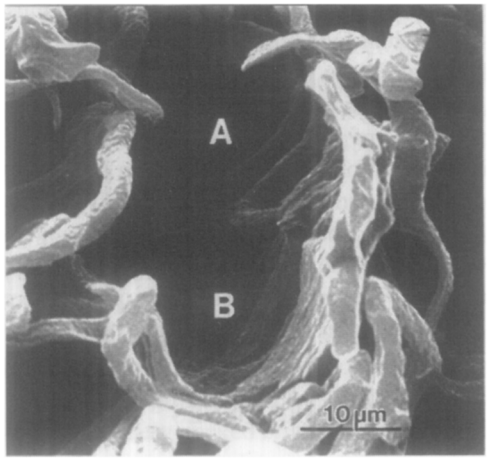


Fig. 6. Scanning electron micrograph of a cross-sectional view of a corrosion cast from skipjack tuna (*Katsuwonus pelamis*) red muscle. Note the dense envelope formed by capillaries. Based on fiber dimensions, two muscle fibers (A and B) could be contained in the empty space. From Mathieu-Costello *et al.* (1992) with permission.

2.98; Bone, 1978b; Mosse, 1979). Further increasing the area of the capillary–muscle fiber interface in skipjack red muscle is the geometry of the capillaries. The red muscle capillaries have numerous venular branches, which run perpendicular to the fiber axis (Mathieu-Costello *et al.,* 1992). These form dense clusters called capillary manifolds, increasing capillary surface area around the muscle fiber (Figure 6). Interestingly, capillary manifolds have also been found in the flight muscles of birds, but it is not known if they are present in other active fishes. The manifolds potentially increase the oxygen flux to the muscle fiber by increasing the area for exchange and increasing capillary transit time (Mathieu-Costello *et al.,* 1992).

Although the capillary density in the white muscle of skipjack (543 mm^{-2}; Mathieu-Costello *et al.,* 1992) is less than that of the red muscle, it is relatively high compared with other fishes. The mean number of capillaries surrounding each white muscle fiber in skipjack (4.8; Mathieu-Costello *et al.,* 1992) is greater than that in other teleosts (0.3–1.6; Mosse, 1979). However, capillarity in albacore white muscle (1.2; Dickson, 1988) is more similar to other teleosts, including the Australian mackerel *Scomber australasicus* (1.1; Mosse, 1979).

In muscle, uptake of oxygen from the blood and diffusive transport within the tissue are facilitated by an oxygen-binding molecule, myoglobin (M_b; Stevens and Carey, 1981; Stevens, 1982). Compared with other fishes, including scombrids, tuna red and white muscle have high concentrations of M_b (reviewed by Dickson,

1996; Marcinek, 2000). The concentration of M_b in the red muscle of Pacific bluefin (40 mg g^{-1}) is more than twice that of Pacific bonito (15 mg g^{-1}; Marcinek 2000). Although less than in the red muscle, the white muscle of tunas also has relatively high M_b concentrations (1–6 mg g^{-1}; reviewed by Dickson, 1996; Marcinek, 2000). Comparisons of M_b concentrations from near the skin and toward the backbone indicate a twofold increase in Pacific bluefin, while no difference was observed in bonito (Marcinek, 2000). Interestingly, a similar pattern was observed for activity of the mitochondrial enzyme citrate synthase (CS), with 30% greater activity in the deep white muscle of the bluefin. Whether the increase in M_b with tissue depth has roots in oxygen storage or aerobic capacity, or acts to compensate for the increase in temperature, remains to be determined.

V. METABOLIC CAPACITY OF TISSUES

Although the features discussed above are critical for the delivery of oxygen and metabolic substrates, ultimately the capacity for energy utilization by a tissue will depend on its total mass, temperature, and specific metabolic capacity. Indexes of tissue aerobic metabolic capacity include capillarity and myoglobin contents (discussed above), as well as mitochondrial volume density and *in vitro* activities of key metabolic enzymes—often the mitochondrial enzyme citrate synthase. Estimates of anaerobic metabolic capacity come from intracellular buffering capacities and activities of lactate dehydrogenase (LDH), which catalyzes the final step of anaerobic glycolysis (Torres and Somero, 1988). Most studies of tuna tissue metabolic capacity have focused on cardiac muscle (see Brill and Bushnell, this volume) and the swimming musculature, with little information for other tissues.[2]

A. Red Muscle

Depending on species, the total mass of red muscle in tunas is similar to or greater than that of other teleosts. The relative contribution of red muscle to total body mass can be as low as 4% in albacore (Graham *et al.*, 1983), or as high as 10 to 13% in black skipjack (*Euthynnus lineatus*), bullet (*Auxis rochei*), and frigate tuna (*Auxis thazard;* Magnuson, 1973; Graham *et al.*, 1983). Values for bigeye, skipjack, yellowfin, and kawakawa tuna fall between these two extremes (6–9%;

[2]For clarity and brevity, we focus our review of enzymatic activities on CS and LDH. These two indicators of aerobic and anaerobic activity, respectively, are the most common enzymes studied. However, other enzymes from both aerobic and anaerobic pathways have been studied in tunas, and, in general, they support conclusions based on CS and LDH. We refer the reader to Guppy and Hochachka (1978), Hochachka *et al.* (1978), Guppy *et al.* (1979), Moyes *et al.* (1992), and Dickson (1995) for additional enzymatic profiles of tuna muscle.

Magnuson, 1973; Graham *et al.*, 1983; Freund, 1999). This range of relative red muscle mass for tunas overlaps values reported for ectothermic scombrids (2–7%, *Scomber, Sarda,* and *Acanthocybium* spp.), blue marlin (*Makaira nigricans,* 5%), yellowtail (5%), and salmonids (3–4%; Magnuson, 1973; Graham *et al.*, 1983; Johnston and Salamonski, 1984; Tsukamoto, 1984; Tang and Wardle, 1992; Dickson, 1995; Freund, 1999). Thus, inferences about differences in red muscle mass depend strongly on the comparisons made.

Relative mitochondrial volume densities in skipjack tuna red muscle (16.4–38%; Bone, 1978b; Hochachka *et al.*, 1978; Hulbert *et al.*, 1979; Mathieu-Costello *et al.*, 1992; Moyes *et al.*, 1992) are within the range reported for most other fishes (8–36%; Johnston, 1981; Johnston *et al.*, 1998), but are less than that in the anchovy (46%; Johnston, 1982). However, relative amounts of mitochondrial protein (48 mg g^{-1}) are high in skipjack (80% higher than in the carp *Cyprinus carpio*) as a result of densely packed cristae within the mitochondria (Moyes *et al.*, 1992). Mitochondrial inner membrane surface area per unit mitochondrial volume in skipjack red muscle (63–71 m^2 cm^{-3}) is higher than that in other fishes (36–50 m^2 cm^{-3}; Johnston *et al.*, 1998) and even the skeletal muscles of birds and mammals (20–60 m^2 cm^{-3}; Hoppeler and Lindstedt, 1985; Suarez *et al.*, 1991). This cristae surface density is possibly approaching the maximum for the given space (Moyes *et al.*, 1992). Although no data are available for cristae surface densities in other scombrids, there are data on the specific activities of mitochondrial enzymes.

When compared at the same temperature, maximal *in vitro* specific activities of CS are greater in the red muscle of tunas than that in billfishes or sluggish fish species (Dickson, 1995). However, comparison with the ectothermic scombrids (*Sarda, Scomberomorus,* and *Scomber* spp.) is not straightforward. Red muscle CS activities are higher in some species of tunas, such as skipjack and frigate tuna (Figure 7). When compared as a group, however, tunas have red muscle CS activities that are not significantly different from those of ectothermic scombrids (Figure 7; Dickson, 1996; Freund, 1999). This analysis suggests that the intrinsic aerobic metabolic capacity of tuna red muscle tissue, while high compared with fishes in general, is more similar to that of some other active pelagic teleosts (Dickson, 1996).

One clear difference between the tunas and other teleosts is tunas' ability to elevate the temperature of the red muscle. The extent to which muscle temperature is elevated (from less than 1°C up to 20°C) varies among species, and is influenced by body mass, ambient temperature, and swimming activity (Carey and Teal, 1969; Carey *et al.*, 1971; Graham, 1975; Graham and Dickson, 1981; Dewar *et al.*, 1994; Dickson, 1994; Holland and Sibert, 1994). The increase in temperature will increase the aerobic capacity of the red muscle. Correcting for the differences in red muscle temperature, CS capacities in tunas are, on average, 70% higher than those in ectothermic scombrids (Dickson, 1996).

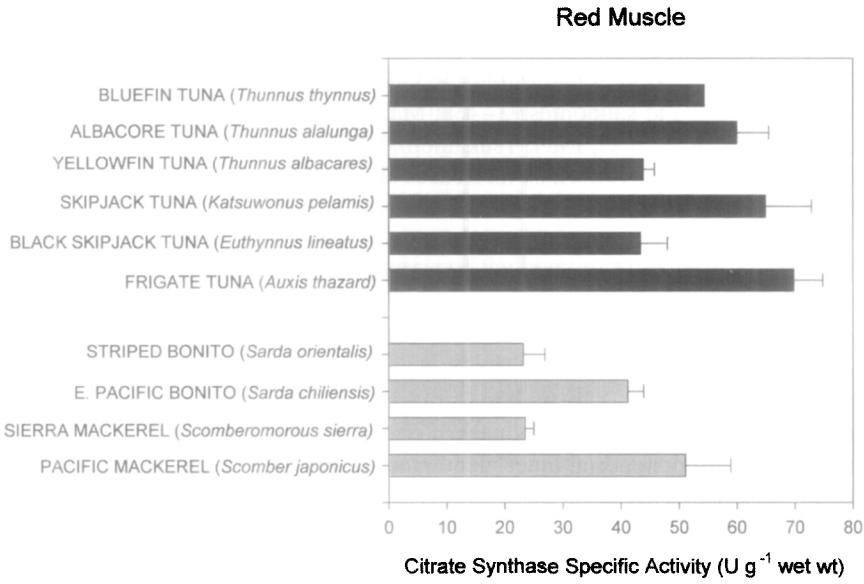


Fig. 7. Mean (±SE) citrate synthase (CS) specific activity [international units, or μmol substrate converted to product min^{-1} (gram wet weight of muscle tissue)$^{-1}$] measured at 20°C in the red myotomal muscle of tunas (solid bars) and ectothermic scombrid species (shaded bars). Overall, red muscle CS activity in tunas does not differ significantly from that in ectothermic scombrids. Data from Dickson (1996 and unpublished observations).

Thus, while the intrinsic metabolic capacity of tuna red muscle is similar to that of other active pelagic fishes, regional endothermy, and in some species greater amounts of tissue, significantly elevates the aerobic capacity of the tuna's red swimming musculature relative to other teleosts (Dickson, 1996). Graham *et al.* (1983) found a negative correlation between the relative amount of red muscle and the total surface area of the heat exchanger among the tuna species. This relationship suggests that species with better heat conservation (and therefore greater red muscle temperatures) require a smaller amount of red muscle tissue to support sustained swimming (Graham *et al.*, 1983; Dickson, 1995).

B. White Muscle

The white muscle has a high anaerobic capacity fueled by glycogen (Guppy *et al.*, 1979; Hulbert *et al.*, 1979; Arthur *et al.*, 1992). Specific activities of LDH are extraordinarily high in tuna, exceeding values from other scombrids (at the same temperature—see Figure 8; Guppy and Hochachka, 1978; Dickson, 1995, 1996). This, in addition to large glycogen stores in the white muscle (145 μmol

g^{-1} in skipjack, compared with 34 μmol g^{-1} in rainbow trout; Arthur *et al.,* 1992; Schulte *et al.,* 1992), indicates a high capacity for very fast, short-duration, swimming bursts. This anaerobic swimming activity, and depletion of glycogen to produce ATP, can produce large amounts of muscle lactate (over 100 μmol g^{-1}, compared with 42 μmol g^{-1} in trout; Guppy *et al.,* 1979; Arthur *et al.,* 1992; Schulte *et al.,* 1992), and presumably a large metabolic acid load.

The resulting acidification from lactic acid production during burst swimming activity is minimized by high blood and intracellular buffering capacities in tuna (Perry *et al.,* 1985; Dickson and Somero, 1987; Brill *et al.,* 1992). The importance of buffering in support of anaerobic glycolysis is indicated by the positive correlation between buffering capacity and LDH activity in muscle of both marine fishes and mammals (Castellini and Somero, 1981; Dickson, 1995). In an analysis of five tuna and four ectothermic scombrid species, Dickson and Somero (1987) found white muscle buffering capacity in tunas to be significantly higher (112 slykes compared with 99.5 slykes). By minimizing disruption of intra- and extracellular pH that occurs during anaerobiosis, tunas may be able to increase the duration, frequency, or velocities of burst swimming (Dickson, 1996).

In addition to a high anaerobic capacity, the white muscle of tunas also has

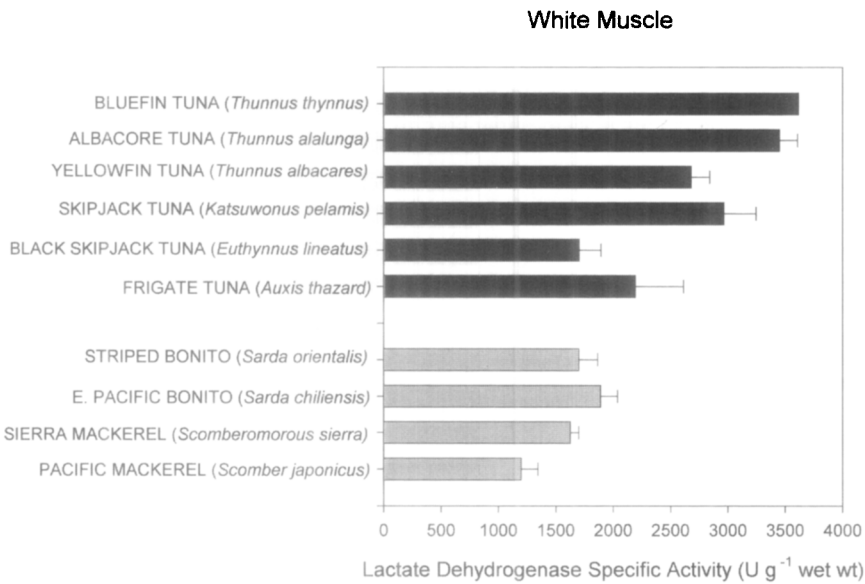


Fig. 8. Mean (±SE) lactate dehydrogenase (LDH) specific activity at 20°C in the white myotomal muscle of tunas (solid bars) and ectothermic scombrid species (shaded bars). The white muscle LDH activity in tunas is significantly greater than that for ectothermic scombrids. Data from Dickson (1996 and unpublished observations).

higher aerobic capacities compared with other fishes, including ectothermic scombrids (Guppy and Hochachka, 1978; Moyes *et al.*, 1992; Dickson, 1996; Freund, 1999). The aerobic capacity is reflected in high M_b contents, and in some species high capillarity (see above). As with the red muscle, mitochondrial volume density in skipjack white muscle (2–2.8%; Hulbert *et al.*, 1979; Mathieu-Costello *et al.*, 1992; Moyes *et al.*, 1992) is within the range reported for other fishes (1–4%; Johnston, 1981) and similar to that in Atlantic mackerel (Bone, 1978b). However, specific CS activities in white muscle of tunas are higher, even when compared with ectothermic scombrids at the same temperature (Figure 9), suggesting the intrinsic aerobic capacity of this tissue is elevated in the tunas (Hulbert *et al.*, 1979; Dickson, 1995, 1996; Freund, 1999; Marcinek, 2000).

Although only the red muscle is supplied by well-developed countercurrent heat exchangers, areas of the surrounding white muscle are also warmed via conduction from the deep red muscle. Recently caught fish or those exercised until exhaustion show white muscle temperatures warmer than ambient water temperature (Carey, 1973; Graham, 1975; Graham and Dickson, 1981; Marcinek, 2000). Archival tags placed beneath several centimeters of white muscle in large (ap-

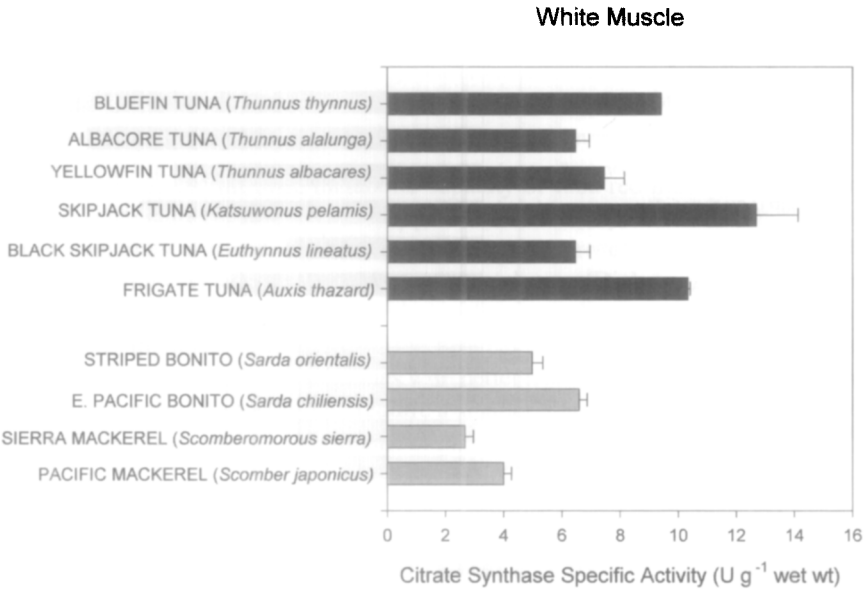


Fig. 9. Mean (±SE) citrate synthase (CS) specific activity at 20°C in the white myotomal muscle of tunas (solid bars) and ectothermic scombrid species (shaded bars). Overall, white muscle CS activity in tunas is significantly greater than that in ectothermic scombrids. Data from Dickson (1996 and unpublished observations).

proximately 100–250 kg) bluefin tuna report temperatures up to 10°C above ambient (Stevens *et al.*, 2000; see Gunn and Block, this volume). The extent of warming will vary with position relative to the body surface and the red muscle, and the extent of red muscle excess temperature. As with the red muscle, an increase in temperature can elevate the metabolic activity of the white muscle.

A clear difference between the endo- and ectothermic scombrids appears to be that the capacity of white muscle to contribute to total aerobic capacity is actually greater than the red muscle in tunas due to its high mass-specific aerobic capacity. Although the aerobic capacity per unit gram of tuna white muscle tissue is less than that of red muscle, because of its much larger mass, the potential contribution of white muscle to total metabolic rate is greater. In tunas and other scombrids, the white muscle accounts for approximately 45 to 55% of total body mass (Graham *et al.*, 1983, Freund, 1999). In skipjack tuna, mass-specific CS activity is only one-fifth that of red muscle (Moyes *et al.*, 1992), but with about seven times as much white muscle (Graham *et al.*, 1983), total aerobic capacity in the white muscle is about 40% greater than that of the red muscle. In yellowfin tuna, white muscle as a whole has 8% higher aerobic capacity than the red muscle (Freund, 1999). In ectothermic scombrids the opposite is true; the red muscle has a greater total aerobic capacity (11% in Pacific bonito and 64% in Pacific mackerel) than the white muscle (Freund, 1999). This high aerobic capacity in tuna white muscle likely supports rapid recoveries following anaerobic swimming bursts (discussed further below). It also is possible that white muscle is recruited aerobically to support high sustainable swimming speeds. In either case, it is clear that both the aerobic and the anaerobic potentials of tuna white muscle are exceptional.

C. Other Tissues

Few studies have made an effort to quantify the activities of systems other than those associated with locomotion or the circulatory system (Dickson, 1988; Freund 1999). Freund (1999) measured aerobic activity levels (i.e., maximal CS activity) and relative mass of the liver, kidney, gills, and caecum for yellowfin tuna and Pacific bonito. From tissue mass and CS activities it was possible to calculate the relative metabolic potential of these tissues (Table I). Freund (1999) found no consistent difference in aerobic capacity, tissue mass, or relative metabolic potential between the two species. Taking relative mass into account, all of these tissues together compose less than 10% of the total CS activity (Freund, 1999). The caecum has the greatest contribution to total CS activity (2.1–3.6%) in both species (Table I).

While CS activity indicates the potential for maximum aerobic activity, it is not clear at what level these tissues regularly operate. The relative contribution of each tissue to total metabolism will depend on the activity being performed and its intensity.

Table I
Fractional Contribution (±SE) of Four Tissues to Total Citrate Synthase Activity (at 20°C) from Yellowfin Tuna *Thunnus albacares* (4.74 ± 0.77 kg) and Pacific Bonito *Sarda chiliensis* (2.69 ± 0.55 kg)

	Fractional contribution of each tissue (%)	
Tissue	Yellowfin	Bonito
Liver	0.5 ± 0.06	0.3 ± 0.04
Kidney	0.53 ± 0.07	0.45 ± 0.0
Pyloric caecum	2.13 ± 0.25	3.57 ± 0.57
Gill	1.2 ± 0.1	0.87 ± 0.15
Total	4.36	5.19

Data from Freund (1999).

VI. MULTIPLE METABOLIC DEMANDS

Although much of the interest in tuna physiology has centered on swimming adaptations, this is not the only metabolic cost that must be supported. Other, often simultaneous, activities such as digestion and assimilation of prey, investment into growth and reproduction, and repayment of the oxygen debt incurred during anaerobic swimming bursts also will contribute to aerobic metabolic demands.

Currently there are no measures of metabolic rate in tunas that can separate out the costs of specific functions other than swimming and SMR. However, the biochemical indexes of various tissues discussed above, as well as other evidence (discussed below), indicate that metabolic processes other than aerobic swimming are "high performance" in tuna with concomitant high energy costs (Brill, 1996; Korsmeyer *et al.*, 1996a). In tunas, as well as other fishes, these metabolic functions may account for a large proportion of total metabolic rate, and can result in conflicts if total demand exceeds aerobic metabolic scope (Priede, 1985).

We can divide the total respiratory or aerobic metabolism of a tuna into its component parts (Priede, 1985; Korsmeyer *et al.*, 1996a),

$$R = R_S + R_F + R_A + R_D + R_{G\&R},$$

where R is the total aerobic metabolic rate, R_S is the standard metabolic rate, R_F is the metabolic rate attributable to the activities of digestion and assimilation, also termed specific dynamic action (SDA), R_A is metabolism due to aerobic locomotor activity, R_D is due to recovery from oxygen debt, and $R_{G\&R}$ is growth and reproduction.

The metabolic costs of R_S (= SMR) and R_A (aerobic swimming activity) are discussed above. The following sections will discuss what is known about each of the other metabolic components in tuna.

A. Specific Dynamic Action (R_F)

A portion of ingested energy is lost due to the mechanical and biochemical costs associated with digestion and assimilation, and this is defined as specific dynamic action (SDA or R_F; Jobling, 1981). R_F in fishes accounts for about 15% of ingested energy (Brett and Groves, 1979; Jobling, 1981). Maximum $\dot{M}O_2$ following feeding in fishes generally ranges between 1.5 and 2.5 times SMR (Jobling, 1981). In some fishes the $\dot{M}O_2$ due to R_F can equal the maximum active $\dot{M}O_2$ (Beamish, 1974; Priede, 1985).

Although no direct measurements have been made for tunas, R_F is likely to be a large component of aerobic metabolism because these fishes have high rates of both consumption and digestion. Tunas can consume up to 30% of their body mass per day (Kitchell *et al.*, 1978), although the estimated daily ration for yellowfin in the wild is between 4 and 7% of body mass (Olson and Boggs, 1986). Based on postfeeding stomach contents, captive skipjack and yellowfin (24°C) were found to empty their gut in an average of 12 and 10.4 h, respectively (Magnuson, 1969; Olson and Boggs, 1986). This rate of gut clearance is 4 to 5 times faster than for other piscivores of comparable size (Magnuson, 1969). In addition, some species of tunas have the ability to elevate visceral temperature with vascular retia (Collette, 1978; Stevens and Neill, 1978; Carey *et al.*, 1984), presumably to aid rapid digestion and assimilation. Stevens and McLeese (1984) found that the elevated gut temperatures of bluefin tuna could increase the activity of digestive peptidases by threefold. The ability to consume large amounts and rapidly clear the gut enables tunas to take advantage of prey aggregations that are patchily distributed, and still meet their high metabolic demands (Olson and Boggs, 1986). No examination of gut clearance or SDA has been made for ectothermic scombrids.

B. Growth and Reproduction ($R_{G\&R}$)

Tunas have relatively high rates of both somatic and gonadal growth (see Sharp, this volume, and Schaefer, this volume). Growth rates vary considerably between species and are linked to maximum size, which ranges from only a few kilograms for *Auxis* sp. to over 680 kg for bluefin tuna (Collette and Nauen, 1983). At an age of 1 year, yellowfin and skipjack tunas will have reached a mass of 2.3 and 1.3 kg, respectively (Wild, 1986; Uchiyama and Struhsaker, 1980). High growth rates also are documented for other pelagic fishes. Dolphinfish and the

blue marlin will be 10 and 43 kg at 1 year, and reach maximum sizes of 46 and 580 kg, respectively (Palko *et al.*, 1982; Uchiyama *et al.*, 1986; Prince *et al.*, 1990; Nakamura, 1985).

In addition to growth, reproduction can be very costly. Skipjack produce about 100,000 eggs per kilogram per spawning (equal to approximately 2% of body mass) and at times may spawn on a near daily basis over a 3-month period, producing tens of millions of eggs annually (Forsbergh, 1980; Hunter *et al.*, 1986). For mature yellowfin tuna, the annual costs of spawning are estimated to be equivalent to 254% of body mass in females and 120% in males (Schaefer, this volume). These annual reproductive costs as a proportion of total energy expenditure are estimated to be 17.5 and 8.8% in females and males, respectively. Although the metabolic costs for growth and reproduction in tunas are high, other large, tropical, pelagic fishes may have similar costs.

C. Oxygen Debt Recovery (R_D)

Anaerobic metabolism can elevate energy expenditure beyond the aerobic scope, but ultimately will result in the aerobic costs associated with R_D. Short periods of high-intensity swimming, powered by anaerobic metabolism of the white muscle, result in depletion of glycogen reserves, buildup of lactate, depression of blood pH, and ionic and osmotic disturbances (Wood, 1991). These physiological disturbances may result in exhaustion and inability to perform further burst swimming activity. Recovery from exhaustive exercise is associated with an elevation in $\dot{M}O_2$, "repaying" the oxygen debt, while restorative processes take place.

Recovery from anaerobic activity involves removal of lactate and return of acid–base balance, processes which require energy provided by oxidative (aerobic) metabolism (Moyes *et al.*, 1993). Despite generation of high, postexercise lactate levels, these processes occur very rapidly in skipjack tuna (<90 min; Perry *et al.*, 1985; Arthur *et al.*, 1992), many times faster than in rainbow trout (6–24 h; Milligan, 1996). The majority of lactate is resynthesized to glycogen within the white muscle (Weber *et al.*, 1986; Arthur *et al.*, 1992; Buck *et al.*, 1992). Rates of lactate clearance from white muscle in skipjack (1.3 μmol g^{-1} min^{-1}; Arthur *et al.*, 1992) are 10- to 100-fold greater than those in other fishes (0.011–0.125 μmol g^{-1} min^{-1}; reviewed by Moyes *et al.*, 1993), and there is a close correlation with the repletion of muscle glycogen and phosphocreatine (Arthur *et al.*, 1992). These rates were measured in fish prevented from swimming, which may have impeded recovery. Milligan *et al.* (2000) recently found that rainbow trout allowed to swim at low speeds recovered much faster (<2 h) than those held in still water (>6 h). The rapid recovery in tuna permit burst swimming to occur with greater frequency.

White muscle aerobic capacity strongly correlates with the rate of lactate

clearance in fishes (Moyes *et al.*, 1993). This suggests that the high aerobic capacity of tuna white muscle may function for rapid recovery from the large lactate load generated in the white muscle during burst swimming (Dickson, 1995; Korsmeyer *et al.*, 1996a). It also suggests that oxygen debt recovery in tunas can be a major component of total oxygen demand (Bushnell and Brill, 1991; Brill, 1996; Korsmeyer *et al.*, 1996a).

D. Modeling Multiple Metabolic Costs

Based on measured rates of growth, caloric intake and digestion, lactate clearance and creatine rephosphorylation, and swimming metabolism, Korsmeyer *et al.* (1996a,b) calculated estimates of the average potential aerobic costs associated with each metabolic component (Figure 10).[3] This model of tuna metabolic demands is based on a 2-kg yellowfin tuna, because the best estimate of swimming metabolic rates and most other physiological data are from tunas of this size and at a temperature of about 25°C. Actual measurements of the metabolic costs associated with these processes in tunas and other pelagic fishes would be a useful area for future research. However, this model analysis provides us with an estimate of how various metabolic functions of tunas contribute to total energetic demands, and how they may fit within the aerobic scope.

It is clear that tunas have elevated energy demands for many metabolic processes in addition to aerobic swimming and SMR (Figure 10). This is particularly true for oxygen debt recovery. The estimated $\dot{M}O_2$ required for oxygen debt recovery (840 mg O_2 kg^{-1} h^{-1}) approaches that of high-velocity aerobic swimming (1100 mg O_2 kg^{-1} h^{-1} above SMR at 3.5 L s^{-1}). This is not surprising given that the total aerobic potential of white muscle, the site of glycogen resynthesis, exceeds that of red muscle in tunas (see above).

All fishes have a potential power budgeting problem in that the combined capacities for R_A, R_D, and R_F, in addition to R_S, will likely exceed maximum aerobic capacity (Priede, 1985). Conflicts in oxygen demand between digestion and swimming activity, for example, have been demonstrated in a number of fishes. In the sablefish *Anaplopoma fimbria*, as swimming oxygen demand increases, the proportion allocated to digestion decreases until swimming consumes all of the metabolic scope (Furnell, 1987). Alternatively, in rainbow trout the costs

[3]These values must be taken only as a first approximation as none of the estimated values will be constant. $\dot{M}O_2$, due to R_F increases to a maximum following feeding and then declines over many hours, and its magnitude will depend on the quantity and quality of prey (Jobling, 1981). Growth rates are higher in younger tuna and decrease with age (Wild, 1986), and part of this cost may be included in SMR or R_F (Jobling, 1981). Oxygen debt recovery is maximal just after intense exercise and declines with time, and additional costs are associated with readjustment of ion, acid–base, and fluid volume disturbances (Wood, 1991). Therefore, these values may actually underestimate costs in many cases.

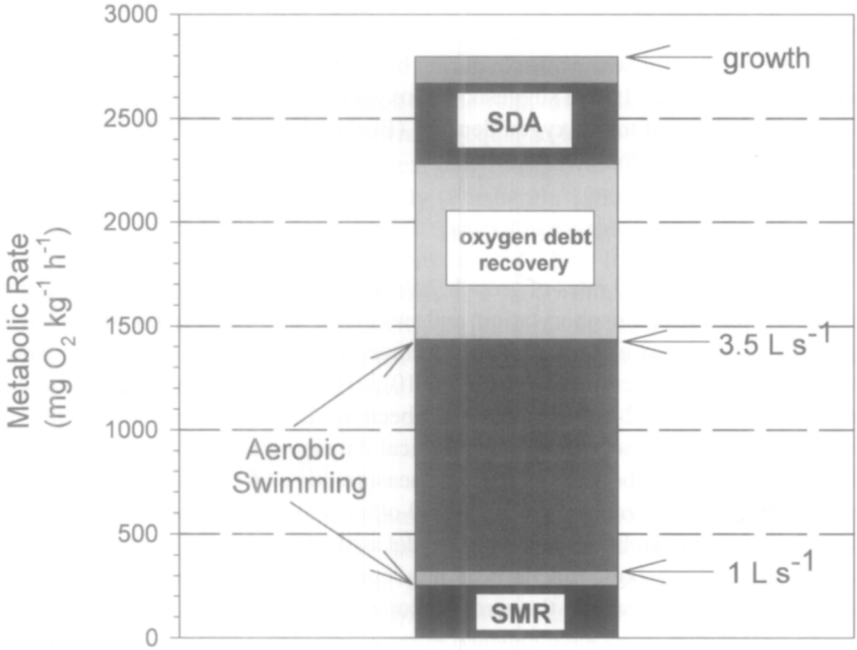


Fig. 10. Potential aerobic energetic costs estimated for a 2.1-kg (50 cm) yellowfin tuna (*Thunnus albacares)* at 25°C. Included are standard metabolic rate (SMR), aerobic swimming costs, oxygen debt recovery, specific dynamic action (SDA), and growth (Korsmeyer *et al.,* 1996a,b). Swimming costs are given at both 1.0 body length (L) per second and at 3.5 L s^{-1}, which is predicted to be near the maximal sustained swimming speed (Korsmeyer *et al.,* 1996b; Brill, 1996). Total aerobic costs, if all processes occur simultaneously (2731 mg O_2 kg^{-1} h^{-1}), are near estimates for maximal metabolic rate in tuna (2500 mg O_2 kg^{-1} h^{-1}). This suggests that the tuna's aerobic scope can support multiple metabolic processes without conflicts in oxygen delivery.

of R_F are not reduced, but instead limit swimming velocities once maximal $\dot{M}O_2$ is reached (Alsop and Wood, 1997).

These conflicts occur due to limitations of the cardiorespiratory system to deliver sufficient oxygen to competing tissues. During exercise in fishes, blood flow to the viscera is reduced and redistributed to the red muscle (Randall and Daxboeck, 1982; Axelsson *et al.,* 1989; Axelsson and Fritsche, 1991; Thorarensen *et al.,* 1993). This redistribution likely reflects the inability of the circulatory system to supply sufficient oxygen to viscera (for digestion) while also supporting the aerobic locomotory muscles. In fish with higher oxygen delivery capacities (higher hematocrit), there is less reduction in visceral blood flow (Thorarensen *et al.,* 1993). Clearly, aerobic scope determines the extent to which multiple functions can occur simultaneously.

In tunas this problem is made especially acute by a high R_S and the constant swimming requirements (R_A) required for gill ventilation and hydrodynamic lift (Magnuson, 1973). After feeding, tunas must be able to repay any oxygen debt incurred during prey capture and rapidly complete the processes of digestion to prepare the gut for the next prey encounter. All of these various metabolic oxygen requirements can and do occur simultaneously, heightening potential conflicts in oxygen demand.

Total aerobic metabolic costs, however, cannot exceed the MMR. If, however, as data from skipjack suggest, MMRs for tuna are 2500 mg O_2 kg^{-1} h^{-1} (see above), then significant aerobic scope (2200 mg O_2 kg^{-1} h^{-1}) would be available to support multiple metabolic functions, even beyond that required for high sustained swimming speeds. For example, a tuna could support its SMR, deliver sufficient oxygen to the red muscle for swimming continuously at moderate velocities, and still have sufficient aerobic scope to support rapid lactate clearance in the white muscle tissue (Figure 10; Bushnell and Brill, 1991). In this way, tunas do not need to rest (something they cannot do) following exhaustive exercise, but can continue to search for prey to support their high energy demands while clearing the gut and replenishing white muscle glycogen stores in preparation for the next bout of burst swimming. In fact, the highest measured $\dot{M}O_2$ in tuna was from skipjack that were just caught from a feeding frenzy and were therefore likely repaying an oxygen debt and digesting prey, while also swimming at 3.5 L s^{-1} (Gooding *et al.*, 1981). The large aerobic metabolic scope of tunas may, therefore, be an adaptation to limit conflicts among the simultaneous requirements of multiple metabolic demands (Priede, 1985; Brill, 1996; Korsmeyer *et al.*, 1996a).

VII. DISCUSSION AND CONCLUSIONS

Above we have summarized the available information examining the metabolic costs in tuna, the associated adaptations, and the estimated relative contributions of different components. Tuna energetics has a long history and much has been learned in the last 20 years. The recent addition of data from ectothermic scombrids and other active teleosts provides greater power for examining the significance of different traits and compels us to reexamine conclusions based only on comparisons with salmonids. Much remains to be done, but for now let us revisit the questions posed in the Introduction.

A. How Does the Metabolic Rate of Tunas Compare with Other Fishes?

Regardless of the method used it is clear that tunas have high energetic costs. The primary basis for this is the elevated SMR, which is also reflected in an ele-

vated swimming metabolic rate. While the SMR in tuna is higher than that found in many species, comparable values are found in other large, active (but ectothermic) species such as the dolphinfish and bonito. In general, fishes with a greater aerobic scope for activity also have a high SMR (Priede, 1985). This relationship suggests that a high SMR is related to the costs of supporting the physiological systems required for a high MMR, and would agree with MMR estimates for tunas. Consequently, an elevated metabolic rate does not depend on endothermy, but may be associated with capabilities for enhanced activity and an increased metabolic scope (i.e., permits higher MMRs).

What accounts for the high SMR of tunas and some other pelagic fishes? One hypothesis is that the large surface area and thin epithelia of the gills entails a high osmoregulatory cost and consequently an elevated SMR (Brill, 1987, 1996). For some fish there appears to be a general positive correlation between SMR and gill surface area (Brill, 1996). For others this does not hold true. Both the mackerel and the menhaden (*Brevoortia tyrannus*) have mass-specific gill surface areas that exceed either the bonito or the dolphinfish (Gray, 1954), yet they have lower metabolic rates (Figure 1; Sepulveda and Dickson, 2000; Freund, 1999). Elevated osmoregulatory costs in tunas are suggested by high estimates for gill $\dot{M}O_2$ in spinally blocked skipjack and yellowfin tunas (50–70% of $\dot{M}O_2$; Bushnell and Brill, 1992) compared with other fishes (27% of $\dot{M}O_2$ in rainbow trout; Daxboeck *et al.*, 1982). However, estimates based on tuna gill Na^+-K^+ ATPase activity are much lower (9–13% of SMR; Brill and Bushnell, this volume). Other factors which could cause elevation of SMR include an increase in the proton leak across the inner mitochondrial membranes (Brand, 1990), costs of maintaining metabolic machinery (e.g., enzyme turnover), and high rates of growth.

Although the SMR and RMR of tunas may be comparable to some other active fishes, we predict that MMR will be greater. The total aerobic metabolic potential in tunas is increased, even in comparison with ectothermic scombrids, by red muscle endothermy and an extraordinary white muscle aerobic capacity.

B. What Are the Adaptations Related to Supporting the Energetic Demands of Swimming and Other Metabolic Processes?

Each step in the oxygen cascade from the gill to the mitochondria is specialized to enhance oxygen flux in tuna. The structure of the gills facilitates increased levels of oxygen uptake from the water. A large heart generates high rates of blood flow, and oxygen uptake at the tissue is improved by the capillary structure and tissue M_b concentrations. In the tissue, the ability to produce ATP is enhanced by elevated activities of metabolic enzymes. Compared to other scombrids, tuna red muscle aerobic capacity is elevated not by great increases in specific enzyme activities, but by a greater amount of tissue in some species, and the ability to

increase the temperature of this tissue. The white muscle of tunas has higher intrinsic anaerobic and aerobic capacities than other fishes, including scombrids. Interestingly, these same patterns have been observed in white muscle of endothermic and ectothermic sharks (Dickson *et al.*, 1993).

C. How Do Tuna Energetics Relate to Their Swimming Performance?

Perhaps the most surprising finding is that, based on the available data, tuna are no more efficient swimmers than other active fish, including mackerel and salmon. This seems unlikely given the suite of apparent hydrodynamic and biomechanic specializations in tunas. There are a number of possible reasons why this is the case: (1) It may be that any energetic advantages are slight, and that our current data are constrained by the technical challenge of working with these fishes and limited comparative data on large, active fish at the same temperature. (2) The energetic advantages may not be apparent during the steady swimming recorded in a swim flume or metabolic chamber, but instead are manifested during a swim-and-glide mode of swimming which is hypothesized to increase efficiency (Weihs, 1973). The extensive streamlining may act to minimized drag during periods of gliding, rather than when the body is undulating. Observations of free-swimming captive fish and during acoustic telemetry in the field indicate that tunas use this mode of travel (Holland *et al.*, 1990; Block *et al.*, 1998; H. Dewar, personal observation). (3) Alternatively, tuna morphology may be an adaptation for rapid *accelerations,* aiding anaerobically powered, high-speed burst swimming and prey capture. (4) Finally, tuna specializations may allow higher sustainable (aerobic) swimming speeds, without improving efficiency. For example, elevated red muscle temperatures could increase power output, without necessarily reducing the cost per unit power produced. This will increase the speed at which the transition to white muscle recruitment must occur. For this last possibility, some limited data are available.

Maximal sustained[4] swimming speed (U_{ms}) has not been directly measured for

[4]Swimming activity is usually classified into several categories which define the duration over which the fish can perform at that level of activity, as well as the metabolic pathways which provide the energy for the different types of swimming. Sustained swimming is that which can be maintained indefinitely (for practical purposes, considered 200 min or longer) without resulting in fatigue and which is supported by aerobic metabolism. Prolonged swimming is that which results in fatigue between 20 s and 200 min. Prolonged speeds are supported by aerobic metabolism as well as some anaerobic component. The critical swimming speed (U_{crit}) is a subcategory of prolonged swimming and is determined experimentally by enforcing stepwise increments in swimming velocity until fatigue occurs. The U_{crit} is then calculated as the highest velocity the fish could maintain for a defined period of time (usually 30 to 60 min). Burst swimming speeds are the highest speeds of which the fish is capable, result in rapid fatigue (<20 s), and are predominately supported by anaerobic metabolism (Jobling, 1994).

tunas, although claims of extraordinary values (6–10 L s^{-1}) have been reported (Yuen, 1970; Beamish, 1978; Dizon *et al.*, 1978; Magnuson, 1978). However, the highest swimming velocities of tunas (30–200 cm in length) tracked in the wild or held in captivity are generally less than 3 L s^{-1} (reviewed in Bushnell, 1988, and Korsmeyer *et al.*, 1996a; Block *et al.*, 1998; Brill *et al.*, 1999). The highest velocities achieved in a water tunnel for skipjack and yellowfin tuna (30–51 cm) were 3 L s^{-1} or less, for periods of 40 to 60 min (Dewar and Graham, 1994). Models of oxygen uptake, swimming energetics, and tissue oxygen delivery suggest that tunas have a U_{ms} between 2 and 4 L s^{-1} (for ~50-cm tuna; Brill, 1996; Korsmeyer *et al.*, 1996b). These data suggest that U_{ms} values in tunas are much less than early reports suggested.

Comparison of these estimates with U_{ms} in other fishes is complicated by lack of data for similarly sized fish at the same temperature. However, the above values for tuna overlap measured U_{ms} values for other fishes. In a summary of 25 fish species, ranging from 5 to 55 cm, Videler (1993) found an average U_{ms} of 3.3 L s^{-1}, varying from 1.4 to 4.8 L s^{-1}. Among fish of larger size (~55 cm), U_{ms} was as high as 3.1 and 3.3 L s^{-1} in sockeye salmon (18°C), and pink salmon (*Oncorhynchus gorbuscha,* 20°C), respectively (Brett, 1982). Therefore, U_{ms} in tunas appears to be similar to or only slightly higher than that in other fishes. Further indicating that swimming performance in tunas is not exceptional, critical swimming velocities[4] (maintained for 30 min) among small (18–22 cm) kawakawa and yellowfin tuna (U_{crit} = 3.2–4.7 L s^{-1}) are not significantly different from another scombrid, the Pacific mackerel (3.8–5.8 L s^{-1}; Sepulveda and Dickson, 2000).

Tunas do have higher *optimal* swimming velocities, suggesting they are adapted for higher routine swimming speeds, but this is accompanied by higher swimming costs (Figure 5). Clearly, to resolve the question of swimming efficiency, additional research is required. Potential lines of research include: (1) studies with free-swimming tuna using an indicator of energetic output (e.g., tail beat or heart rates), (2) experiments with larger fish, given the changes in morphology (Magnuson, 1978) and potential increases in excess muscle temperatures with body size, and (3) advancement of biomechanical models that allow indirect estimates of thrust and drag based on kinematics.

D. What Metabolic Processes Account for the Total Energetic Costs in Tunas?

Although we cannot produce an energy budget for tunas because we do not know how much time is spent in any particular activity, the information reviewed above provides us with an estimate of the potential metabolic costs. SMRs in combination with aerobic swimming costs are high. U_{opt} for a 2-kg (~50 cm) yellowfin tuna is similar to routine speeds measured in the field (2 L s^{-1}, Holland

et al., 1990). At this velocity, two-thirds of the total costs (~700 mg O_2 kg^{-1} h^{-1}) are associated with locomotion and one-third with SMR (Dewar and Graham, 1994). Although MMR is not well defined, it appears that even at this speed a considerable fraction of aerobic scope remains.

As maximal sustained swimming speeds in tunas do not appear to be extraordinary, their high aerobic scope could be an adaptation that permits the provision for other metabolic costs on top of a high SMR and continuous locomotion. The potential contributions of reproduction, growth, digestion, and recovery from anaerobiosis are likely also high in tunas. A high aerobic scope would limit potential conflicts in energy demand, including that required for growth and reproduction (= Darwinian fitness). Among these other metabolic costs, recovery from intense anaerobic activity has the highest potential for oxygen demand.

Tuna white muscle differs from that of other fish, including other scombrids, in that in conjunction with a high anaerobic capacity, this tissue has an extraordinary aerobic capacity. Total aerobic capacity of the white muscle in tunas exceeds that of the red. This aerobic capacity is likely associated with the tuna's capabilities for rapid oxygen debt recovery. Rapid recovery, while also swimming at moderate aerobic velocities, will permit more frequent swimming bursts (~10 L s^{-1}; Magnuson, 1978), and can therefore result in higher *average* swimming velocities. Videler and Weihs (1982) have proposed that use of the white muscle in a burst-and-coast mode of swimming would be more efficient than swimming continuously at high velocities. This may account for the extraordinarily high speeds reported for some schools of tuna (Yuen, 1970).

E. Finally, How Does the Metabolism of Tunas Relate to Their Pelagic Existence and the Evolution of Regional Endothermy?

This question is best separated into two sections. First we examine the tuna's adaptations in relation to their pelagic existence. Tunas are often called energy speculators (Stevens and Neill, 1978), investing large amounts of energy (high SMR) on the potential for high energy returns in prey capture. Although it may appear that a high SMR is a disadvantage, this supports the capacity for increased levels of oxygen uptake, delivery, and utilization, and consequently work. The resulting high MMR and aerobic scope not only enable tuna to carry out many metabolic functions at a faster rate than other fish, but to do so simultaneously, reducing energetic compromises. Rates of work are, of course, enhanced by elevated temperature as well. Rather than minimize energy expenditure, tunas maximize energy intake, increasing the ratio of energy income to energy output. In many respects the metabolic intensity of tunas parallels that of other endotherms (mammals and birds); the increase in aerobic scope allows access to greater en-

ergy resources and ultimately increased fitness. The recent similarities observed between tuna and some other active pelagic fishes have not changed this conclusion—it is just clear that tuna are not the only energy speculators.

The evolution of endothermy has been the subject of great interest for scientists focusing on both marine and terrestrial vertebrates. Energetics has been the focal point of many studies of endothermy due to the 5- to 10-fold difference in resting metabolic rate between endo- and ectothermic terrestrial vertebrates (Else and Hulbert, 1981, 1985). In tunas it does not appear that a regional elevation in body temperature necessarily results in an elevated metabolic rate when comparisons are made at the same activity level. The SMR or RMR is similar for tunas, bonito, and the dolphinfish (Figures 1 and 3A). Instead, it is the maintenance of suite of adaptations (SMR) that facilitate a high aerobic scope and account for that elevation (see above). What increases as a result of elevated temperatures is the maximum rate and which functions can be performed, as indicated by thermal affects on muscle performance (Altringham and Block, 1997; see Altringham and Shadwick, this volume) and digestion (Stevens and McLeese, 1984). Thus, while not apparent in the SMR and RMR, when the metabolic costs are measured over a broader range of activities, an elevation in tuna $\dot{M}O_2$ may be apparent.

In addition to examining the potential cost of endothermy, the tunas and their ectothermic sister taxa provide an ideal opportunity to examine the evolution of endothermy (Dickson, 1995, 1996; Freund, 1999). Important questions center around the advantages of endothermy and the necessary physiological precursors. There are two dominant theories as to why endothermy evolved: (1) to expand the thermal niche, and (2) as a byproduct of selection for increased aerobic capacity. We are currently not in a position to resolve this question (but see Block and Finnerty, 1994; Brill *et al.*, 1999), and these two possibilities are not necessarily mutually exclusive. Further information on phylogenetic relationships, metabolic capacity, and thermal range is needed. The high RMRs of bonito, but not mackerel (Freund, 1999), suggest that an increased aerobic capacity evolved prior to the evolution of endothermy within the scombrids. Certainly, one advantage of endothermy is a further increase in the aerobic capacity of the red muscle (Dickson, 1996) and possibly the white muscle, but the consequences on tuna swimming ability remain elusive.

VIII. THE FUTURE

Although our understanding of tuna energetics has been improved, much remains to be done. Actual measurements of many metabolic costs (SDA, oxygen debt recovery, maximal metabolic rates) are needed to fully understand the consequences of a high SMR and tissue aerobic capacities. Our interpretation also has

been restricted by the limited scope of species studied. Most research has been conducted on juveniles of a few tropical species and clearly not all tunas are created equal. Within the tuna clade exists a great deal of morphological and physiological variation. Our conclusions may change when additional data are obtained on other tunas that inhabit cooler waters, such as the albacore, bigeye, and bluefin tunas. These species have greater endothermic capabilities, with greater temperature elevation and more regions served by countercurrent heat exchangers (Carey, 1973; Stevens and Neill, 1978). Comparisons within the thunnini tribe, and over a greater range of size, would be useful for examining the functional significance of endothermy and both scaling and ontogenetic effects. Studies of other pelagic fishes, and the endothermic sharks, will also be of great use in teasing out the selective pressures of an oceanic environment and the evolution of endothermy.

ACKNOWLEDGMENTS

For their helpful comments and critique on drafts of the manuscript, we gratefully thank Rich Brill, Kathy Dickson, Don Stevens, Barb Block, and Tony Farrell. Also, we thank Kathy Dickson, Chugey Sepulveda, Ellen Freund, Dave Marcinek, John Steffensen, and Robert Shadwick for access to unpublished data. Any errors in this chapter, however, are solely those of the authors. Support for the preparation of this manuscript was provided to H.D. by the Pfleger Institute of Environmental Research and to K.E.K. by Hawaii Pacific University Trustees' Scholarly Endeavors Program.

REFERENCES

Alsop, D. H., and Wood, C. M. (1997). The interactive effects of feeding and exercise on oxygen consumption, swimming performance and protein usage in juvenile rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **200,** 2337–2346.

Altringham, J. D., and Block, B. A. (1997). Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200,** 2617–2627.

Arthur, P. G., West, T. G., Brill, R. W., Schulte, P. M., and Hochachka, P. W. (1992). Recovery metabolism of skipjack tuna (*Katsuwonus pelamis*) white muscle: Rapid and parallel changes in lactate and phosphocreatine after exercise. *Can. J. Zool.* **70,** 1230–1239.

Axelsson, M., and Fritsche, R. (1991). Effects of exercise, hypoxia and feeding on the gastrointestinal blood flow in the Atlantic cod *Gadus morhua*. *J. Exp. Biol.* **158,** 181–198.

Axelsson, M., Driedzic, W. R., Farrell, A. P., and Nilsson, S. (1989). Regulation of cardiac output and gut blood flow in the sea raven, *Hemitripterus americanus*. *Fish Physiol. Biochem.* **6,** 315–326.

Beamish, F. W. H. (1970). Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. *Can. J. Zool.* **48,** 1221–1228.

Beamish, F. W. H. (1974). Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. *J. Fish. Res. Bd. Can.* **31,** 1763–1769.

Beamish, F. W. H. (1978). Swimming capacity. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 7, pp. 101–187. Academic Press, New York.

Benetti, D. D., Brill, R. W., and Kraul, S. A. (1995). The standard metabolic rate of dolphin fish. *J. Fish Biol.* **46,** 987–996.

Bennett, A. F., and Ruben, J. A. (1979). Endothermy and activity in vertebrates. *Science* **206,** 649–654.

Blackburn, M. (1968). Micronecton of the eastern tropical pacific ocean: Family composition, distribution, abundance, and relations to tuna. *Fish. Bull.* **67,** 71–115.

Block, B. A., and Finnerty, J. R. (1994). Endothermy in fishes: A phylogenetic analysis of constraints, predispositions, and selection pressures. *Environ. Biol. Fishes* **40,** 283–302.

Block, B. A., Keen, J. E., Castillo, B., Brill, R. W., Dewar, H., Freund, E. V., Marcinek, D. J., and Farwell, C. (1998). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of their range. *Mar. Biol.* **130,** 119–132.

Boggs, C. H. (1984). Tuna bioenergetics and hydrodynamics. Ph.D. dissertation, University of Wisconsin, Madison.

Boggs, C. H., and Kitchell, J. F. (1991). Tuna metabolic rates estimated from energy losses during starvation. *Physiol. Zool.* **64,** 502–524.

Bone, Q. (1978a). Locomotor muscle. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 7, pp. 361–424. Academic Press, New York.

Bone, Q. (1978b). Myotomal muscle fiber types in *Scomber* and *Katsuwonus*. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 183–205. Academic Press, New York.

Brand, M. D. (1990). The contribution of the leak of protons across the mitochondrial inner membrane to standard metabolic rate. *J. Theoret. Biol.* **145,** 267–286.

Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Can.* **21,** 1183–1226.

Brett, J. R. (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Can.* **22,** 1491–1501.

Brett, J. R. (1972). The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. *Respir. Physiol.* **14,** 151–170.

Brett, J. R. (1982). The swimming speed of adult pink salmon, *Oncorhynchus gorbuscha,* at 20°C and a comparison with sockeye salmon, *O. nerka. Can. Tech. Rep. Fish. Aquatic Sci.* **1143,** 1–37.

Brett, J. R., and Glass, N. R. (1973). Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Bd. Can.* **30,** 379–387.

Brett, J. R., and Groves, T. D. D. (1979). Physiological energetics. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Brett, J. R., Eds.), Vol. 8, pp. 279–352. Academic Press, New York.

Brill, R. W. (1979). The effect of body size on the standard metabolic rate of skipjack tuna, *Katsuwonus pelamis. Fish. Bull.* **77,** 494–498.

Brill, R. W. (1987). On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. *Fish. Bull.* **85,** 25–35.

Brill, R. W. (1992). The Kewalo Research Facility, 1958–92: Over 30 Years of Progress. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, Honolulu.

Brill, R. W. (1994). A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fish. Oceanogr.* **3,** 204–216.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. *Comp. Biochem. Physiol.* **113A,** 3–15.

Brill, R. W., and Bushnell, P. G. (1991). Metabolic and cardiac scope of high energy demand teleosts, the tunas. *Can. J. Zool.* **69,** 2002–2009.

Brill, R. W., Bushnell, P. G., Jones, D. R., and Shimizu, M. (1992). Effects of acute temperature

change, *in vivo* and *in vitro*, on the acid-base status of blood from yellowfin tuna (*Thunnus albacares*). *Can. J. Zool.* **70,** 654–662.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: Implications for the physiological ecology of pelagic fishes. *Mar. Biol.* **133,** 395–408.

Brown, C. E., and Muir, B. S. (1970). Analysis of ram ventilation of fish gills with application to skipjack tuna (*Katsuwonus pelamis*). *J. Fish. Res. Bd. Can.* **27,** 1637–1652.

Buck, L. T., Brill, R. W., and Hochachka, P. W. (1992). Gluconeogenesis in hepatocytes isolated from the skipjack tuna (*Katsuwonus pelamis*). *Can. J. Zool.* **70,** 1254–1257.

Bushnell, P. G. (1988). Cardiovascular and respiratory responses to hypoxia in three species of obligate ram ventilating fishes, skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*T. obesus*). Ph.D. dissertation, University of Hawaii, Honolulu.

Bushnell, P. G., and Brill, R. W. (1991). Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas to acute hypoxia, and a model of their cardiorespiratory function. *Physiol. Zool.* **64,** 787–811.

Bushnell, P. G., and Brill, R. W. (1992). Oxygen transport and cardiovascular responses in skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) exposed to acute hypoxia. *J. Comp. Physiol. B* **162,** 131–143.

Bushnell, P. G., and Jones, D. R. (1994). Cardiovascular and respiratory physiology of tuna: Adaptations for support of exceptionally high metabolic rates. *Environ. Biol. Fishes* **40,** 303–318.

Bushnell, P. G., Steffensen, J. G., and Johansen, K. (1984). Oxygen consumption and swimming performance in hypoxia-acclimated rainbow trout, *Salmo gairdneri*. *J. Exp. Biol.* **13,** 225–235.

Bushnell, P. G., Brill, R. W., and Bourke, R. E. (1990). Cardiorespiratory responses of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) to acute reductions of ambient oxygen. *Can. J. Zool.* **68,** 1857–1865.

Carey, F. G. (1973). Fishes with warm bodies. *Sci. Am.* **228,** 36–44.

Carey, F. G., and Teal, J. M. (1969). Regulation of body temperature by the bluefin tuna. *Comp. Biochem. Physiol.* **28,** 205–213.

Carey, F. G., Teal, J. M., Kanwisher, J. W., and Lawson, K. D. (1971). Warm-bodied fish. *Am. Zool.* **11,** 135–145.

Carey, F. G., Kanwisher, J. W., and Stevens, E. D. (1984). Bluefin tuna warm their viscera during digestion. *J. Exp. Biol.* **109,** 1–20.

Carroll, R. L. (1988). "Vertebrate Paleontology and Evolution," Chap. 7. Freeman, New York.

Castellini, M. A., and Somero, G. N. (1981). Buffering capacity of vertebrate muscle: Correlations with potentials for anaerobic function. *J. Comp. Physiol. B* **143,** 191–198.

Clarke, A., and Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *J. Anim. Ecol.* **68,** 893–905.

Collette, B. B. (1978). Adaptations and systematics of the mackerels and tunas. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 7–39. Academic Press, New York.

Collette, B. B., and Nauen, C. E. (1983). FAO species catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. *FAO Fish. Synop.* **125,** 1–137.

Davis, J. C., and Cameron, J. N. (1971). Water flow and gas exchange at the gills of rainbow trout, *Salmo gairdneri*. *J. Exp. Biol.* **54,** 1–18.

Daxboeck, C., Davie, P. S., Perry, S. F., and Randall, D. J. (1982). Oxygen uptake in a spontaneously ventilating, blood-perfused trout preparation. *J. Exp. Biol.* **101,** 35–45.

Dewar, H., and Graham, J. B. (1994). Studies of tropical tuna swimming performance in a large water tunnel. I. Energetics. *J. Exp. Biol.* **192,** 13–31.

Dewar, H., Graham, J. B., and Brill, R. W. (1994). Studies of tropical tuna swimming performance in a large water tunnel. II. Thermoregulation *J. Exp. Biol.* **192,** 33–44.

Dewar, H., Deffenbaugh, M., Thurmond, G., Lashkari K. G., and Block. B. (1999). Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. *J. Exp. Biol.* **202,** 2693–2699.

Dickson, K. A. (1988). Why are some fishes endothermic? Interspecific comparisons of aerobic and anaerobic metabolic capacities in endothermic and ectothermic scombrids. Ph.D. dissertation, Scripps Institution of Oceanography, University of California, San Diego.

Dickson, K. A. (1994). Tunas as small as 207mm fork length can elevate muscle temperatures significantly above ambient water temperature. *J. Exp. Biol.* **190,** 79–93.

Dickson, K. A. (1995). Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environ. Biol. Fishes* **42,** 65–97.

Dickson, K. A. (1996). Locomotor muscle of high-performance fishes: What do comparisons of tunas with ectothermic sister taxa reveal? *Comp. Biochem. Physiol.* **113A,** 39–49.

Dickson, K. A., and Somero, G. N. (1987). Partial characterization of the buffering components of the red and white myotomal muscle of marine teleosts, with special emphasis on scombrid fishes. *Physiol. Zool.* **60,** 699–706.

Dickson, K. A., Gregorio, M. O., Gruber, S. J., Loefler, K. L., Tran, M., and Terrell, C. (1993). Biochemical indices of aerobic and anaerobic capacity in muscle tissues of California elasmobranch fishes differing in typical activity level. *Mar. Biol.* **117,** 185–193.

Dizon, A. E. (1977). Effect of dissolved oxygen concentration and salinity on swimming speed of two species of tunas. *Fish. Bull.* **75,** 649–653.

Dizon, A. E., Brill, R. W., and Yuen, H. S. H. (1978). Correlations between environment, physiology and activity and the effects on thermoregulation in skipjack tuna. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 233–259. Academic Press, New York.

Egginton, S., and Johnston, I. A. (1983). An estimate of capillary anisotropy and determination of surface and volume densities of capillaries in skeletal muscles of the conger eel (*Conger conger* L.). *Quart. J. Exp. Physiol.* **68,** 603–617.

Else, P. L., and Hulbert, A. J. (1981). Comparison of the "mammal machine" and the "reptile machine": Energy production. *Am. J. Physiol.* **240,** R3–R9.

Else, P. L., and Hulbert, A. J. (1985). An allometric comparison of the mitochondria of mammalian and reptilian tissues: The implications for the evolution of endothermy. *J. Comp. Physiol. B* **156,** 3–11.

Fierstine, H. L., and Walters, V. (1968). Studies in locomotion and anatomy of scombroid fishes. *Memoirs South. Calif. Acad. Sci.* **6,** 1–31.

Forsbergh, E. D. (1980). Synopsis of biological data on the skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758), in the Pacific ocean. *Inter-Am. Trop. Tuna Commission, Spec. Rep.* **2,** 295–360.

Freund, E. V. (1999). Comparisons of metabolic and cardiac performance in scombrid fishes: Insights into the evolution of endothermy. Ph.D. dissertation, Biological Sciences, Stanford University, Stanford, CA.

Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 6, pp. 1–99. Academic Press, San Diego.

Furnell, D. J. (1987). Partitioning of locomotor and feeding metabolism in sablefish (*Anoplopoma fimbria*). *Can. J. Zool.* **65,** 486–489.

Gooding, R. M., Neill, W. H., and Dizon, A. E. (1981). Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis. Fish. Bull.* **79,** 31–48.

Goolish, E. M. (1991). Aerobic and anaerobic scaling in fish. *Biol. Rev.* **66,** 33–56.

Gordon, M. S. (1968). Oxygen consumption of red and white muscles from tuna fishes. *Science* **159,** 87–90.

Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares,* and skipjack tuna,

Katsuwonus pelamis, and the adaptive significance of elevated body temperatures in scombrid fishes. *Fish. Bull.* **73,** 219–229.

Graham, J. B., and Dickson, K. A. (1981). Physiological thermoregulation in the albacore *Thunnus alalunga. Physiol. Zool.* **54,** 470–486.

Graham, J. B., and Laurs, R. M. (1982). Metabolic rate of the albacore tuna *Thunnus alalunga. Mar. Biol.* **72,** 1–6.

Graham, J. B., Koehrn, F. J., and Dickson, K. A. (1983). Distribution and relative proportions of red muscle in scombrid fishes: Consequences of body size and relationships to locomotion and endothermy. *Can. J. Zool.* **61,** 2087–2096.

Graham, J. B., Lowell, W. R., Lai, N. C., and Laurs, R. M. (1989). O_2 tension, swimming-velocity, and thermal effects on the metabolic rate of the Pacific albacore *Thunnus alalunga. Exp. Biol.* **48,** 89–94.

Graham, J. B., Dewar, H., Lai, N. C., Lowell, W. R., and Arce, S. M. (1990). Aspects of shark swimming performance determined using a large water tunnel. *J. Exp. Biol.* **151,** 175–192.

Gray, I. E. (1954). Comparative study of the gill area of marine fishes. *Biol. Bull. Mar. Biol. Lab.* **107,** 219–225.

Guppy, M., and Hochachka, P. W. (1978). Controlling the highest lactate dehydrogenase activity known in nature. *Am. J. Physiol.* **234,** R136–R140.

Guppy, M., Hulbert, W. C., and Hochachka, P. W. (1979). Metabolic sources of heat and power in tuna muscles. II. Enzyme and metabolite profiles. *J. Exp. Biol.* **82,** 303–320.

Heisler, N. (1989). Interactions between gas exchange, metabolism, and ion transport in animals: An overview. *Can. J. Zool.* **67,** 2923–2935.

Herskin, J., and Steffensen, J. F. (1998). Energy savings in sea bass swimming in a school: Measurements of tail beat frequency and oxygen consumption at different swimming velocities. *J. Fish Biol.* **53,** 366–376.

Hochachka, P. W., Hulbert, W. C., and Guppy, M. (1978). The tuna power plant and furnace. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 153–174. Academic Press, New York.

Holland, K. N., and Sibert, J. R. (1994). Physiological thermoregulation in bigeye tuna, *Thunnus obesus. Environ. Biol. Fishes* **40,** 319–327.

Holland, K. N., Brill, R. W., and Chang, R. K. C. (1990). Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish. Bull.* **88,** 493–507.

Hoppeler, H., and Lindstedt, S. L. (1985). Malleability of skeletal muscle in overcoming limitations: Structural elements. *J. Exp. Biol.* **115,** 355–364.

Hughes, G. M. (1984). General anatomy of the gills. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 10, pp. 1–72. Academic Press, New York.

Hulbert, W. C., Guppy, M., Murphy, B., and Hochachka, P. W. (1979). Metabolic sources of heat and power in tuna muscles. I. Muscle fine structure. *J. Exp. Biol.* **82,** 289–301.

Hunter, J. R., Macewicz, B. J., and Sibert, J. R. (1986). The spawning frequency of skipjack tuna, *Katsuwonus pelamis,* from the South Pacific. *Fish. Bull.* **84,** 895–903.

Jobling, M. (1981). The influences of feeding on the metabolic rate of fishes: A short review. *J. Fish Biol.* **18,** 385–400.

Jobling, M. (1994). "Fish Bioenergetics." Chapman and Hall, New York.

Johnston, I. A. (1981). Structure and function of fish muscles. *Symp. Zool. Soc. Lond.* **48,** 71–113.

Johnston, I. A. (1982). Quantitative analyses of ultrastructure and vascularization of the slow muscle fibres of the anchovy. *Tissue Cell* **14,** 319–328.

Johnston, I. A., and Salamonski, J. (1984). Power output and force-velocity relationship of red and white muscle fibres from the Pacific blue marlin (*Makaira nigricans*). *J. Exp. Biol.* **111,** 171–177.

Johnston, I. A., Calvo, J., Guderley, H., Fernandez, D., and Palmer, L. (1998). Latitudinal variation in

the abundance and oxidative capacities of muscle mitochondria in perciform fishes. *J. Exp. Biol.* **201,** 1–12.

Kiceniuk, J. W., and Jones, D. R. (1977). The oxygen transport system in trout (*Salmo gairdneri*) during sustained exercise *J. Exp. Biol.* **69,** 247–260.

Kitchell, J. F., Neill, W. H., Dizon, A. E., and Magnuson, J. J. (1978). Bioenergetic spectra of skipjack and yellowfin tunas. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 357–368. Academic Press, New York.

Korsmeyer, K. E. (1996). A study of cardiovascular function in swimming tuna. Ph.D. dissertation, Scripps Institution of Oceanography, University of California, San Diego.

Korsmeyer, K. E., Dewar, H., Lai, N. C., and Graham, J. B. (1996a). The aerobic capacity of tunas: Adaptation for multiple metabolic demands. *Comp. Biochem. Physiol.* **113A,** 17–24.

Korsmeyer, K. E., Dewar, H., Lai, N. C., and Graham, J. B. (1996b). Tuna aerobic swimming performance: Physiological and environmental limits based on oxygen supply and demand. *Comp. Biochem. Physiol.* **113B,** 45–56.

Korsmeyer, K. E., Lai, N. C., Shadwick, R. E., and Graham, J. B. (1997). Oxygen transport and cardiovascular responses to exercise in the yellowfin tuna *Thunnus albacares. J. Exp. Biol.* **200,** 1987–1997.

Macy, W. K., Durbin, A. G., and Durbin, E. G. (1999). Metabolic rate in relation to temperature and swimming speed, and the cost of filter feeding in Atlantic menhaden, *Brevoortia tyrannus. Fish. Bull.* **97**(2), 282–293.

Magnuson, J. J. (1969). Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). *Trans. Am. Fish. Soc.* **98,** 379–392.

Magnuson, J. J. (1973). Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. *Fish. Bull.* **71,** 337–356.

Magnuson, J. J. (1978). Locomotion by scombrid fishes: Hydromechanics, morphology, and behavior. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 7, pp. 239–313. Academic Press, New York.

Marcinek, D. J. (2000). The physiological ecology of myoglobin in scombrid fish. Ph.D. dissertation, Biological Sciences, Stanford University, Stanford, CA.

Mather, F. J. (1962). Transatlantic migration of two large bluefin tuna. *Cons. Perm. Int. Explor. Mer.* **27,** 325–327.

Mathieu-Costello, O., Agey, P. J., Logemann, R. B., Brill, R. W., and Hochachka, P. W. (1992). Capillary-fiber geometrical relationships in tuna red muscle. *Can. J. Zool.* **70,** 1218–1229.

Milligan, C. L. (1996). Metabolic recovery from exhaustive exercise in rainbow trout. *Comp. Biochem. Physiol.* **113A,** 51–60.

Milligan, C. L., Hooke, G. B., and Johnston, C. (2000). Sustained swimming at low velocity following a bout of exhaustive exercise enhances metabolic recovery in rainbow trout. *J. Exp. Biol.* **203,** 921–926.

Mosse, P. R. L. (1979). Capillary distribution and metabolic histochemistry of the lateral propulsive musculature of pelagic teleost fish. *Cell Tissue Res.* **203,** 141–160.

Moyes, C. D., Mathieu-Costello, O. A., Brill, R. W., and Hochachka, P. W. (1992). Mitochondrial metabolism of cardiac and skeletal muscles from a fast (*Katsuwonus pelamis*) and a slow (*Cyprinus carpio*) fish. *Can. J. Zool.* **70,** 1246–1253.

Moyes, C. D., Schulte, P. M., and West, T. G. (1993). Burst exercise recovery metabolism in fish white muscle. *In* "Surviving Hypoxia" (Hochachka, P. W., Lutz, P. L., Sick, T., Rosenthal, M., and van den Thillart, G., Eds.), pp. 527–539. CRC Press, Boca Raton.

Muir, B. S., and Hughes, G. M. (1969). Gill dimensions for three species of tunny. *J. Exp. Biol.* **51,** 271–285.

Muir, B. S., and Kendall, J. I. (1968). Structural modifications in the gills of tunas and some other oceanic fishes. *Copeia,* 388–398.

Nakamura, E. L. (1972). Development and uses of facilities for studying tuna behavior. *In* "Behavior of Marine Animals" (Winn, H. E., and Olla, B. L., Eds.), Vol. 2, pp. 245–277. Plenum Press, New York.

Nakamura, I. (1985). FAO species catalogue. Vol.5. Billfishes of the world. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes and swordfishes known to date. *FAO Fish. Synop.* **125**(5).

Olson, R. J., and Boggs, C. H. (1986). Apex predation by yellowfin tuna (*Thunnus albacares*): Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Can. J. Fish. Aquatic Sci.* **43,** 1760–1775.

Palko, B. J., Beardsley, G. L., and Richards, W. J. (1982). "Synopsis of the Biological Data on Dolphin Fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus," NOAA Technical Report, NMFS Circular 443, National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Seattle.

Perry, S. F., Daxboeck, C., Emmett, B., Hochachka, P. W., and Brill, R. W. (1985). Effects of exhausting exercise on acid-base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. *Physiol. Zool.* **58,** 421–429.

Priede, I. G. (1985). Metabolic scope in fishes. *In* "Fish Energetics: New Perspectives" (Tyler, P., and Calow, P., Eds.), pp. 33–64. John Hopkins University Press, Baltimore.

Prince, E. D., Lee, D. W., Zweifel, J. R., and Brothers, E. B. (1990). Ageing young Atlantic blue marlin (*Makaira nigricans*) from otolith microstructure (summary paper). *In* "Planning the Future of Billfishes, Part 2" (Stroud, R. H., Ed.), pp. 295–304. National Coalition for Marine Conservation, Inc., Savannah.

Randall, D. J., and Daxboeck, C. (1982). Cardiovascular changes in the rainbow trout (*Salmo gairdneri* Richardson) during exercise. *Can. J. Zool.* **60,** 1135–1140.

Randall, D. J., Burggren, W., and French, K. (1997). "Eckert Animal Physiology." Freeman, New York.

Schulte, P. M., Moyes, C. D., and Hochachka, P. W. (1992). Integrating metabolic pathways in post-exercise recovery of white muscle. *J. Exp. Biol.* **166,** 181–195.

Sepulveda, C. A., and Dickson, K. D. (2000). Maximum sustainable speeds and cost of swimming in juvenile Kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J. Exp. Biol.,* **203,** 3089–3101.

Stevens, E. D. (1972). Some aspects of gas exchange in tuna. *J. Exp. Biol.* **56,** 809–823.

Stevens, E. D. (1982). The effect of temperature on facilitated oxygen diffusion and its relation to warm tuna muscle. *Can. J. Zool.* **60,** 1148–1152.

Stevens, E. D., and Carey, F. G. (1981). One why of the warmth of warm-bodied fish. *Am. J. Physiol.* **240,** R151–R155.

Stevens, E. D., and McLeese, J. M. (1984). Why bluefin tuna have warm tummies: Temperature effect on trypsin and chymotrypsin. *Am. J. Physiol.* **246,** R487–R494.

Stevens, E. D., and Neill, W. H. (1978). Body temperature relations of tuna, especially skipjack. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 7, pp. 316–360. Academic Press, New York.

Stevens, E. D., Kanwisher, J. W., and Carey, F. G. (2000). Muscle temperature in free-swimming giant Atlantic bluefin tuna (*Thunnus thynnus* L.). *J. Thermal Biol.,* **25,** 419–423.

Suarez, R. K., Lighton, J. R. B., Brown, G. S., and Mathieu-Costello, O. (1991). Mitochondrial respiration in hummingbird flight muscles. *Proc. Natl. Acad. Sci. USA* **88,** 4870–4873.

Tang, J., and Wardle, C. S. (1992). Power output of two sizes of Atlantic salmon (*Salmo salar*) at their maximum sustained swimming speeds. *J. Exp. Biol.* **166,** 33–46.

Thorarensen, H., Gallaugher, P. E., Kiessling, A. K., and Farrell, A. P. (1993). Intestinal blood flow in swimming Chinook salmon *Oncorhynchus tshawytscha* and the effects of haematocrit on blood flow distribution. *J. Exp. Biol.* **179,** 115–139.

Torres, J. J., and Somero, G. N. (1988). Metabolism, enzymatic activities and cold adaptation in Antarctic mesopelagic fishes. *Mar. Biol.* **98,** 169–180.

Townsend, C. R., and Winfield, I. J. (1985). The application of optimal foraging theory to feeding behavior in fish. *In* "Fish Energetics: New Perspectives" (Tyler, P., and Calow, P., Eds.), pp. 67–78. John Hopkins University Press, Baltimore.

Tsukamoto, K. (1984). Contribution of the red and white muscles to the power output required for swimming by the yellowtail. *Bull. Jpn. Soc. Sci. Fish.* **50,** 2031–2042.

Tucker, V. A. (1975). The energetic cost of moving about. *Am. Sci.* **63,** 413–419.

Uchiyama, J. H., and Struhsaker, P. (1980). Age and growth of skipjack tuna, *Katsuwonus pelamis,* and yellowfin tuna, *Thunnus albacares,* as indicated by daily growth increments of sagittae. *Fish. Bull.* **79,** 151–162.

Uchiyama, J. H., Burch, R. K., and Kraul, S. A. (1986). Growth of dolphins, *Coryphaena hippurus* and *C. equiselis* in Hawaiian waters as determined by daily increments on otoliths. *Fish. Bull.* **84,** 186–191.

Videler, J. J. (1993). "Fish Swimming." Chapman and Hall, New York.

Videler, J. J., and Nolet, B. A. (1990). Costs of swimming measured at optimum speed: Scale effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. *Comp. Biochem. Physiol.* **97A,** 91–99.

Videler, J. J., and Weihs, D. (1982). Energetic advantages of burst-and-coast swimming of fish at high speeds. *J. Exp. Biol.* **97,** 169–178.

Walters, V., and Fierstine, H. L. (1964). Measurements of swimming speeds of yellowfin tuna and wahoo. *Nature* **202,** 208–209.

Wardle, C. S., Soofiani, N. M., O'Neill, F. G., Glass, C. W., and Johnstone, A. D. F. (1996). Measurements of aerobic metabolism of a school of horse mackerel at different swimming speeds. *J. Fish Biol.* **49,** 854–862.

Webb, P. W. (1971). The swimming energetics of trout. II: Oxygen consumption and swimming efficiency. *J. Exp. Biol.* **55,** 521–540.

Webb, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *J. Fish. Res. Bd. Can.* **190.**

Weber, J. M. (1992). Pathways for oxidative fuel provision to working muscles: Ecological consequences of maximal supply limitations. *Experientia* **48,** 557–564.

Weber, J., Brill, R. W., and Hochachka, P. W. (1986). Mammalian metabolite flux rates in a teleost: Lactate and glucose turnover in tuna. *Am. J. Physiol.* **250,** R452–R458.

Weihs, D. (1973). Mechanically efficient swimming techniques for fish with negative buoyancy. *J. Mar. Res.* **31,** 194–209.

Wild, A. (1986). Growth of yellowfin tuna, *Thunnus albacares,* in the eastern tropical Pacific Ocean based on otolith increments. *Inter-Am. Trop. Tuna Commission, Bull.* **18,** 422–479.

Wood, C. M. (1991). Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. *J. Exp. Biol.* **160,** 285–308.

Yamamoto, K., Itazawa, Y., and Kobayashi, H. (1981). Gas exchange in the gills of yellowtail, *Seriola quinqueradiata,* under resting and normoxic condition. *Bull. Jpn. Soc. Sci. Fish.* **47,** 447–451.

Yuen, H. S. H. (1970). Behavior of skipjack tuna, *Katsuwonus pelamis,* as determined by tracking with ultrasonic devices. *J. Fish. Res. Bd. Can.* **27,** 2071–2079.

3

THE CARDIOVASCULAR SYSTEM OF TUNAS

RICHARD W. BRILL
PETER G. BUSHNELL

I. Introduction
II. Cardiovascular Function at Routine Activity Levels
  A. Oxygen Transport from Water to Tissues
  B. High Blood Pressures and the Maintenance of Tissue Fluid Balance
III. Maximal Rates of Cardiovascular Function in Tunas
  A. How Skipjack and Yellowfin Tunas Achieve High Maximum Metabolic Rates
  B. Elevated Hematocrit, Oxygen Transport, and Blood Viscosity
IV. Tuna Cardiac Function
  A. Stroke Volume
  B. Maximal Heart Rates in Tunas and Other Teleosts
  C. Sarcoplasmic Reticulum
  D. Mechanical and Electrical Coupling of Myocytes
  E. Biochemical Adaptations of Tuna Hearts for High Power Output
  F. Ventricular and Arterial Dynamics and Functions of the Bulbus Arteriosus
V. Cardiac Function and the Physiological Ecology of Tunas—A Possible Connection
VI. Summary and Conclusions

I. INTRODUCTION

Tunas (family *Scombridae,* tribe *Thunnini*) have high metabolic rates (Korsmeyer and Dewar, this volume) and are obligate ram ventilators (Brown and Muir, 1970; Roberts, 1975, 1978). They suffocate rapidly if prevented from swimming so special care must be taken to ensure that ventilatory requirements are met during all stages of an experiment. Tunas also struggle violently during any restraining procedure. It is impossible to use completely intact, unanesthetized, "resting" fish to make even the simplest cardiorespiratory measurements using techniques commonly employed with other species (e.g., Smith and Davie, 1984; Smatresk, 1986). Some data have been obtained on swimming tunas (Jones *et al.,* 1990, 1993; Bushnell and Brill 1991; Korsmeyer *et al.,* 1997a,b) but these procedures are inherently very difficult and fish can carry only minimal instrumentation with-

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

out impacting hydrodynamics and increasing metabolic energy demand (Kiceniuk and Jones, 1977; Jones *et al.,* 1990). Much of the data on tuna cardiovascular function has, therefore, been recorded in somewhat unusual circumstances such as total neuromuscular blockade with forced ventilation (Stevens, 1972; White *et al.,* 1988) or spinal blockade with fish in a water stream (Bushnell and Brill, 1992). Tunas are also expensive to acquire, difficult to maintain in captivity, and are routinely kept in shore side tanks at only a handful of laboratories (Nakamura, 1972; Brill, 1999; Farwell, this volume). The difficulties of working with individual fish are compounded because relatively few animals are available for study.

As a result, our understanding of cardiovascular function in tunas is incomplete. This should not be construed to mean that it remains a mystery. On the contrary, in spite of the difficulties of working with these fishes, there exists a significant body of publications that range from the molecular and biochemical to whole-animal physiology. In this chapter we synthesize the more recent of these diverse studies and endeavor to show how they are beginning to present a unified picture of these fascinating animals.

We start our discussion by attempting to distinguish which aspects of the cardiovascular system of tunas are clearly enhanced compared to other teleosts. For the following reasons, however, we do so with only a modest degree of certainty. Rates of virtually all physiological functions are influenced by temperature and scale nonlinearly with body mass. Yet correcting for these variables, and making appropriate comparisons, can be problematic because temperature effects and scaling relationships are often ill-defined (Packard and Boardman, 1999). This is especially true when comparing rates of cardiovascular function in tunas to those of other teleosts. Because of their accessibility, most of our knowledge of teleost cardiovascular physiology comes from measurements made on temperate (i.e., at $<20°C$), small (<1 kg body mass), freshwater fishes (e.g., rainbow trout, *Oncorhynchus mykiss*). In contrast, information on tuna cardiovascular function comes mostly from measurements made on 1- to 3-kg skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) at 25°C. Data at $\approx 15°C$ are available for albacore (*Thunnus alalunga*), but are from fish of $\approx$7–10 kg body mass (Lai *et al.,* 1987; White *et al.,* 1988; Graham *et al.,* 1989). Also, albacore are not routinely maintained in captivity and all *in vivo* data have been collected at sea on recently captured fish when they may have been physiologically stressed and recovering from exhaustive exercise. The different methods used to quantify cardiovascular function in tunas and other teleosts can also generate what appear to be species-specific differences, but that are artifactual (Metcalf and Butler, 1982; Kalinin *et al.,* 1999). Therefore, as in all experiments involving whole animals, but more so with tunas, the anesthesia, surgical, handling, and instrumentation procedures required to make cardiovascular measurements can easily distort the very processes being evaluated.

We also attempt to discern the important functional adaptations that set tunas

apart from other teleosts. In theory, this type of analysis should involve comparisons of more than two or three species, include data from "primitive" members of the clade, and employ statistical procedures that take phylogenetic distances into account (Garland and Adolph, 1994). In our case, the application of these principles is problematic as the *in vivo* data on tuna cardiovascular physiology come from only three species: skipjack tuna, yellowfin tuna, and albacore. Moreover, although critical for discerning the evolution of cardiovascular function, the physiology of primitive members of the family *Scombridae* (the so-called "ectothermic scombrids") remains almost unstudied. [The ectothermic scombrids include the bonitos (tribe *Sardini*), seerfishes (tribe *Scomberomorini*), and mackerel (tribe *Scombrini*).]

II. CARDIOVASCULAR FUNCTION AT ROUTINE ACTIVITY LEVELS

Besides being obligate ram ventilators, tunas also depend on constant forward motion to produce lift from their pectoral fins for hydrostatic equilibrium (Magnuson, 1978; Magnuson and Weininger, 1978). If tunas stop swimming they sink as well as suffocate. As a result, throughout this review we refer to "routine" rates of cardiovascular function. By this we mean those associated with swimming speeds ranging from 1 to 2 body lengths s^{-1}. This level of activity is commonly recorded when skipjack and yellowfin tunas are able to set their swimming speeds either in the laboratory, or when fish carrying ultrasonic transmitters are followed in the open ocean (e.g., Dizon *et al.*, 1978; Dizon and Brill, 1979; Gooding *et al.*, 1981; Holland *et al.*, 1990b; Block *et al.*, 1997; Brill *et al.*, 1999; Freund, 1999).

Table I summarizes the anatomical and physiological descriptors of cardiovascular function in tunas that we regard as the most reflective of unstressed animals. We have highlighted in bold those values we consider unusual in tunas, and on which we will focus. For comparison, we have included data from yellowtail (*Seriola* spp.) and rainbow trout. We selected the former because they are active, pelagic, warm-water, marine fishes, and because data are available from a range of body masses similar to those of skipjack and yellowfin tunas commonly used in physiological experiments. We chose the latter because it is the most well-studied teleost species in terms of its physiology, and because data are available on minimal as well as maximal rates of cardiovascular function.

The standard metabolic rates (i.e., those measured in fish paralyzed with neuromuscular blocking agents) of skipjack and yellowfin tuna are 412 and 286 mg O_2 kg^{-1} h^{-1}, respectively (Brill, 1987), values several times those of yellowtail at "rest." At routine swimming speeds ($\approx$1–2 body lengths s^{-1}), the metabolic rates of skipjack and yellowfin tunas are 974 and 776 mg O_2 kg^{-1} h^{-1}, which are approximately six to eight times that of yellowtail, a marine species living at a

Table I
Cardiorespiratory Function in Tunas and Other Teleosts

	Yellowfin tuna[a]	Skipjack tuna[a]	Yellowtail[b]	Rainbow trout[c]	
Temperature	25°C	25°C	19–25°C	10°C	10°C
Body mass (kg)	≈1–2	≈1–2	≈1	0.9–1.5	0.9–1.5
Swimming speed (body lengths s^{-1})	1.0–1.3	1.6–2.2	—	—	≈0.5–1.5[g]
Activity level	Routine[h]	Routine	Rest	Rest	Maximum sustainable
Total O_2 consumption (mg O_2 kg^{-1} h^{-1})	**776**	**974**	138	48	372
Gill O_2 consumption (mg O_2 kg^{-1} h^{-1})	**362**	**420**	2	≈0	213
Body O_2 consumption (mg O_2 kg^{-1} h^{-1})	**414**	**554**	136	54	159
Ventilation volume (liter min^{-1} kg^{-1})	**2.4–4.7**	**3.8**	0.46	0.5	1.7
Utilization (%)	**51–59**	**52**	25	33	33
TO_2 (mg O_2 min^{-1} kPa^{-1} kg^{-1})[d]	**0.030**	**0.056**	—	0.00076	0.0038
E_w (%)[d]	**63**	**67**	—	42	37
E_b (%)[d]	89	74	73	100	—
P_aO_2 (kPa)[e]	10–12	9.3	10.6	18.3	16.8
P_vO_2 (kPa)[e]	5.2–5.3	4.9	—	4.4	2.1
C_aO_2 (mg dl^{-1})[e]	18	20	16	15	14
C_vO_2 (mg dl^{-1})[e]	12	13	9.5	10	1.9
O_2 delivery (mg O_2 min^{-1} kg^{-1})[e]	**21**	**26**	5.6	2.7	7.4
Ventilation perfusion capacity-rate ratio[d]	0.73	1.1	0.55	1.2–2.0	2.2
Hematocrit (%)[e]	27–35	34–38	29	23	27
Hemoglobin concentration (g dl^{-1})[e]	11–12	13	11	6.4	—
Mean cell hemoglobin concentration (g dl^{-1})	31–44	34–38	38	29	—
Gill surface area (cm^2/kg body mass)	**14,380**	**18,400**	—	≈2000	—
Gill blood–water barrier thickness (μm)	**0.533**	**0.596**	—	6.37	—
Blood volume (ml kg^{-1})	31–54	≈50	58	41–52	—

Cardiac output (ml min^{-1} kg^{-1})[e]	**115**	**132**	35	18	53
Heart rate (beats min^{-1})[e]	62–97	79	96	38	51
Stroke volume (ml kg^{-1})[e]	**1.1**	**1.3**	0.35	0.46	1.03
Mean VA blood pressure (kPa)[e]	**10.8–11.8**	**11.6**	5.8	5.2	8.3
Mean DA blood pressure (kPa)[e]	**6.7–6.8**	**5.3**	1.4	4.1–4.5	—
Gill resistance (kPa ml^{-1} min^{-1} kg^{-1})[e]	0.035–0.044	0.047	0.12	0.039–0.061	—
Systemic resistance (kPa ml^{-1} min^{-1} kg^{-1})[e]	0.058–0.059	0.040	0.040	0.23–0.25	—
Total resistance (kPa ml^{-1} min^{-1} kg^{-1})[e]	**0.094–0.10**	**0.088**	0.17	0.29	0.16
Ventricle mass (% body mass)	**0.29**	**0.38**	0.11	0.08–0.13	0.08–0.13
Cardiac power output (mW kg^{-1} body mass)[f]	**21–23**	**26**	3.4	1.6	7.7
Cardiac power output (mW g^{-1} ventricle mass)	**7.1–7.8**	**6.7**	3.1	1.2–1.9	5.6–9.1

Note: Those parameters that we consider clearly enhanced in skipjack and yellowfin tunas are printed in bold.

[a]Data for yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas compiled from Muir and Hughes (1969); Bushnell (1988); Bushnell *et al.* (1990); Jones *et al.* (1986, 1990, 1993); Brill and Bushnell (1991); Bushnell and Brill (1991, 1992); Dewar (1993); Brill and Jones (1994); Dewar and Graham (1994); Korsmeyer *et al.* (1997a,b); Brill *et al.* (1998); Lowe *et al.* (1998); and R. Brill, T. Lowe, and K. Cousins (unpublished data).

[b]Data for yellowtail (*Seriola* spp.) compiled from Yamamoto *et al.* (1981); Itazawa *et al.* (1983); and Ishimatsu *et al.* (1990, 1997).

[c]Data for rainbow trout (*Oncorhynchus mykiss*) compiled from Holeton and Randall (1967); Randall *et al.* (1967); Stevens and Randall (1967); Kiceniuk and Jones (1977); Gngerich *et al.* (1987, 1990); Tetens and Christensen (1987); Palzenberger and Pohola (1992); and Farrell and Jones (1992).

[d]Data for skipjack and yellowfin tunas from spinally blocked (i.e. nonswimming) fish.

[e]Data for skipjack tuna from spinally blocked (i.e., nonswimming) fish.

[f]Cardiac power output is calculated as cardiac output multiplied by mean ventral aortic (VA) pressure.

[g]As a result of the extra hydrodynamic drag induced by the catheters and wires required to measure heart rate, blood pressures, etc., maximum sustainable swimming speeds were below those of uninstrumented fish (~2 body lengths s^{-1}).

similar temperature (Table I). Clearly, the cardiovascular and respiratory systems of skipjack and yellowfin tunas must supply oxygen and metabolic substrates to the tissues at exceptional rates, and hence we often use the term "high-energy-demand fishes" as a general descriptor (e.g., Brill and Bushnell, 1991; Brill *et al.*, 1998). Interestingly, the metabolic rates of resting yellowtail and rainbow trout are comparable when corrected for temperature (assuming a Q_{10} of 2; Boehlert, 1978; Moffitt and Crawshaw, 1983).

A. Oxygen Transport from Water to Tissues

The rate of oxygen movement across the gill respiratory epithelium is directly proportional to functional surface area and inversely proportional to the thickness of the diffusion barrier (Wood and Perry, 1985). Tunas have gill surface areas approximately seven to nine times larger, and gill blood–water barrier thicknesses approximately an order of magnitude less, than those of rainbow trout (Table I). These anatomical adaptations appear to be required for the relatively elevated rate of gas transfer across tuna gills occurring even at routine activity levels (Hughes, 1984; Perry, 1992). Skipjack and yellowfin tunas have ventilation volumes approximately 5 to 10 times those of other teleosts (Table I), yet because of their large thin gills, both are able to extract approximately 50% of the oxygen from the ventilatory water stream (utilization, Table I). The effectiveness of oxygen transfer from water (E_w) is the ratio of the actual rate of removal of oxygen from the ventilatory water stream to the theoretically maximum possible rate. E_w in tunas (>60%) is substantially higher than that in trout (33%), indicating that a larger fraction of the ventilatory water stream is in effective contact with the gas exchange surface in tunas.

Oxygen diffusing across the lamella is carried away from the gill by red blood cells. Contrary to much of the speculation in the early literature, the oxygen content of arterial blood (C_aO_2) in tunas is not unusual (Bushnell and Brill, 1992; Korsmeyer *et al.*, 1997b). This is because the elevated hematocrit and hemoglobin levels reported originally were based on blood samples taken from highly stressed, recently boated fish (Klawe *et al.*, 1963). Neither are seen in catheterized tunas that are fully recovered from handling and surgery (Bushnell and Brill, 1992; Brill and Jones, 1994; Lowe *et al.*, 1998). High rates of oxygen delivery to the tissues (O_2 delivery, Table I) at routine activity levels are, therefore, sustained by high cardiac output (approximately three times those of other teleosts). This, in turn, is made possible by large stroke volumes, rather than elevated heart rates (when comparisons are made at equivalent body temperatures). It should be noted, however, that the cardiac output of rainbow trout has been shown to be linearly related to acclimation temperature, with a Q_{10} of $\approx$4 (Barron *et al.*, 1987). When extrapolated to an acclimation temperature of 25°C (skipjack and yellowfin tunas' normal water temperature), the cardiac output of rainbow trout (80–90 ml

$min^{-1}\ kg^{-1}$) could theoretically approach those of tunas. This cardiac output, however, more likely reflects maximum, rather than routine, outputs in trout (Farrell *et al.*, 1996).

Elevated cardiac outputs increase the transfer factors (TO_2; i.e., the rate of oxygen transfer from the water to the blood per unit O_2 partial pressure difference between the water and venous blood) of skipjack and yellowfin tunas to approximately two orders of magnitude above those measured in other fishes (Bushnell and Brill, 1992). High cardiac outputs also ensure that ventilation and perfusion capacities in tunas are well matched, since the rate at which oxygen is delivered to the gills by the ventilatory water stream will be equivalent to the rate oxygen can be transported away by the blood. To express this more formally, the ventilation perfusion capacity–rate ratio (i.e., the ratio of the oxygen content of the inhalant water multiplied by the ventilation volume to the oxygen content of arterial blood multiplied by the cardiac output) is close to the theoretically ideal value of one (Piiper and Scheid, 1984).

B. High Blood Pressures and the Maintenance of Tissue Fluid Balance

Skipjack and yellowfin tunas' high cardiac outputs also generate unusually high (for a teleost) arterial blood pressures (Table I). Although blood pressure is the product of cardiac output and total peripheral resistance, the elevated dorsal and ventral aortic blood pressures of tunas are solely a result of the former, as the total vascular resistance is actually below that of other fishes (Bushnell *et al.*, 1992). The tunas' large gills and vascular countercurrent heat exchangers both contain numerous parallel blood flow channels (Kishinouye, 1923; Muir and Hughes, 1969; Muir, 1970; Muir and Brown, 1971; Stevens *et al.*, 1974; Graham and Diener, 1978) and have large total cross-sectional areas. Therefore, they do not add significantly to total vascular resistance.

The high arterial blood pressures may, however, have consequences with respect to tissue fluid balance. Although our understanding of this aspect of tuna cardiovascular function remains incomplete, recent progress has been made. Plasma colloid osmotic pressure (COP) works in opposition to capillary hydrostatic pressure to maintain tissue fluid balance. At the arterial end of the capillary, where capillary hydrostatic pressure exceeds COP, fluid filtration results and there is transfer of extracellular fluid from the plasma to interstitium. At the venous end of the capillary, when COP exceeds capillary hydrostatic pressure, fluid reabsorption occurs (Friedman, 1976). The net fluid flux during the passage of blood through capillaries, therefore, depends on arterial blood pressure (the primary determinant of capillary hydrostatic pressure) and permeability of the capillaries to blood proteins and their concentration (the primary contributors to plasma COP). Hargens *et al.* (1974) found protein concentrations in cod (*Gadus morhua*) and

flounder (*Pleuronectes platessa*) plasma, interstitial, and peritoneal fluid to be essentially identical and concluded that capillary permeability of fishes was high, and therefore, effective COP across the capillaries was low. In general, it appears that if capillary hydrostatic pressure is low, a high COP may not be needed to ensure adequate fluid reabsorption.

Following this chain of logic, high blood pressure (i.e., capillary hydrostatic pressure) in tunas could result in elevated rates of net fluid transfer from the capillaries to the interstitium. In mammals, fluid not reabsorbed by the capillaries is drained from the interstitial space by the lymph system. Fish do not have a lymph system anatomically identical to that of higher vertebrates, but rather a "secondary circulatory system" which appears to play a similar role (Steffensen and Lomholt, 1992; Olson, 1996). The vessels of the secondary circulation arise from the walls of various arteries as arteriolar-sized vessels that coalesce into larger trunks. Dewar *et al.* (1994) described vessels of a secondary circulation in the central vascular heat exchangers of skipjack tuna similar to those seen in other teleosts (e.g., Chopin *et al.*, 1998). There is no evidence, however, that the secondary circulation is more developed in tunas than in other teleosts (Brill *et al.*, 1998), as would be expected if tunas had significantly high rates of net fluid transfer out of the capillaries.

We have attempted to measure capillary pressures in skipjack and yellowfin tunas (along with coinvestigators D. R. Jones and J. F. Steffensen), but have not yet succeeded. Our recent work on the relative capillary permeability and protein concentrations of plasma and various interstitial fluids of yellowfin tuna, cod, and rainbow trout, however, suggests tuna capillaries have low protein permeability (Jones *et al.*, 2000). Figure 1 shows that capillaries of yellowfin tuna are far less permeable to large molecules (e.g., 40-kDa dextran) than those of the other two species. In yellowfin tuna, plasma COP is thus maintained during passage through the capillaries, and net fluid transfer out of the vascular system is not excessive. As might be expected, Figure 1 also suggests that capillary permeability is inversely related to dorsal aorta blood pressure ($\approx$7, $\approx$5, and $\approx$4 kPa in yellowfin tuna, rainbow trout, and cod, respectively), and presumably capillary pressure. Bluefish (*Pomatomus saltatrix*) have mean ventral aortic blood pressures approaching those of tunas ($\approx$10 kPa; Ogilvy *et al.*, 1988), and a study of their capillary permeability could be useful to test the hypothesis that the capillary permeability and blood pressures are indeed inversely related.

III. MAXIMAL RATES OF CARDIOVASCULAR FUNCTION IN TUNAS

To take advantage of the resources of the pelagic environment, skipjack, yellowfin, and bigeye tunas are highly aggregated and highly mobile. Although

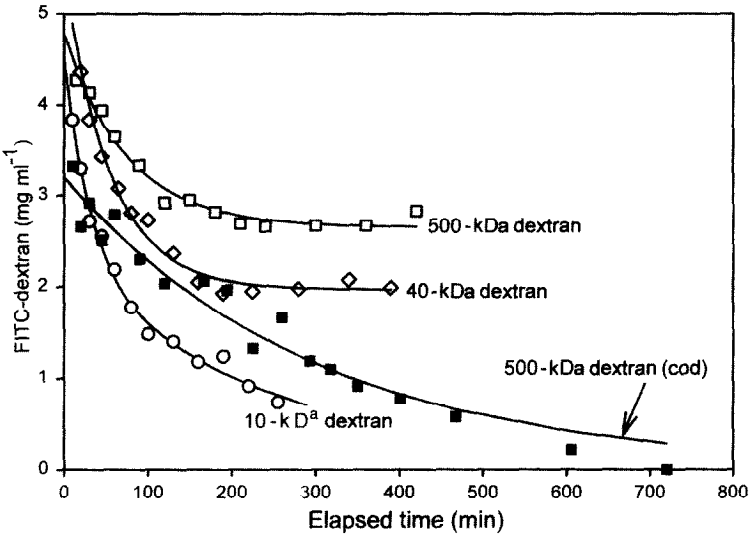


Fig. 1. Plasma concentration of fluorescein-isothiocyanate-labeled dextran (FITC-dextran) following a bolus injection of the marker into the ventral aorta. The initial rapid drop is most likely a result of the marker equilibrating within the circulatory system. In yellowfin tuna (open symbols), dextran molecules as small as 40 kilo-Daltons (kDa) remain within the vascular compartment, as demonstrated by constant plasma concentrations after 200 min. In cod (filled symbols), even with molecules as large as 500 kDa, plasma concentration continues to decline, indicating a leak from the vascular compartment, most likely into the interstitial space. Plasma decay curves for rainbow trout (data not shown) injected with 500-kDa dextran were similar to those for cod. The data clearly show the capillaries of yellowfin tuna are less permeable than are those of other teleosts, a characteristic which is important for maintaining tissue fluid balance in the face of elevated blood pressures (data from Jones *et al.*, 2000).

the former makes them an exploitable, economically important resource (Sharp, 1978), it is the latter that has shaped much of the thinking about tuna biology. As a result, there has been a general focus on what initially appeared to be their exceptional locomotor abilities (e.g., Walters, 1962; Carey, 1973; Graham, 1975; Magnuson, 1978; Stevens and Carey, 1981; Sharp, 1983; Bushnell and Holland, 1989; Block, 1991). While they are certainly capable of high burst and cruising speeds, there is little evidence that maximum burst and maximum sustainable swimming speeds of skipjack and yellowfin tunas are significantly above those of other active teleosts living at similar temperatures (Brill, 1996). Rather, as first recognized by Bushnell and Brill (1991) and later reinforced by Korsmeyer *et al.* (1996a), the cardiovascular systems of skipjack and yellowfin tunas appear capable of delivering oxygen and metabolic substrates at exceptionally high rates to meet multiple metabolic demands simultaneously (e.g., rapid lactate metabolism,

rapid digestion, and high growth rates) rather than to allow exceptionally high sustained swimming speeds. For example, based on data presented in Guppy *et al.* (1979), Arthur *et al.* (1992), Dewar (1993), Brill (1994), and Bushnell and Jones (1994), during recovery from exhaustive exercise, skipjack tuna swimming at about 1.5 body lengths s^{-1} would have to reach a total metabolic rate of 2276 mg O_2 kg^{-1} h^{-1} to metabolize white muscle lactate over the observed 2-h time course. This prediction closely approaches the highest metabolic rate thus far measured in tunas—≈2500 mg O_2 kg^{-1} h^{-1} in skipjack tuna immediately after capture at sea and which were presumably recovering from exhaustive exercise (Gooding *et al.*, 1981). In contrast, the highest metabolic rate of which other teleosts of approximately equivalent body mass are capable is approximately 1000 mg O_2 kg^{-1} h^{-1} (Brett, 1972).

A. How Skipjack and Yellowfin Tunas Achieve High Maximum Metabolic Rates

Although routine rates of cardiovascular function (Table I) have been quantified in skipjack and yellowfin tunas with at least some degree of certainty, maximal rates have not. Rather, they are based on a limited number of observations (Korsmeyer, 1996; Korsmeyer *et al.*, 1997a,b) and extrapolations (Brill and Bushnell, 1991; Brill, 1994; Bushnell and Jones, 1994; Korsmeyer *et al.*, 1996a,b). To date, Graham *et al.* (1989), Dewar and Graham (1994), and Korsmeyer *et al.* (1997a,b) are the only investigators to have successfully measured changes in metabolic rate and cardiovascular function in tunas swimming at various velocities in a water tunnel. Unfortunately, the range of speeds at which the instrumented fish would swim was limited (≈0.8–2.4 body lengths s^{-1}), and it remains unclear if metabolic demand and associated rates of cardiovascular function were indeed maximal and representative of rates in free-swimming tunas in the wild. Regardless, the experimental observations and mathematical extrapolations are now beginning to form a reasonably consistent picture of tunas' physiological capabilities.

The relationship between metabolic rate, cardiac output, and blood oxygen-carrying capacity can be described by three equations,

$$\dot{V}O_2 = Q \cdot ([O_2]_{\text{arterial blood}} - [O_2]_{\text{venous blood}}), \quad (1)$$

$$Q = HR \cdot SV, \quad (2)$$

$$[O_2]_{max} = MCHC \cdot HCT \cdot [O_{2\ Hb}], \quad (3)$$

where:

$\dot{V}O_2$ is metabolic rate;
Q, cardiac output;

$[O_2]_{arterial\ blood}$, oxygen content of the arterial blood;
$[O_2]_{venous\ blood}$, oxygen content of the venous blood;
HR, heart rate;
SV, stroke volume;
$[O_2]_{max}$, maximum oxygen-carrying capacity of the arterial blood;
MCHC, mean red blood cell hemoglobin concentration;
HCT, hematocrit; and
$[O_{2\ Hb}]$, oxygen-carrying capacity per unit mass of hemoglobin.

Although tunas could increase any or all of the variables in Equations (1)–(3) to reach their maximum metabolic rates, they appear to attain high rates of oxygen and substrate delivery as a result of (a) three anatomical adaptations (large gill surface area, thin blood–water barrier in the gills, and enlarged ventricle mass; Table I), (b) the ability to achieve high arterial–venous content difference (Equations 1 and 3), and (c) the ability to reach exceptionally high maximum cardiac outputs through high heart rates and large stroke volumes (Equation 2; Brill and Bushnell, 1991; Bushnell and Jones, 1994; Farrell, 1991, 1996).

The cardiac outputs required to meet tunas' estimated maximum metabolic rates, and how these are achieved, are relevant to several other aspects of tuna biology and therefore we examine these subjects in some detail. Unfortunately, the maximum cardiac output of any tuna species has never been measured. By combining available data from a number of sources, however, we can use Equation (1) to model an upper, physiologically reasonable limit that can be tested in future experiments. As is clear from Equation (1), in addition to knowing maximal $\dot{V}O_2$, an estimate of the maximal $([O_2]_{arterial\ blood} - [O_2]_{venous\ blood})$ is also required. While this too has never been measured, previous studies give us some insight into tuna blood oxygen-carrying capacity as well as oxygen extraction potential at the tissues.

The maximal $([O_2]_{arterial\ blood} - [O_2]_{venous\ blood})$ will be determined in part by $[O_2]_{max}$, which, in turn, is determined by hematocrit (Equation 3). The normal hematocrits of skipjack and yellowfin tuna range from 27 to 34% (Bushnell and Brill, 1992; Korsmeyer *et al.*, 1997b). An hematocrit of ≈50% is seen during recovery from exhaustive exercise (White *et al.*, 1988) due to red cell ejection from the spleen, red cell swelling, loss of plasma volume, or (more likely) a combination of all three (Yamamoto and Itazawa, 1989). A HCT of 50% and a MCHC of 370 g liter^{-1} (Korsmeyer *et al.*, 1997b; Lowe *et al.*, 1998) would result in a blood hemoglobin concentration of 185 g liter^{-1}, a value within the range of those measured in tunas recently boated at sea (141–207 g liter^{-1}; Klawe *et al.*, 1963). At 25°C, the oxygen-carrying capacity of hemoglobin is 1.25 ml O_2 g^{-1} (Ganong, 1973), resulting in a maximum predicted $[O_2]_{arterial\ blood}$ of 231 ml O_2 liter^{-1}. It is unlikely that tuna could produce a $[O_2]_{venous\ blood}$ of zero. The lowest values for skipjack and yellowfin tuna reported in the literature are ≈70–80 ml O_2 liter^{-1}—

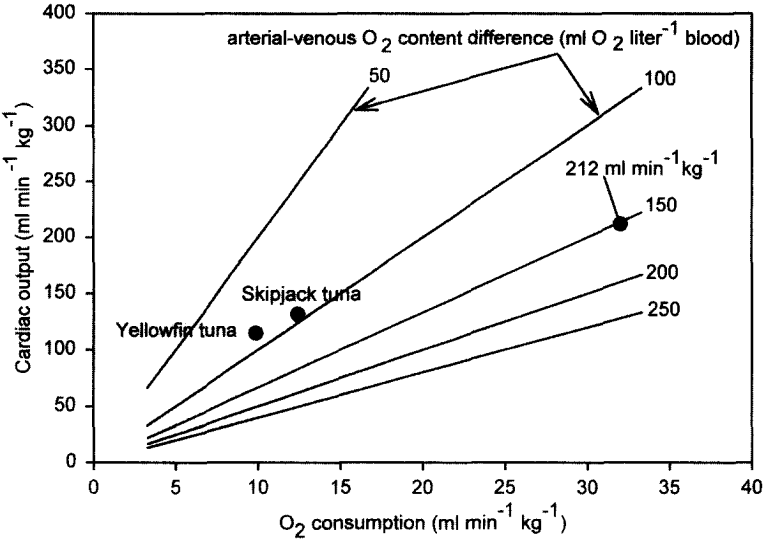


Fig. 2. Predicted cardiac outputs required to reach various rates of oxygen consumption in skipjack and yellowfin tuna as a function of the arterial–venous (A-V) blood oxygen content difference. At a reasonable maximum A-V blood oxygen content difference (150 ml O_2 liter^{-1} blood), estimated maximum metabolic rates could be achieved by doubling routine cardiac output. Figure is adapted from Bushnell and Jones (1994); reprinted with permission.

values recorded during severe hypoxia (Bushnell and Brill, 1992) and recovery from anesthesia (Korsmeyer *et al.*, 1997b). Based on these estimates, maximum ($[O_2]_{\text{arterial blood}} - [O_2]_{\text{venous blood}}$) in tunas is most likely about 151–161 ml O_2 liter^{-1}.

By applying these data to Figure 2, in order to generate their maximum documented metabolic rate (32 ml O_2 min^{-1} at ≈25°C; Gooding *et al.*, 1981), skipjack tuna would have to attain a cardiac output of 212 ml min^{-1} kg^{-1}, or an increase of approximately 1.6 times their routine cardiac output (Table I). The predicted increase in cardiac output is less than that measured by Kiceniuk and Jones (1977) in freshwater rainbow trout going from rest to maximum sustainable swimming speed (3× increase), but it is similar to that observed by Thorarensen *et al.*, (1996) in seawater-acclimated rainbow trout (1.8× increase).

The limited amount of data collected *in vivo* supports the model's predictions. For instance, the maximum increases in cardiac output and heart rate in yellowfin tuna observed by Korsmeyer *et al.* (1997a) during exercise was approximately about 1.3 and 1.5 times above those seen in slowly swimming fish. Moreover, the maximum increase in heart rate observed in swimming yellowfin tuna matches that seen in nonswimming fish whose vagal control of heart rate has been blocked by injection of atropine (Keen *et al.*, 1995). Since stroke volume appears to be

fixed in skipjack and yellowfin tunas (discussed in detail in next section), cardiac output mirrors changes in heart rate. Taken together, both the model and data suggest that the ratio of maximal to routine cardiac output in tunas is similar to that of other active teleosts. It should be noted, however, that the predicted maximum cardiac output of skipjack tuna (>200 ml min^{-1} kg^{-1} at 25°C) is still substantially higher (≈3 to 4 times) than those of other fishes (Table I).

B. Elevated Hematocrit, Oxygen Transport, and Blood Viscosity

The positive impact of high maximum hematocrit (≈50% in tunas) on maximum blood oxygen-carrying capacity can potentially be offset by the resulting increase in blood viscosity which raises blood pressure, a primary determinant of cardiac work and maximum cardiac output. As a result, increases in blood viscosity could reduce maximum cardiac output and actually impair blood flow and oxygen delivery (Egginton, 1998). In tuna (as well as all vertebrates studied to date), blood viscosity increases exponentially with hematocrit (Figure 3A), while maximum blood oxygen content increases linearly (Fletcher and Hedrich, 1987; Wells and Baldwin, 1990). The relationship between the two is reflected in the blood oxygen transport capacity, which is the quotient of maximum blood oxygen capacity divided by viscosity. When plotted against hematocrit (Figure 3B), blood oxygen transport capacity is highly nonlinear, with maximal blood oxygen transport capacity representing the theoretically "optimal" hematocrit.

Interestingly, the increase in viscosity with hematocrit in yellowfin tuna blood (Figure 3A) is clearly less than that in blood from other fishes (Brill and Jones, 1994). As a result, increases in hematocrit above ≈30% have little effect on blood oxygen transport capacity (Figure 3B). The hematocrit likely occurring in yellowfin tuna during periods of maximal metabolic rates (≈50%) would still, therefore, be considered "optimal." Mention should be made, however, that contrary to the predicted detrimental effects of high viscosity, *in vivo* studies of rainbow trout show that increases in hematocrit from ≈30% to over 50% had no effect on maximum rates of oxygen uptake. The expected decrease in maximum cardiac output with increase in hematocrit did not occur, and increased blood viscosity actually had a slight positive effect on maximum sustainable swimming speeds (Gallaugher *et al.*, 1995). It is, therefore, an open question if the concept of "optimal hematocrit" is applicable *in vivo*, and the reason(s) for the unusual behavior of yellowfin tuna blood remains unexplained.

IV. TUNA CARDIAC FUNCTION

Tuna cardiac anatomy and physiology have been the subject of comprehensive reviews (Brill and Bushnell, 1991; Farrell, 1991, 1996; Bushnell *et al.*, 1992;

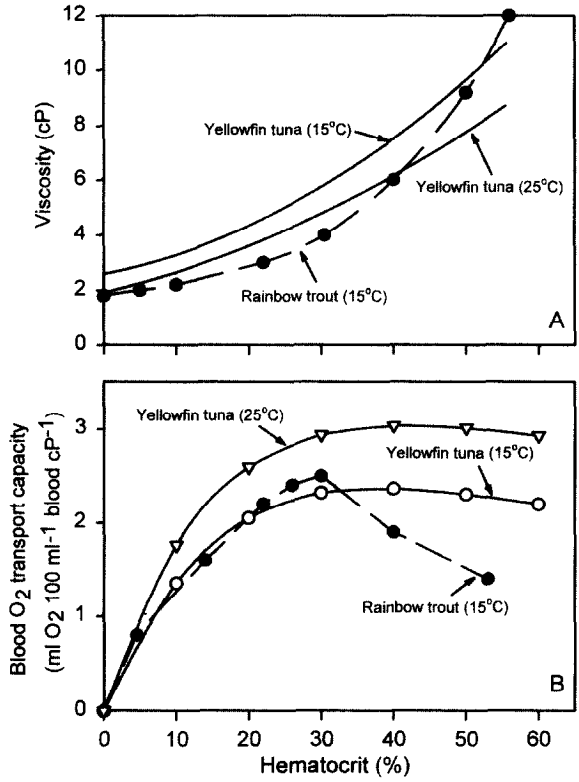


Fig. 3. (A) Effects of hematocrit on viscosity of yellowfin tuna blood at 15 and 25°C, and equivalent data for rainbow trout (at 15°C). (The shear rate in both instances was 90 s^{-1}.) (B) Effects of hematocrit on blood oxygen transport capacity in yellowfin tuna at 15 and 25°C and rainbow trout (at 15°C). The increase in blood viscosity with increasing hematocrit is less steep in yellowfin tuna blood than in rainbow trout blood. As a result, in yellowfin tuna, increases in hematocrit above 30% have almost no influence on blood oxygen transport capacity. Figure redrawn from data present in Wells and Weber (1991) and Brill and Jones (1994).

Bushnell and Jones, 1994; Agnisola and Tota, 1994; Moyes, 1996; Tibbits, 1996). We have, however, chosen to examine this subject in some detail because cardiac function is central to understanding of cardiovascular physiology and perhaps even the physiological ecology of tunas (Brill *et al.*, 1999).

As described in Sanchez-Quintana and Hurle (1987) and Farrell and Jones (1992), tuna ventricles are large (Table I), thick walled, and pyramidal, characteristics required to produce high ventricular pressures. The inner compact muscle

fibers surrounding the vertices have a coil-like arrangement. The more superficial compact layer muscle fibers form loops around the ventricle, but with a transverse fiber orientation on the caudal face. This fiber morphology is thought to provide the necessary mechanical advantage for rapid ejection of stroke volume, since the ventricle can contract simultaneously in the longitudinal and transverse directions.

According to the classification scheme developed by Tota *et al.* (1983) and Tota (1983, 1989), tunas have type IV hearts typical of high-energy-demand teleosts—hearts with more than 30% compact myocardium and coronary arteries in the compact and spongy myocardium. The fraction of ventricular mass composed of compact myocardium is, however, clearly elevated only in bigeye tuna (>70%) compared to other fishes (≈15–50%; Brill and Bushnell, 1991). The tuna myocardium is very well vascularized, with highly branched arterioles and venules, and extensive capillarization which extends even into the spongy myocardium (Tota, 1983). Not surprisingly, tuna hearts may be more dependent on coronary circulation than other teleosts (Farrell *et al.*, 1992). Whereas in other active fishes an intact coronary circulation is important only during strenuous exercise or severe hypoxia (Farrell and Steffensen, 1987), *in vitro* experiments have shown that skipjack tuna hearts depend on an intact coronary circulation for normal function (Farrell *et al.*, 1992). This presumably is also the case *in vivo*. As expected, the estimated coronary blood flow rate (ml blood g^{-1} ventricle min^{-1}) is approximately twice as great in skipjack tuna hearts as in those of rainbow trout (Farrell, 1996). No work has been conducted on factors controlling coronary blood flow in tunas.

A. Stroke Volume

The routine stroke volume of skipjack and yellowfin tuna hearts (≈1 ml kg^{-1}) approaches the maximum stroke volume of other fishes (Table I). More importantly, however, both *in vivo* and *in vitro* data suggest that tuna hearts normally function at close to their maximum stroke volumes. In other words, unlike hearts of other teleosts, tuna ventricles appear to have a very limited ability to increase stroke volume. This was first noted during experiments to quantify hypoxia tolerance. Bushnell *et al.* (1990) and Bushnell and Brill (1992) found hypoxic bradycardia occurring in skipjack and yellowfin tunas to be accompanied by nearly equivalent reductions in cardiac output. In other fishes (e.g., cod and lingcod *Ophiodon elongatus*) hypoxic bradycardia is accompanied by compensatory increases in stroke volume sufficient to maintain cardiac output (Farrell, 1982; Fritsche and Nilsson, 1989). Yellowfin and skipjack tunas' limited ability to increase stroke volume is also observed in fish subjected to acute reductions in ambient temperature (from 25 to ≈18°C; Korsmeyer *et al.*, 1997a; R. Brill, K. Cousins, and T. Lowe, unpublished observations). Under these conditions too, decreases in

heart rate result in nearly parallel reductions in cardiac output because of only modest (≈15%) increases in stroke volume. In contrast, when porgy (*Pagrus major*) are subjected to a similar acute reduction in ambient temperature, the fall in heart rate is accompanied by an increase in stroke volume sufficient to maintain cardiac output (Azuma *et al.*, 1998). This compensatory response to acute temperature changes is not universal, however. Although hypoxic bradycardia in lingcod results in increased stroke volume, bradycardia accompanying acute reductions in ambient temperatures does not, and cardiac output decreases in almost direct proportion to heart rate (Stevens *et al.*, 1972).

The limited ability of tunas to elevate stroke volume *in vivo* is also apparent during forced activity. While elevated activity levels in yellowfin tuna result in increases in cardiac output (Korsmeyer *et al.*, 1997a,b), as they do in other teleosts (Farrell and Jones, 1992), increases in cardiac output are accomplished solely by increases in heart rate with no measurable change in stroke volume (Figure 4A). In contrast, rainbow trout increase cardiac output during exercise by doubling stroke volume and only fractionally changing heart rate (Figure 4B). In general, in teleosts other than tunas, ≈40–60% of the increase in cardiac output during exercise is due to a rise in stroke volume, with the remainder due to elevations in heart rate (Farrell, 1991).

The tuna heart's limited ability to increase stroke volume can also be demonstrated *in vitro*. In fish hearts, as in mammalian hearts, there is a positive correlation between end diastolic ventricular volume (preload) and stroke volume (Farrell, 1984). The phenomenon is intrinsic to the myocardium (Harwood *et al.*, 1999) and is referred to as the "Frank–Starling mechanism," after its discoverers. *In vitro,* end diastolic ventricular volume is altered by changing ventricular filling pressure, and the resultant relationship of ventricular filling pressure to stroke volume is referred to as a "Starling curve." Examples from several teleosts are shown in Figure 5. Note that the Starling curve for skipjack tuna ventricles has the same shape as those for other fishes, but only at subambient filling pressures. Unfortunately, with skipjack tuna hearts *in vitro,* raising filling pressures above ambient results in ventricular failure, possibly due to the inability to adequately perfuse the coronary circulation in these circumstances (Farrell *et al.*, 1992). Lai *et al.* (1987) have reported subambient pericardial pressures in albacore, although these were subsequently not observed in yellowfin tuna (Jones *et al.*, 1993). Regardless of these inconsistencies, it is important to appreciate the fact that over the range of input pressures needed to produce near-routine stroke volume (≈1 ml kg^{-1}), stroke volume appears almost insensitive to filling pressure (i.e., to end diastolic ventricular volume) in skipjack tuna hearts. We surmise that, in general, both skipjack and yellowfin tuna hearts normally function on the upper flat portion of their Starling curve where stroke volume is insensitive to preload filling pressure or filling time (i.e., cardiac interval). Other teleost hearts function on the "steeper" parts of their Starling curves (Figure 5).

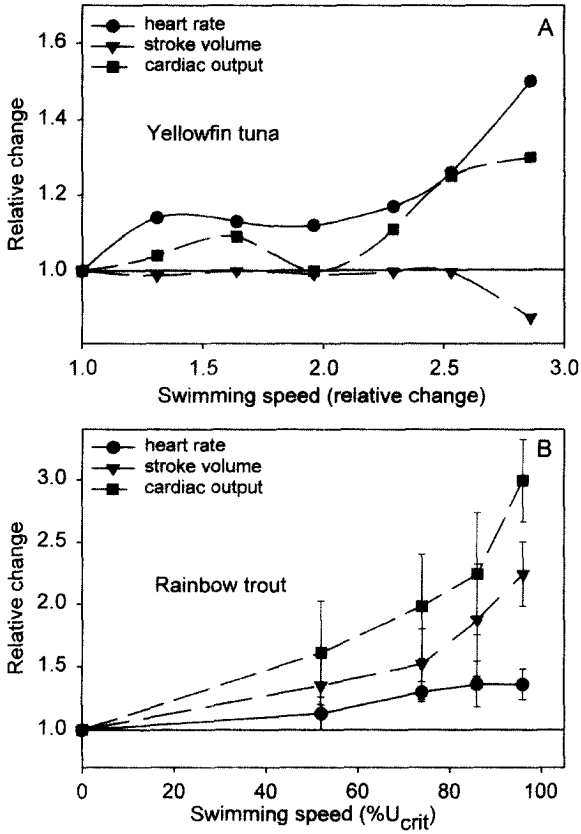


Fig. 4. Effect of swimming speed on the relative change in cardiac output, heart rate, and stoke volume in a yellowfin tuna (A) and rainbow trout (B). Note that in yellowfin tuna increases in cardiac output are accomplished by increases in heart rate alone, whereas in rainbow trout both heart rate and stoke volume increase with increases in swimming speed. Data for yellowfin tuna are from Korsmeyer *et al.* (1997a), and those for rainbow trout from Kiceniuk and Jones (1977).

B. Maximal Heart Rates in Tunas and Other Teleosts

Because maximum heart rates in fishes are temperature labile, comparisons of maximum heart rates in tunas to those of other species are somewhat difficult. In general, the maximum heart rate of teleosts has been reported to be 120 beats min^{-1} (Farrell, 1991), even at temperatures as high as 35°C (Gehrke and Fielder, 1988). The maximum heart rates of skipjack tuna ($\approx$200 beats min^{-1}; Kanwisher *et al.*, 1974; Keen *et al.*, 1995) have, therefore, been considered to be the highest

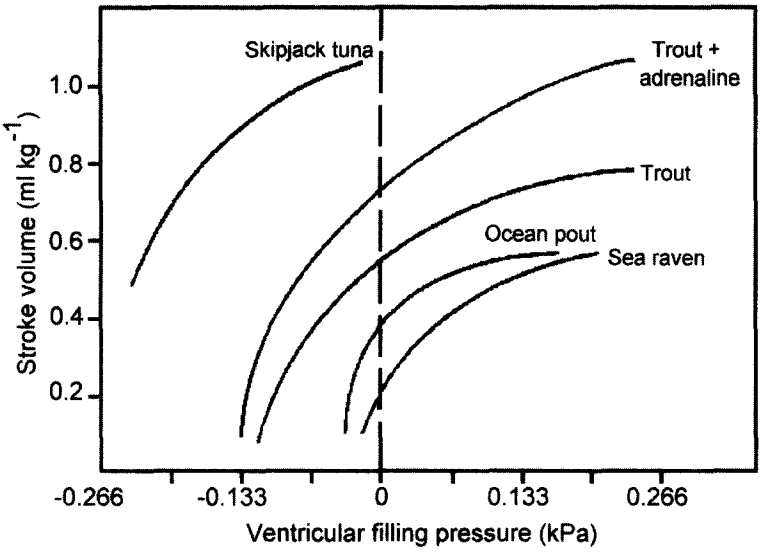


Fig. 5. Effects of filling pressure on cardiac stroke volume (i.e., Starling curves) of isolated perfused hearts from several species of teleosts. With the exception of tunas, teleost hearts normally operate over the steep portion of their Starling curves. Tuna hearts, however, normally operate at nearly maximum stroke volumes (i.e., at positive ventricular filling pressures where the Starling curves are relatively flat). Figure is from Farrell (1991); reprinted with permission.

among teleosts. This may no longer strictly be the case since a tropical tide pool goby, *Bathygobius soporator,* has now been reported to have maximum heart rates of 225 beats min^{-1} (at 35°C; Rantin *et al.,* 1998).

In addition to having heart rates that are generally higher than most other teleosts, there are also clear differences in the neural control of heart rate in tunas. The intrinsic activity of the teleost heart's pacemaker cells can be influenced by several factors, including temperature, adrenergic stimulation, and cholinergic stimulation (Farrell and Jones, 1992). Tunas are unusual among teleosts in that cholinergic inhibitory tone (via the vagus nerve) is the predominate controller of heart rate. Blocking vagal activity with atropine causes a 58% (75 to 120 beats min^{-1}) and 143% (79 to 193 beats min^{-1}) increase in heart rate in yellowfin and skipjack tunas, respectively (Keen *et al.,* 1995). In other teleosts (excluding the antarctic icefishes, *Pagothenia* spp.), the same treatment generally results in less than a 30% increase in heart rate (Farrell and Jones, 1992). Adrenergic blocking agents in tunas have minimal influence on resting heart rates (Keen *et al.,* 1995), and clearly less than that seen in other teleosts (Farrell and Jones, 1992). The

predominant vagal control of heart rate in tunas begs the question, "What (if any) is the role of sympathetic, adrenergic stimulation on routine or maximum heart rates of tunas?" Injection of a sympathomimetic, epinephrine, is vasoactive and can increase ventral aortic blood pressure (to >25 kPa), heart rate, and cardiac output in skipjack and yellowfin tunas, although none of these effects have been quantitatively investigated (Bushnell and Brill, unpublished observations). To our knowledge the sympathetic system's influence on blood flow distribution to various vascular beds in tunas remains unstudied.

In spite of a fixed stroke volume, the skipjack tuna's high heart rate can easily accommodate its documented maximum metabolic demand. As shown in Figure 6, assuming no increase in stroke volume, maximum heart rate (≈200 beats min^{-1}) is more than sufficient to account for the cardiac output (212 ml min^{-1} kg^{-1}; Figure 2) accompanying the estimated maximum metabolic rate. Also as shown in Figure 6, this is in direct contrast to observed changes with exercise occurring in trout, where increased cardiac output is accomplished by increases in both stroke volume and heart rate.

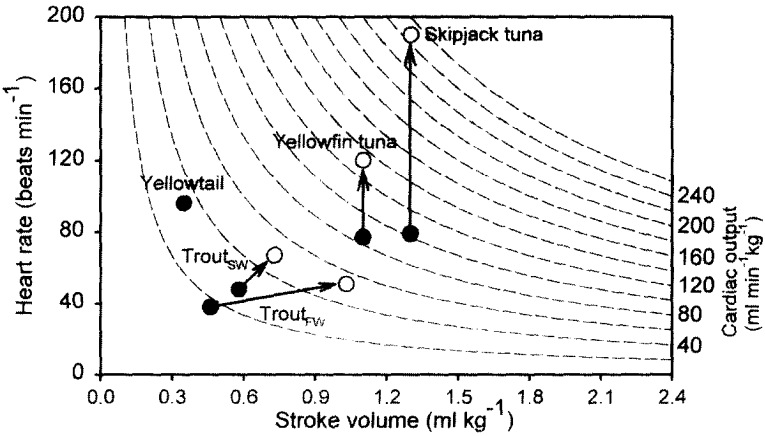


Fig. 6. Relationship of heart rate, stroke volume, and cardiac output in freshwater (Trout$_{FW}$)- and seawater (Trout$_{SW}$)-adapted rainbow trout, yellowtail, yellowfin tuna, and skipjack tuna. Filled circles show minimal values, and open circles maximal values. In fish other than tunas, increases in cardiac output accompanying increases in activity are accomplished primarily by increases in stoke volume (Trout$_{FW}$) or approximately equal increases in stoke volume and heart rate (Trout$_{SW}$). In contrast, the predicted cardiac output (>200 ml min^{-1} kg^{-1}) required to meet skipjack tuna's observed maximum metabolic rates can be met by maximum observed heart rates, with no increase in stroke volume. Data for freshwater-adapted trout are from Kiceniuk and Jones (1977), seawater-adapted trout from Thorarensen *et al.* (1996), yellowtail from Ishimatsu *et al.* (1997), and skipjack and yellowfin tuna from Bushnell and Brill (1992).

C. Sarcoplasmic Reticulum

A key factor influencing rates of ventricular contraction and relaxation is the cycling of calcium ions (Ca^{2+}) into and out of the cardiac muscle cells (myocytes). In mammalian myocardium, Ca^{2+} influx is initiated through sarcolemmal voltage-gated Ca^{2+} channels which serve to trigger a larger Ca^{2+} release from the sarcoplasmic reticulum (SR). This process is referred to as "Ca^{2+}-induced Ca^{2+} release" (Fabiato, 1983). Since SR-Ca^{2+} stores are intracellular, diffusion distances are relatively short, and the time course of Ca^{2+} release and resequestering can be rapid. When myocyte volumes are small relative to their surface areas, however, a well-developed SR may not be necessary. As a consequence of a high ratio of sarcolemmal (i.e., cell surface) area to myocyte volume, extracellular Ca^{2+} alone can be sufficient to initiate myofibrillar contraction (Tibbits *et al.,* 1992b). Anatomical studies tend to support this idea. Fish myocyte diameters range from approximately 2 to 10 μm, compared with 10 to 25 μm in mammals (Santer, 1985; Satchell, 1991), and the SR in teleost hearts is generally considered to be not well developed (Yamamoto, 1967; Santer, 1974; Breisch *et al.,* 1983; Satchell, 1991). Myocyte diameters in albacore, the only tuna species from which we currently have data, range from 2.5 to 6 μm and therefore are not unique in this regard (Breisch *et al.,* 1983).

Although there are some species-specific differences in the extent of SR development among the teleosts, it is unclear if SR volume is related to general activity level as might be expected. For example, electron micrograph studies by Yamamoto (1967) and Santer (1974) indicate that the SR is less extensive in the ventricle of goldfish (*Carassius auratus*) than in that of the more active rainbow trout. In contrast, Breisch *et al.* (1983) stated that in albacore, "the sarcoplasmic reticulum, although present, is very poorly developed." More recently, preliminary studies (K. L. Cousins, unpublished observations) suggest that the yellowfin tuna ventricle (Figure 7) has a SR at least as well developed as that of rainbow trout or carp (*Cyprinus carpio*), but all are clearly less developed than the rat's (Santer, 1974; Chugun *et al.,* 1999). Electron microscopy quantitatively comparing the development of the SR in skipjack tuna, yellowfin tuna, the ectothermic scombrids, and several other fish (including those of different activity levels) seems clearly warranted.

While anatomical studies can be used to establish the distribution and development of SR, accompanying physiological studies on the importance of SR-derived Ca^{2+} in initiating contraction are required. The latter involve the use of ryanodine, which, at high concentrations, locks the SR Ca^{2+}-gated Ca^{2+}-release channel in a subconducting state, making the SR ineffective with respect to Ca^{2+} release or sequestering (Rousseau *et al.,* 1987). Decreases in peak tension developed by isolated atrial or ventricular strips exposed to ryanodine can be used to assess the relative contribution of extracellular (sarcolemmal)- and SR-derived

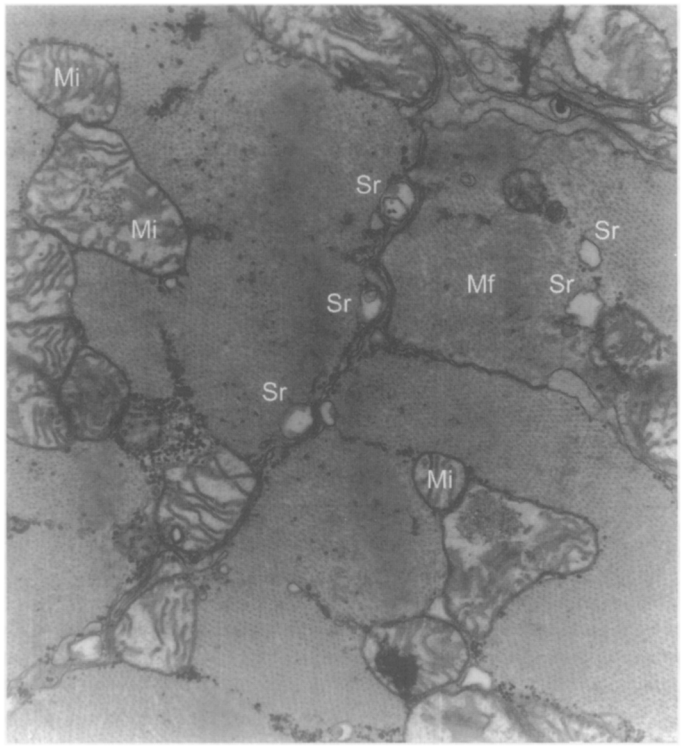


Fig. 7. Transmission electron micrograph of yellowfin tuna ventricle (compact myocardium) with myofibers cut in transverse section (original magnification 15,900×). Although sarcoplasmic reticulum (SR) is clearly evident, pending a careful quantitative study, it remains an open question if the SR is more developed in tuna myocardium than in the hearts of other active teleosts (K. Cousins, unpublished observations). Mi indicates mitochondria, Mf myofilaments.

Ca^{2+}. These types of studies have shown that SR-Ca^{2+} release in teleosts myocardium is negligible except in nonphysiological circumstances such as supraphysiological temperatures or subphysiological pacing frequencies (Tibbits *et al.*, 1992b; Keen *et al.*, 1994; Gesser, 1996; Shiels and Farrell, 1997). In contrast, Keen *et al.* (1992) and Shiels *et al.* (1999) demonstrated that in skipjack and yellowfin tuna atrial strips, SR-Ca^{2+} release contributes ≈30% and ≈60% (respectively) of activator Ca^{2+} under normal operating temperatures (15–25°C) and pacing frequencies (up to 2.5 Hz).

Interpretation of these findings is somewhat obfuscated by the apparent temperature sensitivity of the ryanodine response. Hove-Madsen (1992) found that the ryanodine sensitivity of rainbow trout myocardium was negligible at 15°C,

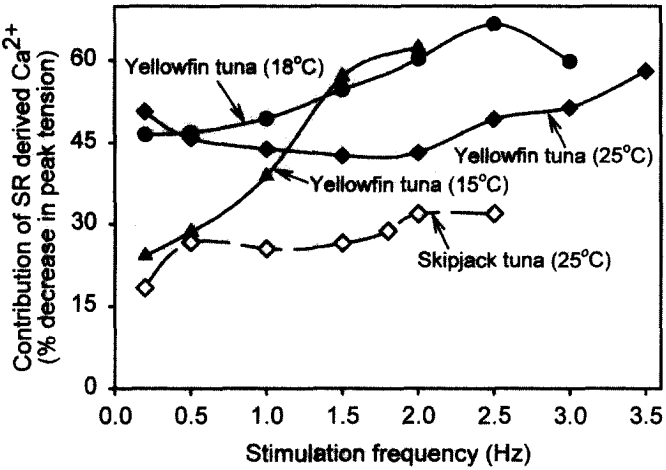


Fig. 8. Contribution of SR-Ca^{2+} release to force development in isolated myocardial strips from yellowfin tuna at 15, 18, and 25°C (from Shiels *et al.*, 1999) and from skipjack tuna at 25°C (from Keen *et al.*, 1992). Data are presented as the fractional reductions in force resulting from exposure to ryanodine. Error bars have been omitted for clarity. Note that contribution of SR-derived Ca^{2+} is less in skipjack tuna than in yellowfin tuna myocardial strips. The contribution of SR-derived Ca^{2+} is greater at lower temperatures in yellowfin tuna, which is in direct contrast to results from other teleosts. In rainbow trout myocardium, the importance of SR-derived Ca^{2+} is greater at higher temperatures.

while at 25°C, SR-Ca^{2+} release accounted for 40% of activator Ca^{2+}. The lack of ryanodine sensitivity at 15°C most likely results from locking the SR-Ca^{2+} release channel in the open position (Tibbits, 1996). In contrast, the temperature sensitivity of ryanodine response in tuna hearts appears to be exactly the opposite, as Shiels *et al.* (1999) found yellowfin tuna atrial strips to have a greater ryanodine sensitivity at 15°C than at 25°C (Figure 8). The implied fundamental differences between SR-Ca^{2+} release channels in tuna and those in other teleosts are obviously another avenue that needs to be explored, perhaps at the molecular level (e.g., Tibbits *et al.*, 1992a).

Temperature effects not withstanding, there appear to be substantial differences in the importance of SR-Ca^{2+} release just within tuna species. Shiels *et al.* (1999) found a greater importance of SR-Ca^{2+} release in atrial strips from yellowfin tuna (≈60%; Figure 8) than in those from skipjack tuna (≈30%) studied by Keen *et al.* (1995). Given the differences in maximum heart rates of yellowfin (120–140 beats min^{-1}) and skipjack (≈200 beats min^{-1}) tunas, the opposite relative SR-Ca^{2+} contributions would be predicted as higher maximum heart rates should be more dependent on SR-Ca^{2+} release and resequestering (Farrell, 1996). It is possible that these findings may result from different techniques; Shiels *et al.*

(1999) used 1 nM adrenaline in their tissue bathing medium whereas Keen *et al.* (1995) did not. If in tuna myocardium adrenaline is required to enhance extracellular Ca^{2+} release enough so as to fully stimulate SR-Ca^{2+} release, then its absence may cause the contribution SR-Ca^{2+} release to be underestimated. Freund (1999), however, also found that increasing extracellular Ca^{2+} has no effect on force of contraction of ventricular strips from yellowfin tuna at high pacing frequencies, as it does in atrial strips from skipjack tuna (Keen *et al.*, 1992) and cod (Driedzic and Gesser, 1985). These data also indicate a larger dependence on SR-Ca^{2+} release in yellowfin tuna than in skipjack tuna myocardium. A dependence on SR-Ca^{2+} may, however, not be strictly necessary for high maximum heart rates. SR-Ca^{2+} release and resequestering do not appear to be important in the tide pool goby (*Bathygobius soporator*) even though maximum heart rates in this species exceed 225 beats min^{-1}. The functioning of ventricular strips isolated from this species are nearly insensitive to ryanodine (Rantin *et al.*, 1998).

A second method of evaluating SR-Ca^{2+} release is postrest potentiation, a technique that monitors the increase in twitch tension of isolated myocardial strips following a single 20-s "rest" period between twitches (Driedzic and Gesser, 1988). Freund (1999) has recently used this procedure to demonstrate that ventricular strips of Pacific mackerel (*Scomber japonicus*) are equally dependent on SR-Ca^{2+} release as those of yellowfin tuna. These data imply that some of the unusual characteristics of SR-Ca^{2+} release channels may have developed early in scombrid evolution, as they are appear to be present in even primitive members of the family *Scombridae*. Shiels and Farrell (2000), however, also using ventricular trabeculae from Pacific mackerel, found ryanodine induced significantly smaller (20%) reductions in peak tension than those observed in similarly treated tuna myocardium. To the best of our knowledge, there are no data on routine or maximal cardiac function in mackerel, so these observations are yet to be put in an *in vivo* physiological context. Moreover, mammalian atrial muscle shows a greater ryanodine sensitivity than ventricular muscle (Bers, 1991). If the same occurs in teleosts, conclusions based on the various studies could be compromised, as some investigators have used atrial muscle and others ventricular muscle. A comparative study of ryanodine sensitivity of tunas, ectothermic scombrids, and other teleosts using the same methodology throughout is clearly needed.

D. Mechanical and Electrical Coupling of Myocytes

The high maximum heart rates of skipjack and yellowfin tunas require that all links in the chain of excitation–contraction coupling be enhanced (Satchell, 1991). For example, the short Ca^{2+} diffusion distances from the SR to the myofibrils require the depolarization triggering Ca^{2+} release from the pacemaker tissue to spread around the ventricle with equal rapidity. Small myocyte diameters, however, can result in high electrical resistance and slow conduction velocities (Farrell

and Jones, 1992). Since the rate of increase in ventricular pressure (dP/dt) in yellowfin tuna hearts *in vivo* is rapid (up to 716 kPa s^{-1}) and in the mammalian range (Jones *et al.*, 1993), we conclude that there is indeed near-synchronous contraction of the myocytes. This, in turn, implies the presence of fast conducting fibers analogous to the bundle of His and Purkinje fibers of mammalian hearts. Although such fibers have not been described histologically in any fish species, based on the pathways over which depolarization is known to spread across teleost ventricles, Satchell (1991) concluded that fast conducting fibers "certainly occur." We would not be surprised to find that specialized fast-conducting fibers are especially well developed in tuna cardiac muscle, and encourage investigation in this area.

In addition to rapid electrical conduction from the pacemaker, cells of the cardiac tissue require both mechanical and electrical coupling. Mechanical coupling of myocytes is accomplished via intercalated disks consisting of fasciae adherentes (where actin filaments of adjacent myocytes insert onto a dense fibrous mat) separated by desmosomes (regions of the cell surface specialized for maintaining cell-to-cell cohesion; Bloom and Fawcett, 1975). Intercalated disks are present in the hearts of all vertebrates and are clearly present in albacore (Breisch *et al.*, 1983) and yellowfin tuna (Figure 9). Electrical coupling between myocytes

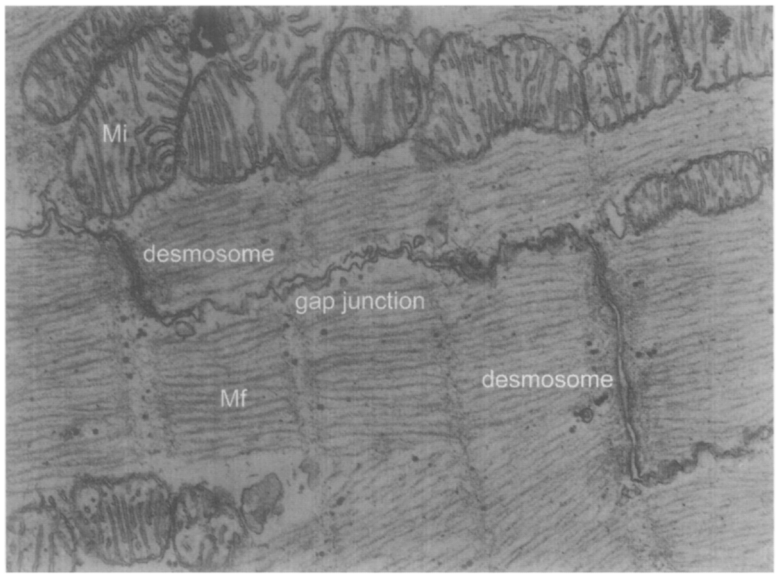


Fig. 9. Transmission electron micrograph of yellowfin tuna ventricle (compact myocardium) with myofibers cut in longitudinal section (original magnification 12,500×). Desmosomes, intercalated disk, and gap junction are shown. Note that, as in mammalian myocardium, gap junctions appear to be part of the intercalated disk. Mi indicates mitochondria, Mf myofilaments (K. Cousins, unpublished observations).

occurs through gap junctions (also referred to as nexus junctions) which have been reported to occur on the lateral walls of adjacent myocytes in several fish species, including albacore (Shibiata and Yamamoto, 1977; Breisch *et al.*, 1983). As can be seen in Figure 9, gap junctions are also present in the compact myocardium of yellowfin tuna and appear to be part of the intercalated disk, as they are in mammalian hearts (Bloom and Fawcett, 1975; Satchell, 1991). Cobb (1974) has reported that in fishes, gap junctions are not associated with the fasciae adherentes of the intercalated disks, but are only on the lateral wall of the myocytes. The physiological implications of the unusual gap junction distribution in yellowfin tuna await further investigation. As with the SR, a quantitative morphological study of gap junctions and intercalated disks involving several species of tunas, ectothermic scombrids, and other teleosts is clearly needed to discern if the ability of tunas to reach high maximum heart rates or cardiac outputs is correlated with more extensive development of these structures.

E. Biochemical Adaptations of Tuna Hearts for High Power Output

Skipjack and yellowfin tunas' high cardiac outputs and ventral aortic blood pressures result in routine cardiac power outputs (per unit body mass) that are approximately seven times those of other teleosts (Table I). Due to their enlarged ventricles, however, power output per gram ventricular mass is only twice that seen in other fishes (Table I). In other words, tunas' elevated cardiac power outputs are achieved primarily through ventricular hyperplasia (Moyes *et al.*, 1992; Farrell, 1996; Tibbits, 1996).

As expected, the levels of aerobic enzyme activity (citrate synthase and 3-hydroxy-o-acyl-CoA dehydrogenase) per gram ventricle mass are likewise all roughly double in tuna hearts compared with hearts of other teleosts (Driedzic, 1992; Moyes *et al.*, 1992; Driedzic and Gesser, 1994; Dickson, 1995). The exception is carnitine-palmitoyl transferase, an enzyme involved in fatty acid metabolism, whose activity is approximately three to seven times higher (Moyes *et al.*, 1992; Dickson, 1995). Tuna hearts, therefore, appear to rely more on fatty acids to power aerobic metabolism than do other teleost hearts (Moyes, 1996; Weber and Haman, 1996). The advantages of fatty acids over glucose as a fuel source are their higher energy content (i.e., moles of ATP derived per gram of substrate) and their ability to be stored in the tissues at high levels. It is also possible that tuna hearts may use lactate as a fuel source, as mitochondria isolated from skipjack tuna ventricle have a higher capacity for lactate oxidation than other metabolic fuels (Moyes *et al.*, 1992). This finding makes intuitive sense since the highest heart rates and cardiac outputs (i.e., highest rates of cardiac energy demand) are likely to occur in tunas during recovery from exhaustive exercise, when plasma lactate levels are elevated (Arthur *et al.*, 1992).

The use of lactate as a metabolic energy source in the heart is also supported

by microanatomical differences which reflect metabolic zonation of compact and spongy myocardium. In albacore, the volume percentage of mitochondria is higher in the spongy layer (31.9%) than in the outer compact myocardium (21.3%; Breisch *et al.*, 1983). While Basile *et al.* (1976) found mitochondrial volume densities (28–32%) in bluefin tuna (*Thunnus thynnus*) hearts to be similar to those of albacore hearts, they did not find differences in mitochondrial volume density between myocardial layers. They did note, however, that the mitochondria from the spongy myocardium had higher cristae density. These anatomical findings support the biochemical observations that the spongy layer has a substantial capacity to oxidize lactate and incorporate it into lipids for possible use by the compact myocardium (Maresca *et al.*, 1976; Gemelli *et al.*, 1980). This implies the possibility of metabolic interactions between the two myocardial layers

Cardiac mitochondrial ATP production capacity can serve as another estimate of cardiac energy demand. As stated earlier, maximum oxygen consumption in skipjack tunas appears to be met by a doubling of cardiac output (Figure 2). In yellowfin tuna (the only species in which this has been measured), there is only a relatively small (>20%) increase in ventral aortic pressure with increasing activity (Korsmeyer *et al.*, 1997a,b). If the same occurs in skipjack tuna, then maximum cardiac power output (per gram ventricle) would be ≈2 times routine levels, and ≈1.5–2.5 times those of other teleosts (Table I). It is not unreasonable to expect that the increase in power output would have to be generated by increases in mitochondrial (i.e., aerobic) ATP production. Studies by Moyes *et al.* (1992) provide evidence that the metabolic support does indeed exist, as the maximal mitochondrial oxygen consumption of skipjack tuna hearts (7 μM O_2 g^{-1} ventricle min^{-1}) is approximately twice the estimated routine consumption rate (3.3 μM O_2 g^{-1} ventricle min^{-1}). This level of oxygen consumption is also about twice that of mitochondria isolated from carp ventricle (per milligram of mitochondrial protein), when corrected for differences in measurement temperature. These data are thus reasonably consistent.

The high maximum power output of tuna hearts may also be supported by the high levels of myoglobin found in tuna ventricles, although exact mechanisms remain unknown. Giovane *et al.* (1980) reported ventricular myoglobin levels in bluefin tuna to be 6–20 mg g^{-1}, a level whose upper range is several times those of other active teleosts (≈1–6 mg g^{-1}; Driedzic, 1983). Driedzic (1983, 1988) has suggested that high ventricular myoglobin levels serve to maintain contractility during episodes of low ambient oxygen. Stevens (1982), however, found that in fish skeletal muscle, elevated myoglobin levels function to facilitate oxygen diffusion from the capillaries to the mitochondria, rather than as an oxygen store utilized during hypoxia. A third possibility, put forth by Tota (1983), is that myoglobin may function as a temporary oxygen store to offset the effects of the brief periods of ischemia occurring during ventricular contraction when coronary blood flow is likely to be diminished.

F. Ventricular and Arterial Dynamics and Functions of the Bulbus Arteriosus

While most of the foregoing discussion has concentrated on how the cardiorespiratory system of tunas achieves high levels of performance, it also important to note that on a second-to-second basis, cardiovascular function involves highly dynamic processes. In this regard, based on tunas' high maximum heart rate it is possible that the complex hemodynamic relationships seen in birds and mammals could be present in the circulatory system of tunas. High heart rates result in short pressure wavelengths, such that length of the arterial tree becomes a significant proportion of the pressure wavelength (Langille *et al.*, 1983; Jones, 1991). As a result, the transmission time of the pressure pulse through the arteries can span a significant portion of the cardiac cycle. In these circumstances, the arterial tree of tunas would not act as a simple elastic reservoir as it does in other fishes (the so-called "Windkessel model"). Rather it would behave as it does in mammals as a wave transmission system with complex wave propagation effects such as pulse amplification, distortion, and wave reflections. Jones *et al.* (1993), however, found no evidence of wave transmission in yellowfin tuna. Rather, pressure and flow waveforms agreed well with theoretical and mathematical Windkessel models. This interesting finding probably results from the functional properties of the bulbus arteriosus, the highly distensible fourth chamber of the teleost heart. In tunas, as in other teleosts, the bulbus arteriosus is capable of stretching to accept an entire stroke volume and recoiling elastically. It thus smooths blood flow pulsatility and maintains blood flow through the gills during diastole (see Figure 5 in Bushnell *et al.*, 1992), which presumably improves gas exchange (Malte, 1992). In contrast, blood flow in the mammalian proximal aorta is highly pulsatile, and often reverses (i.e., momentarily flows backward into the heart) during diastole.

The extreme extensibility of the bulbus arteriosus of yellowfin tuna and albacore is shown in Figure 10A as quasi-static pressure–volume loops and demonstrates how the bulbus arteriosus in tuna is able to maintain blood flow through the gills during diastole (Jones *et al.*, 1993). The initial portion of the compliance curve is very steep (i.e., the bulbus arteriosus is very "stiff" or not very compliant) and pressures remain high even at volumes as low as 10% of maximum injected volume. *In vivo,* this means that during diastole, when the bulbus arteriosus is recoiling, ventral aortic pressure remains elevated until nearly the entire stroke volume has been ejected. This behavior, in turn, provides the motive force to maintain continuous blood flow through the gills between heartbeats. As is the case with most teleosts (Bushnell *et al.*, 1992), the yellowfin tuna bulbus arteriosus is most compliant (i.e., shows relative small increases in pressure with equal increments of inflation) over the range of routine ventral aortic blood pressures (10.8–11.8 kPa, Table I). The plateau phase of the quasi-static pressure–volume loop, therefore, corresponds to ventral aortic systolic pressure. In albacore, how-

ever, the bulbus arteriosus appears to be most compliant at pressures below ventral aortic blood pressure (10–11 kPa; Lai *et al.*, 1987). This result may be somewhat misleading, as blood pressures in albacore were measured on recently boated fish and may have been elevated due to stress. If the compliance characteristics of the bulbus arteriosus are indeed matched to cardiovascular pressures, we would predict that the ventral aortic pressure of unstressed albacore probably lies in the range of 6–8 kPa. We believe the bulbus arteriosus compliance and ventral blood pressure relationship may provide researchers with an *in vitro* experimental tool that can be used to estimate ventral pressures in species which are not amenable to laboratory manipulations because of their size or availability We therefore also present in Figure 10B a series of pressure–volume loops for the bulbi arteriosi from a number of pelagic fishes whose blood pressures have yet to be measured. The data imply that striped marlin (*Tetrapturus audax*), blue marlin (*Makaira nigricans*), and sailfish (*Istiophorus platypterus*) all have blood pressures in the ventral aorta between those of yellowfin tuna and albacore, whereas those of mahimahi (dolphinfish, *Coryphaena hippurus*) and pomfret (*Taractichthys* spp.) are clearly lower.

The highly specialized bulbus arteriosus of tunas most likely performs another very important function: it increases the efficiency of the circulatory system (i.e., the ratio of external cardiac work to cardiac energy demand). The majority of cardiac energy is used to develop systolic blood pressures in the ventricle (i.e., to develop wall tension; Jones, 1991). Therefore, anything that reduces peak systolic pressures, or the time over which they must be generated (i.e., the time–tension index), will reduce cardiac energy demand and thus improve efficiency. Because of the high heart rates, cardiac outputs, and ventral aortic pressures in tunas, adaptations which reduce the myocardial time-tension index should be expected. Mathematical modeling studies have shown that a large, central (rather than peripheral) compliance in the circulatory system is of hemodynamic value as it raises diastolic pressure while effectively lowering peak systole pressures and, thus, the time–tension index of the heart (Campbell *et al.*, 1981). For tunas, which put exceptional demands on their cardiovascular systems (Table I), the energy savings due to the presence of a highly compliant bulbus arteriosus are most likely substantial.

There is, however, a potential problem with having a compliant structure capable of large changes in volume immediately outside the heart. It would remove the ability to regulate blood pressure (beat-to-beat) in an effective manner because any increases in peripheral resistance (or cardiac output), which would normally cause blood pressure to rise, would be damped by the plateau phase of the bulbus arteriosus pressure–volume curve (Figure 10). The solution to the problem lies in having a structure with variable and regulated mechanical properties. This is accomplished by having smooth muscle in the walls of the bulbus arteriosus that is capable of contracting in certain circumstances (Farrell, 1979; Watson and Cobb,

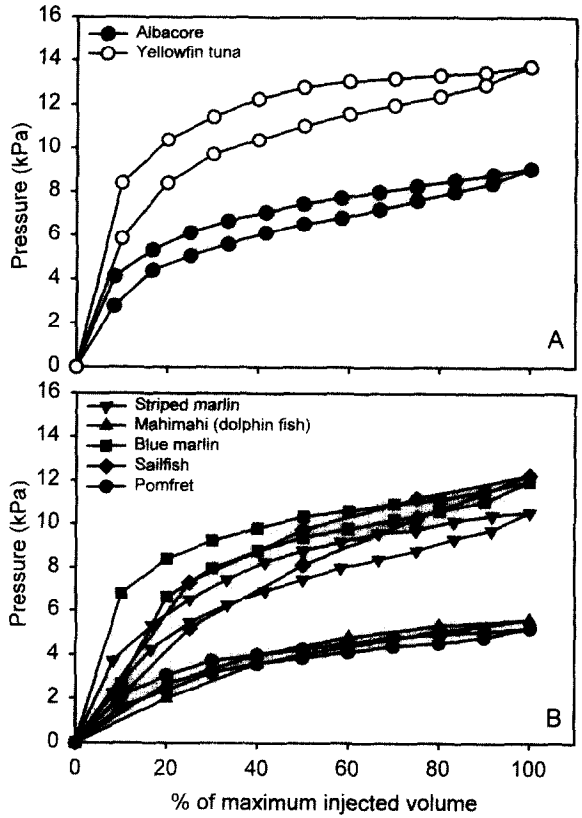


Fig. 10. (A) Pressure–volume loops recorded in isolated bulbi arteriosi taken from yellowfin tuna and albacore. The curves were generated by stepwise injection of measured volumes of saline into isolated sealed vessels, followed by stepwise removal. The pressure–volume curves created during inflation are below those created during deflation. (B) Pressure–volume loops recorded in isolated bulbi arteriosi taken from various pelagic fishes. Based on the tuna data, it is possible that the plateau region of curves shows the normal ventral aortic blood pressures of these fishes. Data from M. Braun, University of British Columbia; reprinted with permission.

1979). Not surprisingly, the bulbus arteriosus of tunas is highly vascular, is well enervated, and possesses significant amounts of smooth muscle (Braun *et al.*, 2000). Presumably, contracting or relaxing this smooth muscle allows subtle manipulation of wall properties and the short-term blood pressure changes necessary to maintain proper function of the cardiovascular system. The regulation of the compliance of the tuna bulbus arteriosus is unstudied, but clearly deserves further investigation.

V. CARDIAC FUNCTION AND THE PHYSIOLOGICAL ECOLOGY OF TUNAS— A POSSIBLE CONNECTION

In the following section we consider how the cardiorespiratory physiology of tunas might impact their behavior and distribution in the open ocean. The ability to apply what we have learned in the laboratory to what we believe is happening in the field is possible because of ultrasonic telemetry and new archival tags (i.e., electronic data recording devices carried by the fish). These allow detailed records to be obtained of the horizontal and vertical movements of tunas and other pelagic fishes in the open sea.

The vertical movements of large adult (≈50 kg) and even juvenile (≈4–6 kg) bigeye tuna are much deeper, and into much colder water, than those of yellowfin tuna (Figure 11). Adult bigeye tuna routinely reach maximum depths of 450–500 m during the day while juvenile fish are commonly found at 350 m (Holland *et al.,* 1990b; Boggs, 1992; R. Brill, M. Musyl, D. Curran, and C. Boggs, unpublished observations). The water temperatures at these depths are ≈5–7°C and ≈15°C, respectively. Ultrasonic tracking studies of large (>25 kg) bigeye tuna near Tahiti show that they follow the daily vertical migrations of the small nektonic organisms (crustaceans, cephalopods, and fishes) of the deep sound-scattering layer even as they descend into deeper and colder water (Josse *et al.,* 1998; Dagorn *et al.,* 2000). Bigeye tuna thus have the ability to exploit a prey source which, during daylight hours, apparently is not normally available to yellowfin tuna (Grundin, 1989; Roger, 1994; Marchal and Lebourges, 1996).

While there are clear instances where the depth distribution of tunas is set by the depth distribution of their prey (e.g., Block *et al.,* 1997; Marcinek *et al.,* 2001), the dichotomous depth distributions of yellowfin and bigeye tunas in exactly the same area near the main Hawaiian Islands (Figure 11) implies that one or more abiotic factors are having an impact on their vertical movements. It is possible that changes in oxygen levels in the water column may be limiting their distribution, but near the main Hawaiian Islands significant decreases in ambient oxygen do not occur in the portion of the water column occupied by yellowfin and juvenile bigeye tunas (Brill *et al.,* 1999). We suggest, as first noted by Brill *et al.* (1993, 1999), that a major limiting factor is the relative change in water temperature occurring between the surface layer and the waters below the thermocline. We believe this to be the case because of the documented effect of acute reductions in ambient temperature on cardiac function. Since tunas' hearts are near the ventral body wall and outside the area warmed by tunas' vascular countercurrent heat exchangers, the temperature of cardiac muscle will almost immediately reflect changes in ambient temperature. This occurs regardless of body size or regional endothermy (Brill *et al.,* 1994).

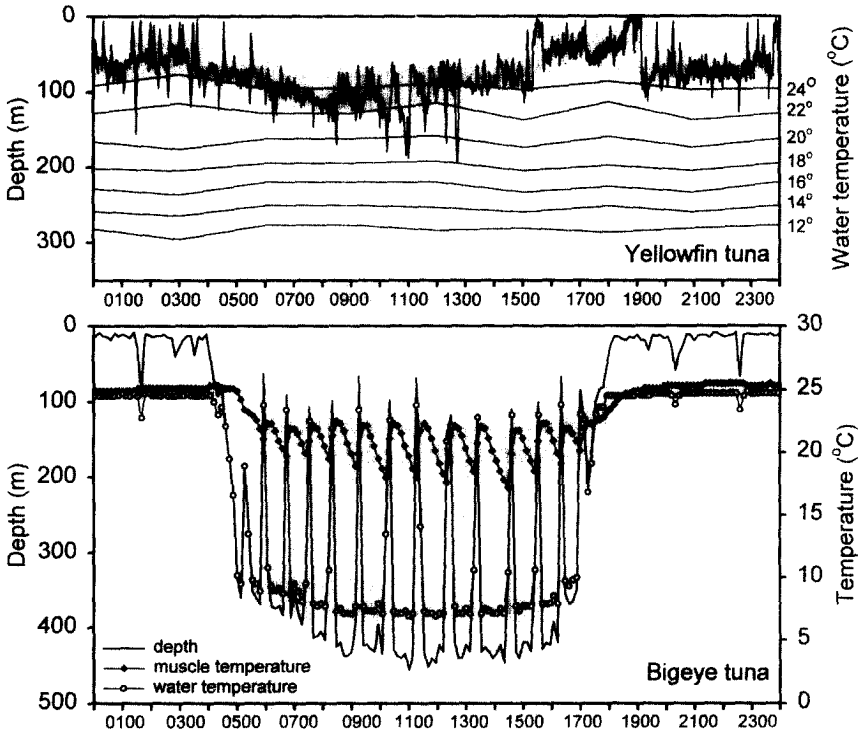


Fig. 11. Representative 24-h records (midnight to midnight) of the vertical movements of adult yellowfin tuna (64 kg estimated body mass) and bigeye tuna (50 kg estimated body mass) in areas near the main Hawaiian Islands. The former was carrying an ultrasonic depth-sensitive transmitter, and swimming depth data were recorded approximately every 10 s onboard a ship that was following the fish. Temperature changes with depth were measured by lowering a temperature probe through the water column and are plotted as 1°C isotherms. (Data replotted from Brill *et al.*, 1999.) The bigeye tuna was implanted with an archival (i.e., electronic data recording) tag that recorded swimming depth, water temperature, and deep red muscle temperature every 8.5 min (R. Brill, M. Musyl, D. Curran, and C. Boggs, unpublished observations). Note that the yellowfin tuna did not descend into water more than ≈8°C below surface layer temperature (≈25°C). In contrast, the adult bigeye tuna repeatedly descended to water as cold as ≈7°C during the day (≈0500–1800 h) and thus repeatedly subjected its heart to ≈18°C temperature changes.

As noted earlier, acute reductions in ambient temperature from 25 to 15°C result in immediate and parallel decreases in heart rate and cardiac output (Q_{10} of ≈2) in both yellowfin and skipjack tunas (Korsmeyer *et al.*, 1997a; R. Brill, K. Cousins, and T. Lowe, unpublished observations). Moreover, these do not appear to be neurally mediated effects, as the decline in heart rate with reductions in

ambient temperature is not counteracted by injection of atropine, a vagolytic drug (Brill, Cousins, and Lowe, unpublished observations). These studies imply, at low ambient temperatures, that skipjack and yellowfin tunas have little or no ability to increase cardiac output. Although they would be able to meet oxygen delivery requirements at low swimming speeds, it seems unlikely that they would be able to increase cardiac output enough to accommodate the doubling (or more) required during high-speed swimming, recovery from exhaustive exercise, and so on. It is interesting to note that the apparent reduction in scope for activity results from two of the facets that make tuna unique: a countercurrent heat exchange system that will maintain metabolism of tissues at higher rates despite the colder ambient temperature, and a heart that operates at maximal stroke volume. In others words, since tuna hearts function on the upper (flat) end of their Starling curves (Figure 5) and heart rate declines immediately with decreases in ambient temperature, then maximal cardiac output declines in direct proportion to ambient temperature. Unfortunately, thanks to the heat exchange system, metabolic demand will not.

The next obvious question is how are bigeye tuna, and possibly other large pelagic species such as bluefin tuna (*Thunnus thynnus;* Lutcavage *et al.,* 2000; Brill *et al.,* 2000) and swordfish (*Xiphias gladius;* Carey, 1990), apparently able to maintain cardiac function in the face of rapid ambient temperature change, and thus achieve their extensive vertical mobility and apparent ability to exploit food resources below the thermocline? There are several possible answers. Heart rates may be less affected by temperature, or like other teleosts, they may be able compensate for reductions in heart rate by increasing stroke volume. In the only *in vivo* study of bigeye tuna physiology, fish exposed to hypoxia responded with a bradycardia that was unaccompanied by increases in stroke volume, and cardiac output fell with heart rate (Bushnell *et al.,* 1990). It should be noted, however, that both Freund (1999) and Shiels *et al.* (1999) found that acute temperature reductions increase Ca^{2+} release from the SR in isolated myocardial strips from yellowfin tuna. The Ca^{2+} sensitivity of isolated myofilaments from catfish (*Pterygoplichthys* spp.) is, however, temperature independent (Meadows *et al.,* 1998). If the same is true in tuna hearts, increased SR-Ca^{2+} release could step up cardiac contractility *in vivo* and potentially offset the decrease in cardiac output resulting from reduced heart rates. Isolated hearts from other teleosts (e.g., pickerel, *Esox niger*) can maintain power output in spite of acute reductions in temperature from 15 to 5°C (Bailey *et al.,* 1991). As stated, however, *in vivo* data suggest that any temperature-induced increases in contractility occurring in yellowfin and skipjack tunas are ineffective in maintaining cardiac output when these fish are subjected to acute temperature changes. Clearly, the influence of environmental temperature changes on cardiac function, both *in vivo* and *in vitro,* in a range of tuna species is a subject that warrants further study.

VI. SUMMARY AND CONCLUSIONS

While significant gaps in our understanding of cardiovascular function in tunas remain, available data, and the extrapolations constructed from them, are now becoming consistent. For example, maximum measured heart rates, stroke volumes, and reasonable arterial–venous oxygen content differences appear sufficient to explain the (admittedly limited) data on maximum metabolic rates.

Several important anatomical adaptations allow tunas to achieve their exceptional rates of oxygen extraction from the ventilatory water stream and delivery to the tissues. Tunas have gill surface areas approximately an order of magnitude larger, and a blood–water barrier thickness up to an order of magnitude less, than those of other teleosts. Tunas also have exceptionally large hearts. As a result, even during periods of routine energy demand, high cardiac outputs are achieved by large stroke volumes. To reach the cardiac outputs necessary to achieve their exceptional maximum metabolic rates, tunas increase heart rate almost exclusively, whereas other teleosts increase stroke volume almost exclusively or stroke volume and heart rate about equally. The hearts of skipjack and yellowfin tunas appear to rely more on sarcoplasmic Ca^{2+} release and resequestering during routine functioning than the myocardium of other fishes, and probably on well-developed specialized electrical conducting pathways as well.

For reasons that are not yet fully understood, tuna hearts normally function on the flat upper limb of their Startling curve (i.e., they have a more limited ability to increase stroke volume than do hearts of other teleosts). This characteristic may, in turn, limit the vertical mobility of some tuna species (e.g., skipjack and yellowfin tunas). As water temperature decreases with depth, decreases in heart rate are necessarily accompanied by decreases in cardiac output. Some tuna species (e.g., bigeye and bluefin tuna) appear to have evolved additional (e.g., Lowe *et al.*, 2000), but as yet mostly unidentified, physiological abilities that allow them to expand their vertical range and thus exploit food resources in ways not available to other tuna species. Due to the paucity of data gathered from members of the family *Scombridae,* a careful comparative study on the physiological/biochemical adaptations of hearts from various tuna and ectothermic scombrids will be fruitful from both an evolutionary and a physiological perspective.

ACKNOWLEDGMENTS

The preparation of this manuscript was funded by National Marine Fisheries Service (Honolulu Laboratory, Southwest Fisheries Science Center) and Cooperative Agreements NA37RJ0199 and NA67RJ0154 from the National Oceanic and Atmospheric Administration with the Joint Institute for

Marine and Atmospheric Research, University of Hawaii. The opinions expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. We gratefully thank Barbara Block, Kathy Cousins, Laurent Dagorn, Heidi Dewar, Tony Farrell, Ellen Freund, David Jones, Dave Marcinek, Holly Shiels, John Steffensen, and Yonat Swimmer for allowing us access to unpublished data, reviewing drafts of this manuscript, and providing important ideas and insights. We especially acknowledge Marvin Braun for his help with the section on the tuna bulbus arteriosus. Any errors of omission or commission are, however, solely ours. This chapter is fondly dedicated to all the colleagues we have had the pleasure and privilege of studying tunas with over the years—but especially to all those old friends who make us laugh.

REFERENCES

Agnisola, C., and Tota, B. (1994). Structure and function of the fish cardiac ventricle: Flexibility and limitations. *Cardioscience* **5,** 145–153.

Arthur, P. G., West, T. G., Brill, R. W., Shulte, P. M., and Hochachka, P. W. (1992). Recovery metabolism in skipjack tuna (*Katsuwonus pelamis*) white muscle; rapid and parallel changes of lactate and phosphocreatine after exercise. *Can. J. Zool.* **70,** 1230–1239.

Azuma, T., Chikushi, Y., and Itazawa, Y. (1998). Effects of acute drop in ambient temperature on respiration and blood circulation of porgy. *Fish. Sci.* **64,** 270–275.

Bailey, J., Septon, D., and Driedzic, W. R. (1991). Impact of an acute temperature change on performance and metabolism of pickerel (*Esox niger*) and eel (*Anguilla rostrata*) hearts. *Physiol. Zool.* **64,** 697–716.

Barron, M. G., Tarr, B. D., and Hayon, W. L. (1987). Temperature-dependence of cardiac output and regional blood flow in rainbow trout, *Salmo gairdneri* Richardson. *J. Fish. Biol.* **31,** 735–744.

Basile, C., Goldspink, G., Modigh, M., and Tota, B. (1976). Morphological and biochemical characterization of the inner and outer ventricular myocardial layers of adult tuna fish (*Thunnus thynnus* L.). *Comp. Biochem. Physiol.* **54B,** 279–283.

Bers, D. M. (1991). "Excitation—Contraction Coupling and Cardiac Contractile Force." Kluwer Scientific, Dordrecht.

Block, B. A. (1991). Endothermy in fish: Thermogenesis, ecology and evolution. *In* "Biochemistry and Molecular Biology of Fishes" (Hochachka, P. W., and Mommsen, T. P., Eds.), Vol. 1. Elsevier, Amsterdam.

Block, B. A., Keen, J. E., Castillo, B., Dewar, H., Freund, E. V., Marcinek, D. J., Brill, R. W., and Farwell, C. (1997). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Mar. Biol.* **130,** 119–132.

Bloom, W., and Fawcett, D. W. (1975). "A Textbook of Histology." Saunders, Philadelphia.

Boehlert, G. W. (1978). Changes in the oxygen consumption of prejuvenile rockfish, *Sebastes diploproa,* prior to migration from the surface to deep water. *Physiol. Zool.* **51,** 56–76.

Boggs, C. H. (1992). Depth, capture time, and hooked longevity of longline-caught pelagic fish: Timing the bites of fish with chips. *Fish. Bull. U.S.* **90,** 642–658.

Braun, M. H., Jones, D. R., Gosline, J. M., and Brill, R. W. (2000). Functional morphology of the bulbous arteriosus. Manuscript.

Breisch, E. A., White, F., Jones, M. H., and Laurs, R. M. (1983). Ultrastructural morphometry of the myocardium of *Thunnus alalunga. Cell Tissue Res.* **233,** 427–438.

Brett, J. R. (1972). The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. *Respir. Physiol.* **14,** 151–170.

Brill, R. W. (1987). On the standard metabolic rate of tropical tunas, including the effect of body size and acute temperature change. *Fish. Bull.* **85,** 25–35.

Brill, R. W. (1994). A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fish. Oceanogr.* **3,** 204–216.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. *Comp. Biochem. Physiol.* **113A,** 3–15.

Brill, R. W. (1999). The Kewalo Research Facility—On the forefront for more than forty years, p. 43. NOAA Technical Memorandum 281. NMFS, Honolulu, Hawaii.

Brill, R. W., and Bushnell, R. W. (1991). Metabolic and cardiac scope of high energy demand teleosts, the tunas. *Can. J. Zool.* **69,** 2002–2009.

Brill, R. W., and Jones, D. R. (1994). The influence of hematocrit, temperature, and shear rate on the viscosity of blood from a high-energy-demand teleost, the yellowfin tuna *Thunnus albacares*. *J. Exp. Biol.* **189,** 199–212.

Brill, R. W., Holts, D. B., Chang, R. K. C., Sullivan, S., Dewar, H., and Carey, F. G. (1993). Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurements of oceanic currents. *Mar. Biol.* **117,** 567–574.

Brill, R. W., Dewar, H., and Graham, J. B. (1994). Basic concepts relevant to heat transfer in fishes, and their use in measuring the physiological thermoregulatory abilities of tunas. *Environ. Biol. Fishes* **40,** 109–124.

Brill, R. W., Cousins, K. L., Jones, D. R., Bushnell, P. G., and Steffensen, J. F. (1998). Blood volume, plasma volume and circulation time in a high-energy-demand teleost, the yellowfin tuna (*Thunnus albacares*). *J. Exp. Biol.* **201,** 647–654.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: Implications for the physiological ecology of pelagic fishes. *Mar. Biol.* **133,** 395–408.

Brill, R., Lutcavage, M., Metzger, G., Stallings, J., Bushnell, P., Arndt, M., Lucy, J., and Watson, C. (2000). Horizontal and vertical movements of juvenile Atlantic bluefin tuna (*Thunnus thynnus*) determined using ultrasonic telemetry, with reference to population assessment by aerial surveys. Manuscript.

Brown, C. E., and Muir, B. S. (1970). Analysis of ram ventilation of fish gills with application to skipjack tuna (*Katsuwonus pelamis*). *J. Fish. Res. Bd. Can.* **27,** 1637–1652.

Bushnell, P. G. (1988). Cardiovascular and respiratory responses to hypoxia in three species of obligate ram ventilating fishes, skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*T. obesus*). Ph.D. dissertation, Department of Physiology, John A. Burns School of Medicine, University of Hawaii, Honolulu, HI.

Bushnell, P. G., and Brill, R. W. (1991). Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas exposed to acute hypoxia, and a model of their cardiorespiratory function. *Physiol. Zool.* **64,** 787–811.

Bushnell, P. G., and Brill, R. W. (1992). Oxygen transport and cardiovascular responses in skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) exposed to acute hypoxia. J. *Comp. Physiol. B* **162,** 131–143.

Bushnell, P. G., and Holland, K. N. (1989). Athletes in a can. *Sea Frontiers* **35,** 43–48.

Bushnell, P. G., and Jones, D. R. (1994). Cardiovascular and respiratory physiology of tuna: Adaptations for support of exceptionally high metabolic rates. *Environ. Biol. Fish.* **40,** 303–318.

Bushnell, P. G., Brill, R. W., and Bourke, R. E. (1990). Cardiorespiratory responses of skipjack tuna *Katsuwonus pelamis;* yellowfin tuna, *Thunnus albacares;* and bigeye tuna, *T. obesus,* to acute reductions in ambient oxygen. *Can. J. Zool.* **68,** 1857–1865.

Bushnell, P. G., Jones, D. R., and Farrell, A. P. (1992). The arterial system. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Farrell, A. P., Eds.), Vol. 12A, pp. 89–139. Academic Press, San Diego.

Campbell, K. B., Rhode, E. A., Cox, R. H., Hunter, W. C., and Noordergraaf, A. (1981). Functional consequences of expanded aortic bulb: A model study. *Am. J. Physiol.* **240,** R200–R210.

Carey, F. G. (1973). Fishes with warm bodies. *Sci. Am.* **228,** 36–44.

Carey, F. G. (1990). Further observations on the biology of the swordfish. *In* "Planning the Future of Billfishes" (Stroud, R. H., Ed.), pp. 102–122. National Coalition for Marine Conservation, Savannah, GA.

Chopin, L. K., Amey, A. P., and Bennett M. B. (1998). A systemic secondary vessel system is present in the teleost fish *Tandanus tandanus* and absent in the elasmobranchs *Carcharinus melanotperus* and *Rhinobatos typus* and in the dipnoan *Neoceratodus forsteri. J. Zool. Lond.* **246,** 105–110.

Chugun, A., Oyamada, T., Temma, K., Hara, Y., and Kondo, H. (1999). Intracellular Ca^{2+} storage sites in the carp heart: Comparison with the rat heart. *Comp. Biochem. Physiol. A* **123,** 61–67.

Cobb, J. L. S. (1974). Gap junctions in the heart of teleost fish. *Cell Tissue Res.* **154,** 131–134.

Dagorn, L., Bach, P., and Josse, E. (2000). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Mar. Biol.* **136,** 361–371.

Dewar, H. (1993). Studies of tropical tuna swimming performance: Thermoregulation, swimming mechanics, and energetics. Ph.D. dissertation, University of California, San Diego.

Dewar, H., and Graham, J. B. (1994). Studies of tropical tuna swimming performance in a large water tunnel. I. Energetics. *J. Exp. Biol.* **192,** 13–31.

Dewar, H., Brill, R. W., and Olson, K. R. (1994). Secondary circulation of the vascular heat exchangers in skipjack tuna (*Katsuwonus pelamis*). *J. Exp. Zool.* **269,** 566–570.

Dickson, K. A. (1995). Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environ. Biol. Fish.* **42,** 65–97.

Dizon, A. E., and Brill, R. W. (1979). Thermoregulation in tunas. *Am. Zool.* **19,** 249–265.

Dizon, A. E., Brill, R. W., and Yuen, H. S. H. (1978). Correlations between environment, physiology, and activity and the effects on thermoregulation in skipjack tuna. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 233–259. Academic Press, New York.

Driedzic, W. R. (1983). The fish heart as a model system for the study of myoglobin. *Comp. Biochem. Physiol.* **76A,** 487–493.

Driedzic, W. R. (1988). Matching of cardiac oxygen delivery and fuel supply to energy demand in teleosts and cephalopods. *Can. J. Zool.* **66,** 1078–1083.

Driedzic, W. R. (1992). Cardiac energy metabolism. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Farrell, A. P., Eds.), Vol. 12A, pp. 219–266. Academic Press, San Diego.

Driedzic, W. R., and Gesser, H. (1985). Ca^{2+} protection form the negative inotropic effect of contraction frequency on teleost hearts. *J. Comp. Physiol. B* **156,** 135–142.

Driedzic, W. R., and Gesser, H. (1988). Differences in force-frequency relationships and calcium dependency between elasmobranch and teleost hearts. *J. Exp. Biol.* **140,** 227–241.

Driedzic, W. R., and Gesser, H. (1994). Energy metabolism and contractility in ectothermic vertebrate hearts: Hypoxia, acidosis, and low temperatures. *Physiol. Rev.* **74,** 221–258.

Egginton, S. (1998). Anatomical adaptations for peripheral oxygen transport at high and low temperatures. *S. Afr. J. Zool.* **33,** 119–128.

Fabiato, A. (1983). Calcium-induced calcium release from the cardiac sarcoplasmic reticulum. *Am. J. Physiol.* **245,** C1—C14.

Farrell, A. P. (1979). The Wind-kessel effect of the bulbus arteriosus in trout. *J. Exp. Zool.* **20,** 169–173.

Farrell, A. P. (1982). Cardiovascular changes in the unanesthetized lingcod (*Ophiodon elongatus*) during short-term progressive hypoxia and spontaneous activity. *Can. J. Zool.* **60,** 933–941.

Farrell, A. P. (1984). A review of cardiac performance in the teleost heart: Intrinsic and humoral regulation. *Can. J. Zool.* **63,** 523–536.

Farrell, A. P. (1991). From hagfish to tuna: A perspective on cardiac function. *Physiol. Zool.* **64,** 1137–1164.

Farrell, A. P. (1996). Features heightening cardiovascular performance in fishes, with special reference to tunas. *Comp. Biochem. Physiol.* **113A,** 61–67.

Farrell, A. P., and Jones, D. R. (1992). The heart. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Farrell, A. P., Eds.), Vol. 12A, pp. 1–87. Academic Press, San Diego.

Farrell, A. P., and Steffensen, J. F. (1987). Coronary ligation reduces maximum sustained swimming speed in Chinook salmon, *Oncorhynchus tshawtscha. Comp. Biochem. Physiol.* **87A,** 35–37.

Farrell, A. P., Davie, P. S., Franklin, C. E., Johansen, J. A., and Brill, R. W. (1992). Cardiac physiology in tunas. I. *In vitro* perfused heart preparations from yellowfin and skipjack tuna. *Can. J. Zool.* **70,** 1200–1210.

Farrell, A. P., Gamperl, A. K., Hicks, J. M. T., Shiels, H. A., and Jain, K. E. (1996). Maximum cardiac performance of rainbow trout (*Oncorhynchus mykiss*) at temperatures approaching their upper lethal limit. *J. Exp. Biol.* **199,** 663–672.

Fletcher, G. L., and Hedrich, R. T. (1987). Rheological properties of rainbow trout blood. *Can. J. Zool.* **65,** 879–883.

Freund, E. V. (1999). Comparison of metabolic and cardiac performance in scombrid fishes: Insights into the evolution of endothermy. Ph.D. dissertation, Stanford University, Stanford, CA.

Friedman, J. J. (1976). Microcirculation. *In* "Physiology" (Selkurt, E. E., Ed.), 4th ed., Chap. 12, pp. 273–288. Little, Brown, and Co., Boston.

Fritsche, R., and Nilsson, S. (1989). Cardiovascular responses to hypoxia in the Atlantic cod, *Gadus morhua. Exp. Biol.* **48,** 153–160.

Gallaugher, P., Thorensen, H., and Farrell, A. P. (1995). Hematocrit in oxygen transport and swimming in rainbow trout (*Oncorhynchus mykiss*). *Respir. Physiol.* **102,** 279–292.

Ganong, W. F. (1973). "Review of Medical Physiology." Lange Medical Publications, Los Altos, CA.

Garland, T., and Adolph, S. C. (1994). Why not to do two-species comparative studies: Limitations on inferring adaptation. *Physiol. Zool.* **67,** 797–828.

Gehrke, P. C., and Fielder, D. R. (1988). Effects of temperature and dissolved oxygen on heart rate, ventilation rate and oxygen consumption of spangled perch, *Leiopotherapon unicolor* (Günther 1959), (*Percoidei, Teraponidae*). *J. Comp. Physiol. B* **157,** 771–782.

Gemelli, L., Martino, G., and Tota, B. (1980). Oxidation of lactate in the compact and spongy myocardium of tuna fish (*Thunnus thynnus* L.). *Comp. Biochem. Physiol.* **65B,** 321–326.

Gesser, H. (1996). Cardiac force-interval relationship, adrenaline and sarcoplasmic reticulum in rainbow trout. *J. Comp. Physiol. B.* **166,** 278–285.

Gingerich, W. H., Pityer, R. A., and Racj, J. J. (1987). Estimates of plasma, packed cell and total blood volume in tissue of the rainbow trout (*Salmo gairdneri*). *Comp. Biochem. Physiol.* **87A,** 251–256.

Gingerich, W. H., Pityer, R. A., and Racj, J. J. (1990). Whole body and tissue blood volumes of two strains of rainbow trout (*Oncorhynchus mykiss*). *Comp. Biochem. Physiol.* **97A,** 615–620.

Giovane, A., Greco, G., and Tota, B. (1980). Myoglobin in the heart ventricle of tuna and other fishes. *Experientia* **36,** 6–7.

Gooding, R. G., Neill, W. H., and Dizon, A. E. (1981). Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis. Fish. Bull.* **79,** 31–47.

Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares,* and skipjack tuna, *Katsuwonus pelamis,* and the adaptive significance of elevated body temperatures in scombrid fishes. *Fish. Bull.* **73,** 219–229

Graham, J. B., and Diener, D. R. (1978). Comparative morphology of the central heat exchangers in

skipjacks *Katsuwonus* and *Euthynnus*. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.). Academic Press, New York.

Graham, J. B., Lowell, R. W., Lai, N. C., and Laurs, R. M. (1989). O_2 tension, swimming velocity, and thermal effects on the metabolic rate of the Pacific albacore, *Thunnus alalunga*. *Exp. Biol.* **48,** 89–94.

Grundin, V. B. (1989). On the ecology of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*). *J. Ichthyol.* **29,** 22–29.

Guppy, M., Hulbert, W. C., and Hochachka, P. W. (1979). Metabolic sources of heat and power in tuna muscles. II. Enzyme and metabolite profiles. *J. Exp. Biol.* **82,** 303–320.

Hargens, A. R., Millard, R. W., and Johansen, K. (1974). High capillary permeability in fishes. *Comp. Biochem. Physiol.* **48A,** 675–680.

Harwood, C. L., Young, I. S., and Altringham, J. D. (1999). Influence of cycle frequency, muscle strain and muscle length on work and power production of rainbow trout (*Oncorhynchus mykiss*) ventricular muscle. *J. Exp. Biol.* **201,** 2723–2733.

Holeton, G. F., and Randall, D. J. (1967). The effect of hypoxia on the partial pressure of gases in the blood and water afferent and efferent to the gills of rainbow trout. *J. Exp. Biol.* **46,** 317–328.

Holland, K. N., Brill, R. W., and Chang, R. K. C. (1990a). Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fish. Bull., U.S.* **88,** 397–402.

Holland, K. N., Brill, R. W., and Chang, R. K. C. (1990b). Horizontal and vertical movements of tunas (*Thunnus spp.*) associated with fish aggregating devices. *Fish. Bull., U.S.* **88,** 493–507.

Hove-Madsen, L. (1992). The influence of temperature on ryanodine sensitivity and the force frequency relationship in the myocardium of rainbow trout. *J. Exp. Biol.* **167,** 47–60.

Hughes, G. M. (1984). General anatomy of the gills (1984). *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 10A. Academic Press, New York.

Ishimatsu, A., Maruta, H., and Tsuchiyama, T. (1990). Respiratory, ionoregulatory and cardiovascular responses of the yellowtail *Seriola quinqueradiata* to exposure to the red tide plankton *Chattonella marina*. *Suisan Gakkaishi* **56,** 189–199.

Ishimatsu, A., Maruta, H., Oda, T., and Ozaki, M. (1997). A comparison of physiological response in yellowtail to fatal environmental hypoxia and exposure to *Chattonella marina*. *Fish. Sci.* **64,** 557–562.

Itazawa, Y., Takeda, T., and Yamamoto, K. (1983). Determination of circulating blood volume in three teleosts, carp, yellowtail and porgy. *Jpn. J. Itcthyol.* **30,** 94–101.

Jones, D. R. (1991). Cardiac energetics and design of the vertebrate arterial systems. *In* "Efficiency and Economy in Animal Physiology" (Blake, R. W., Ed.), pp. 159–168. Cambridge Univ. Press, Cambridge.

Jones, D. R., Brill, R. W., and Mense, D. C. (1986). The influence of blood gas properties on gas tensions and pH of ventral and dorsal aortic blood in free-swimming tuna, *Euthynnus affinis*. *J. Exp. Biol.* **120,** 201–223.

Jones, D. R., Brill, R. W., Butler, P. J., Bushnell, P. G., and Heieis, M. R. A. (1990). Measurement of ventilation volume in swimming tunas. *J. Exp. Biol.* **149,** 491–498.

Jones, D. R., Brill, R. W., and Bushnell, P. W. (1993). Ventricular and arterial dynamics of anaesthetized and swimming tuna. *J. Exp. Biol.* **182,** 97–112.

Jones, D. R., Bushnell, P. G., Brill, R. W., Steffensen, J. F., Cousins, K. L., Duff, D. W., Taxboel, C. D., and Keen, J. E. (2000). Macromolecular capillary permeability of three fishes: Yellowfin tuna, rainbow trout, and Atlantic cod. Manuscript.

Josse, E., Bach, P., and Dagorn, L. (1998). Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* **371/372,** 61–69.

Kalinin, A. L., Glass, M. L., and Rantin, F. T. (1999). A comparison of directly measured and estimated gill ventilation in the Nile tilapia, *Oreochromis niloticus*. *Comp. Biochem. Physiol. A* **122,** 207–211.

Kanwisher, J., Lawson, K., and Sundness, G. (1974). Acoustic telemetry from fish. *Fish. Bull. U.S.* **72,** 251–255.

Keen, J. E., Farrell, A. P., Tibbits, G. F., and Brill, R. W. (1992). Cardiac physiology in tunas. II. Effect of ryanodine, calcium, and adrenaline on force-frequency relationships in atrial strips from skipjack tuna, *Katsuwonus pelamis*. *Can. J. Zool.* **70,** 1211–1217.

Keen, J. E., Ciazon, D.-M., Farrell, A. P., and Tibbits, G. F. (1994). Effect of temperature and temperature acclimation of the ryanodine sensitivity of the trout myocardium. *J. Comp. Physiol. B* **164,** 438–443.

Keen, J. E., Aota, S., Brill, R. W., Farrell, A. P., and Randall, D. J. (1995). Cholinergic and adrenergic regulation of heart rate and ventral aortic pressure in two species of tropical tunas, *Katsuwonus pelamis* and *Thunnus albacares*. *Can. J. Zool.* **73,** 1681–1688.

Kiceniuk, J. W., and Jones, D. R. (1977). The oxygen transport system in trout (*Salmo gairdneri*) during sustained exercise. *J. Exp. Biol.* **69,** 247–260.

Kishinouye, E. (1923). Contributions to the comparative study of the so-called scombroid fishes. *J. Coll. Agric. Imp. Univ. Tokyo* **8,** 293–475.

Klawe, W. L., Barrett, I., and Klawe, B. M. H. (1963). Hæmoglobin content of the blood of six scombrid fishes. *Nature* **198,** 96.

Korsmeyer, K. E. (1996). A study of cardiovascular function in swimming tuna. Ph.D. dissertation. Scripps Institution of Oceanography, University of California, San Diego.

Korsmeyer, K. E., Dewar, H., Lai, N. C., and Graham, J. B. (1996a). The aerobic capacity of tunas: Adaptations for multiple metabolic demands. *Comp. Biochem. Physiol.* **113A,** 17–24.

Korsmeyer, K. E., Dewar, H., Lai, N. C., and Graham, J. B. (1996b). Tuna aerobic swimming performance: Physiological and environmental limits based on oxygen supply and demand. *Comp. Biochem. Physiol.* **113B,** 45–56.

Korsmeyer, K. E., Lai, N. C., Shadwick, R. E., and Graham, J. B. (1997a). Heart rate and stroke volume contributions to cardiac output in swimming yellowfin tuna: Response to exercise and temperature. *J. Exp. Biol.* **200,** 1975–1986.

Korsmeyer, K. E., Lai, N. C., Shadwick, R. E., and Graham, J. B. (1997b). Oxygen transport and cardiovascular responses to exercise in the yellowfin tuna *Thunnus albacares*. *J. Exp. Biol.* **200,** 1987–1997.

Lai, N. C., Graham, J. B., Lowell, W. R., and Laurs, R. M. (1987). Pericardial and vascular pressures and blood flow in the albacore tuna, *Thunnus alalunga*. *Exp. Biol.* **46,** 187–192.

Langille, B. L., Stevens, E. D., and Anataraman, A. (1983). Cardiovascular and respiratory flow dynamics. *In* "Fish Biomechanics" (Web, P. W., and Weihs, D., Eds.), pp. 92–139. Praeger, New York.

Lowe, T. E., Brill, R. W., and Cousins, K. L. (1998). Responses of the red blood cells from two high-energy-demand teleosts, yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*), to catecholamines. *J. Comp. Physiol. B* **168,** 405–418.

Lowe, T. E., Brill, R. W., and Cousins, K. L. (2000). Effects of temperature on blood O_2 binding in bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost with a high blood O_2 affinity. *Mar. Biol.*, **136,** 1087–1098.

Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., Goldstein, J. L., and Tutein, J. (2000). Tracking adult North Atlantic bluefin tuna (*Thunnus thynnus*) in the northwest Atlantic using ultrasonic telemetry. *Mar. Biol.* **137,** 347–358.

Magnuson, J. J. (1978). Locomotion by scombrid fishes: Hydromechanics, morphology, and behavior. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 7, pp. 239–313. New York, Academic Press.

Magnuson, J. J., and Weininger, D. (1978). Estimates of minimum sustained speed and associated body drag of scombrids. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 293–311. Academic Press, New York.

Malte, H. (1992). Effect of pulsatile flow on gas exchange in the fish gill: Theory and experimental data. *Respir. Physiol.* **88,** 51–62.

Marchal, E., and Lebourges, A. (1996). Acoustic evidence of unusual diel behavior of mesopelagic fish (*Vinciguerria nimbaria*) exploited by tuna. *ICES J. Mar. Sci.* **53,** 443–447.

Marcinek, D. J., Blackwell, S. B., Dewar, H., Freund, E. V., Farwell, C., Dau, D. J., Seitz, A. C., and Block, B. A. (2001). Depth and muscle temperatures of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. *Mar. Biol.* **138,** 869–885.

Maresca, B., Modigh, M., Servillo, L., and Tota, B. (1976). Different temperature dependencies of oxidative phosphorylation in the inner and outer layers of tuna heart ventricle. *J. Comp. Physiol.* **105,** 167–172.

Meadows, K. N., Hakkar, R. J., and Gwathmey, J. K. (1998). Effects of pH and temperature on myocardial calcium-activation in *Pterygoplicthys* (catfish). *J. Comp. Physiol. B* **168,** 526–532.

Metcalf, J. D., and Butler, P. J. (1982). Differences between directly measured and calculated values for cardiac output in the dogfish: A criticism of the Fick method. *J. Exp. Biol.* **99,** 255–268.

Moffitt, B. P., and Crawshaw, L. I. (1983). Effects of acute temperature change on metabolism, heart rate, and ventilation frequency in carp *Cyprinus carpio* L. *Physiol. Zool.* **56,** 397–403.

Moyes, C. D. (1996). Cardiac metabolism in high performance fish. *Comp. Biochem. Physiol.* **113A,** 69–75.

Moyes, C. D., Mathieu-Costello, O. A., Brill, R. W., and Hochachka, P. W. (1992). Mitochondrial metabolism of cardiac and skeletal muscles from a fast (*Katsuwonus pelamis*) and a slow (*Cyprinus carpio*) fish. *Can. J. Zool.* **70,** 1246–1253.

Muir, B. S. (1970). Contribution to the study of blood pathways in teleost gills. *Copeia* **1970,** 19–28.

Muir, B. S., and Brown, B. S. (1971). Effects of blood pathways on the blood-pressure drop in fish gills, with special reference to tunas. *J. Fish. Res. Bd. Can.* **28,** 947–955.

Muir, B. S., and Hughes, G. M. (1969). Gill dimensions in three species of tunny. *J. Exp. Biol.* **51,** 271–285.

Nakamura, E. L. (1972). Development and uses of facilities for studying tuna behavior. *In* "Behavior of Marine Animals (Current Perspectives in Research: 2. Vertebrates)" (Winn, W. E., and Olla, B. L., Eds.), pp. 245–277. Plenum, New York.

Ogilivy, C. S., Tremml, P. G., and DuBois, A. B. (1988). Presser and hemodilution responses compensate for acute hemorrhage in bluefish. *Comp. Biochem. Physiol.* **91A,** 807–813.

Olson, K. D. (1996). Secondary circulation in fish: Anatomical organization and physiological significance. *J. Zool., Lond.* **275,** 172–185.

Packard, G. C., and Boardman, T. J. (1999). The use of percentages and size-specific indices to normalize physiological data for variation in body size: Wasted time, wasted effort? *Comp. Biochem. Physiol. A* **122,** 37–44.

Palzenberger, M., and Pohola, H. (1992). Gill surface area of water-breathing freshwater fish. *Rev. Fish Biol., Fish.* **2,** 187–216.

Perry, S. F. (1992). Morphometry of vertebrate gills and lungs: A critical review. *In* "Society for Experimental Biology Seminar Series," Vol. 51: "Oxygen Transport in Biological Systems: Modeling of Pathways from Environment to Cell" (Egginton, S., and Ross, H. F., Eds.), pp. 57–77. Cambridge Univ. Press, Cambridge.

Piiper, J., and Scheid, P. (1984). Model analysis of gas transfer in fish gills. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol 10A, pp. 229–261. Academic Press, New York.

Randall, D. J., Holeton, G. F., and Stevens, E. D. (1967). The exchange of oxygen and carbon dioxide across the gills of rainbow trout. *J. Exp. Biol.* **46,** 339–348.

Rantin, F. T., Gesser, H., Kalinin, A. L., Guerra, C. D. R., De Freitas, J. C., and Driedzic, W. R. (1998). Heart performance, Ca^{2+} regulation and energy metabolism at high temperatures in *Bathygobius soporator,* a tropical marine teleost. *J. Therm. Biol.* **23,** 31–39.

Roberts, J. L. (1975). Active brachial and ram gill ventilation in fishes. *Biol. Bull.* **148,** 85–105.

Roberts, J. L. (1978). Ram gill ventilation in fish. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 83–88. Academic Press, New York.

Roger, C. (1994). Relationships among yellowfin and skipjack tuna, their prey-fish and plankton in the tropical western Indian Ocean. *Fish. Oceangr.* **3,** 133–141.

Rousseau, E., Smith, J. S., and Meissner, G. (1987). Ryanodine modifies conductance and gating behavior of single Ca^{2+} release channels. *Am. J. Physiol.* **253,** C364–C368.

Sanchez-Quintana, D., and Hurle, J. (1987). Ventricular myocardial architecture in marine fishes. *Anat. Rec.* **217,** 263–273.

Santer, R. M. (1974). The organization of the sarcoplasmic reticulum in teleost ventricular myocardial cells. *Cell Tissue Res.* **151,** 395–402.

Santer, R. M. (1985). Morphology and innervation of the fish heart. *Adv. Anat. Embryol. Cell Biol.* **89,** 1–102.

Satchell, G. H. (1991). "Physiology and Form of Fish Circulation." Cambridge Univ. Press, Cambridge.

Sharp, G. D. (1978). Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 397–449. Academic Press, New York.

Sharp, G. D. (1983). Trends in respiratory work and ecological position in the marine ecosystem. *Comp. Biochem. Physiol.* **76A,** 405–411.

Shibata, Y., and Yamamoto, T. (1977). Gap junctions in the cardiac muscle cells of the lamprey. *Cell Tissue Res.* **178,** 477–482. .

Shiels, H. A., and Farrell, A. P. (1997). The effect of temperature and adrenaline on the relative importance of the sarcoplasmic reticulum in contributing Ca^{2+} to force development in isolated ventricular trabeculae from rainbow trout. *J. Exp. Biol.* **200,** 1607–1621.

Shiels, H. A., and Farrell, A. P. (2000). The effect of ryanodine on isometric tension development in isolated ventricular trabeculae from Pacific mackerel (Scomber japonicus). *Comp. Biochem. Physiol.* **125A,** 331–341.

Shiels, H. A., Freund, E. V., Farrell, A. P., and Block, B. A. (1999). The sarcoplasmic reticulum plays a major role in isometric contraction in atrial muscle of yellowfin tuna. *J. Exp. Biol.* **202,** 881–890.

Smatresk, N. J. (1986). Ventilatory and cardiac reflex responses to hypoxia and NaCN in *Lepisosteus osseus,* an air-breathing fish. *Physiol. Zool.* **59,** 385–397.

Smith, F. M., and Davie, P. S. (1984). Effects of sectioning carinal nerves IX and X on the cardiac response to hypoxia in the coho salmon, *Oncorhynchus kisutch. Can. J. Zool.* **62,** 766–768.

Steffensen, J. F., and Lomholt, J. P. (1992). The secondary vascular system in. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 12A, pp. 185–217. Academic Press, New York.

Stevens, E. D. (1972). Some aspects of gas exchange in tuna. *J. Exp. Biol.* **56,** 809–823.

Stevens, E. D. (1982). The effect of temperature on facilitated oxygen diffusion and its relation to warm tuna muscle. *Can. J. Zool.* **60,** 1148–1152.

Stevens, E. D., and Carey, F. G. (1981). One why of the warmth of warm-bodied fish. *Am. J. Physiol.* **240,** R151–155.

Stevens, E. D., and Randall, D. J. (1967). Changes of gas composition in blood and water during moderate swimming activity in rainbow trout. *J. Exp. Biol.* **46,** 329–337.

Stevens, E. D., Bennion, G. R., Randall, D. J., and Shelton, G. (1972). Factors affecting arterial pressures and blood flow from the heart in intact, unrestrained lingcod, *Ophidon elongatus. J. Exp. Biol.* **43A,** 681–695.

Stevens, E. D., Lam, H. J. M., and Kendall, J. (1974). Vascular anatomy of the counter-current heat exchanger of skipjack tuna. *J. Exp. Biol.* **61,** 145–153.

Tetens, V., and Christensen, N. J. (1987). Beta-adrenergic control of blood oxygen affinity in acutely hypoxia-exposed rainbow trout. *J. Comp. Physiol.* **157B,** 667–675.

Thorarensen, H., Galluagher, P., and Farrell, A. P. (1996). Cardiac output in swimming rainbow trout, *Oncorhynchus mykiss,* acclimated to seawater. *Physiol. Zool.* **69,** 139–153.

Tibbits, G. F. (1996). Towards a molecular explanation of the high performance of the tuna heart. *Comp. Biochem. Physiol.* **113A,** 77–82.

Tibbits, G. F., Kashihara, H., and Brill, R. W. (1992a). Myocardial sarcolemma isolated from skipjack tuna, *Katsuwonus pelamis. Can. J. Zool.* **70,** 1240–1245.

Tibbits, G. F., Moyes, C. D., and Hove-Madsen, L. (1992b). Excitation-contraction coupling in the teleost heart. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Farrell, A. P., Eds.), Vol 12A, pp. 267–3040. Academic Press, New York.

Tota, B. (1983). Vascular and metabolic zonation in the ventricular myocardium of mammals and fishes. *Comp. Biochem. Physiol.* **76A,** 423–437.

Tota, B. (1989). Myoarchitecture and vascularization of the elasmobranch heart ventricle *J. Exp. Biol. (Suppl.)* **2,** 122–135.

Tota, B., Cimimi, V., Salvatore, G., and Zummo, G. (1983). Comparative study of the arterial and lacunary systems of the ventricular myocardium of elasmobranch and teleost fishes. *Am. J. Anat.* **167,** 15–32.

Walters, V. (1962). Body form and swimming performance in the scombroid fishes. *Am. Zool.* **2,** 143–149.

Watson, A. D., and Cobb, J. L. S. (1979). A comparative study of the innervation and the vascularization of the bulbus arteriosus in teleost fish. *Cell Tissue Res.* **196,** 337–346.

Weber, J-M., and Haman, F. (1996). Pathways for metabolic fuels and oxygen in high performance fish. *Comp. Biochem. Physiol.* **113A,** 33–38.

Wells, R. M. G., and Baldwin, J. (1990). Oxygen transport potential in tropical reef fish with special reference to blood viscosity and hematocrit. *J. Exp. Mar. Biol. Ecol.* **141,** 131–143.

Wells, R. M. G., and Weber, R. E. (1991). Is there an optimal hematocrit for rainbow trout, *Oncorhynchus mykiss* (Walbaum)? An interpretation of recent data bases on blood viscosity measurements. *J. Fish Biol.* **38,** 53–65.

White, F. C., Kelly, R., Kemper, S., Schumaker, P. T., and Gallagher, K. R. (1988). Organ blood flow hemodynamics and metabolism of the albacore tuna *Thunnus alalunga* (Bonnaterre). *Exp. Biol.* **47,** 161–169.

Wood, C. M., and Perry, S. F. (1985). Respiratory, circulatory, and metabolic adjustments to exercise in fish. *In* "Circulation, Respiration, and Metabolism. Current Comparative Approaches" (Gilles, R., Ed.), pp. 1–22. Springer-Verlag, Berlin.

Yamamoto, T. (1967). Observations on the fine structure of the cardiac muscle cells in goldfish. *In* "Electrophysiology and Ultrastructure of the Heart" (Sano, T., Mizuhira, V., and Matsuda, R., Eds.), pp. 1–13. Grune and Stratton, New York.

Yamamoto, K.-I., and Itazawa, Y. (1989). Erythrocyte supply from the spleen of exercised carp. *Comp. Biochem. Physiol. A* **92,** 139–144.

Yamamoto, K., Itazawa, Y., and Kobayashi, H. (1981). Relationship between gas content and hematocrit value in yellowtail blood. *J. Fac. Agr. Kyushu. Univ.* **26,** 31–37.

4

ANATOMICAL AND PHYSIOLOGICAL SPECIALIZATIONS FOR ENDOTHERMY

JEFFREY B. GRAHAM
KATHRYN A. DICKSON

I. Introduction
II. The Components of Tuna Endothermy
  A. Sustained Swimming, a Continuous Source of Heat, Allows Tunas to Maintain Elevated RM Temperatures
  B. Metabolic Heat Conservation in RM
  C. Maintenance of Elevated Temperatures in Other Tissues
III. A History of Discovery and the Development of Ideas about Tuna Endothermy
  A. Early Observations
  B. The Carey and Teal Era
  C. Thermocentrism: Toward a Modern Synthesis of Tuna Endothermy
IV. Recent Laboratory Studies of Tuna Endothermy
  A. Control of Heat Gain and Loss
  B. Metabolic Performance
  C. Tuna Locomotion, Endothermy, and Evolution
  D. The Ontogeny of Tuna Endothermy
  E. Endothermy in Large Tunas
V. Effects of Endothermy on Some Cardiovascular Characteristics
  A. Endothermy and Heart Function
  B. Endothermy and Hb–O_2 Affinity
VI. Summary, Conclusions, and Future Directions for Laboratory Studies

I. INTRODUCTION

Tunas are endothermic, which means that they utilize metabolic heat to elevate and maintain regional body temperatures (T_b) that are warmer than the ambient seawater temperature (T_w). The objective of this chapter is to review the contributions made by laboratory investigations to our current understanding of endothermy and its biological importance for these fishes. This will complement this volume's chapter by Gunn and Block, which reports on how information obtained from electronic tagging studies has contributed to our knowledge of tuna endothermy.

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

For the purposes of this chapter "laboratory investigations" include dissection, measurement, and any other examination of fresh, frozen, or preserved tunas for the purpose of understanding endothermy. Accordingly, we will discuss the important perspective provided by comparative anatomical studies to current hypotheses about the origin and derivation of endothermy, as well as the ontogeny, control, and biological significance of this specialization for tunas. "Laboratory investigations" also include measurements of T_b, rates of temperature change, and rates of heat production (mainly heat production by red muscle during swimming, but also including that produced by the metabolism of different tissues) conducted on live tunas.

The advantages of laboratory studies are that many of the important variables such as swimming velocity, T_w, and T_b are known and can be experimentally manipulated. Moreover, it is also possible to simultaneously monitor parameters directly relating to the endothermy mechanisms such as cardiac output and blood O_2 levels, and to use animals in replicate experiments (Dewar and Graham, 1994; Dewar *et al.*, 1994; Korsmeyer *et al.*, 1997a,b). By contrast, fewer variables can be known for electronically tagged tunas swimming in the sea and, although future developments in transmitter technology will increase the number of parameters that can be monitored, there is not as much potential for controlled experimentation (Brill *et al.*, 1994; Gunn and Block, this volume).

This does not, however, imply that laboratory studies lack disadvantages. First, not all tuna species can be studied in a laboratory setting. Of the species that can be so investigated, only small specimens can be used, and many factors related to tuna endothermy are influenced by body size. Also, the physiological condition of a laboratory tuna may be affected by diet, exercise regime, confinement within the holding tank, or time in captivity. There is also a high level of stress associated with "recapturing" and anesthetizing a captive tuna in order to affix the experimental monitoring devices used in many studies. Because tunas are powerful and struggle violently during capture, non-steady state conditions may exist for some time after an experimental fish is handled. This and the tuna's requirement for constant swimming in near air-saturated water at the appropriate temperature make laboratory experiments difficult and possibly of limited scope, unless the fish can be stabilized and the experiment conducted for several hours or much longer.

Capture stress and the requirements for swimming and respiration also limit the success of efforts to return freshly caught, healthy tunas to a laboratory, although this has been accomplished. At present three facilities in the western hemisphere hold tunas for research purposes: the National Marine Fisheries Kewalo Basin Tuna Facility in Honolulu, Hawaii, the Inter-American Tropical Tuna Commission Laboratory at Achotines Bay, Panama, and the Stanford University and Monterey Bay Aquarium Tuna Research and Conservation Center in Pacific Grove, California. Studies relevant to tuna thermal biology have been conducted at all three sites (Olson and Scholey, 1990; Brill, 1992; Dewar and Graham, 1994;

Dickson, 1994; Altringham and Block, 1997; Korsmeyer *et al.*, 1997a,b; Farwell, this volume). Tuna research cruises sponsored by the U.S. National Marine Fisheries Service (NMFS) Southwest Fisheries Center have also made important contributions to the current understanding of tuna thermal biology (e.g., Laurs *et al.*, 1977).

This volume's chapter by Collette, Reeb, and Block provides background information about tuna biology, nomenclature, and the evolutionary relationships of tunas (tribe Thunnini) to the other fishes in the family Scombridae. The first objective of the present chapter is to provide a concise overview of the mechanisms of tuna endothermy. This orientation to both the principles of heat transfer and the special mechanisms for heat conservation found in tunas will set the stage for an integrated assessment of the history of discovery and thinking about tuna endothermy, primarily from the standpoint of the contributions made by laboratory research. Then, we summarize what has been learned in more recent laboratory studies of tuna endothermy, and suggest additional studies needed to fill gaps in current knowledge.

II. THE COMPONENTS OF TUNA ENDOTHERMY

Among the tunas, elevation of myotomal muscle, eye, brain, and visceral temperatures above water temperature has been documented. To maintain an elevated temperature within any tissue, two conditions are necessary: (1) a source of metabolic heat and (2) a mechanism to retain that heat. In most cases, the source of heat for a tissue is its own intrinsic metabolic activity and, in all cases, the retention of this metabolic heat within the tissue requires the presence of arterial and venous blood vessels arranged as countercurrent heat exchangers. Because all tunas measured have been shown to conserve metabolic heat within the aerobic, slow-twitch, myotomal muscle fibers (red muscle, RM) that power cruise swimming, we will use information about the elevated T_{RM} of tunas to illustrate heat-transfer principles.

A. Sustained Swimming, a Continuous Source of Heat, Allows Tunas to Maintain Elevated RM Temperatures

Tunas never stop swimming and thus continuously generate heat within the RM. Steady and efficient cruise swimming and a capacity for powerful bursts are fundamental features of tuna biology (Magnuson, 1973, 1978; Block *et al.*, 1993; Dewar and Graham, 1994). Selection for these attributes appears to have played a role in this group's evolutionary divergence from other scombrids about 40 million years ago (Graham and Dickson, 2000). Constant swimming in tunas is, for example, necessitated by the dependence upon ram gill ventilation (Roberts, 1978) and by the requirement of a basal or minimum speed for generating hydrodynamic

lift (Magnuson, 1973, 1978). From an ecological standpoint, continuous swimming in schools is important for tuna feeding success in the open ocean where food resources are patchily distributed (Sund *et al.*, 1981). Sustained cruising also enables migrations to distant, high latitudes to take advantage of seasonally abundant food resources and to make a timely return to warm waters for spawning. Some tunas, for example, migrate across entire ocean basins twice a year (reviewed by Joseph *et al.*, 1988). Tunas also make rapid vertical migrations in search of prey and, in so doing, must be able to adjust to or compensate for changes in light, oxygen, temperature, and hydrostatic pressure—all of which can potentially affect the sensory and motor functions necessary for prey capture.

Because it functions aerobically, RM sustains the power requirements of continuous swimming. Although tuna dependence upon RM for this function is similar to that of other cruise-adapted species, tuna RM has unique properties. When its *in vivo* temperature is taken into account, tuna RM has higher aerobic enzyme activities (and these are matched by higher myoglobin concentrations) relative to the RM of other active fishes, including the ectothermic scombrids (Dickson, 1996). Tuna RM is located in a different position within the body than it is in all other teleosts, (with the exception of the swordfish *Xiphias gladius,* Figure 1). In

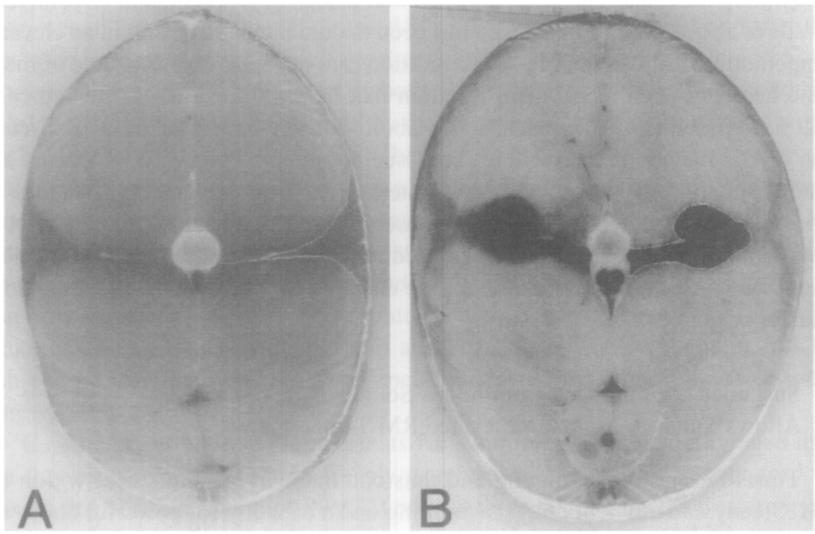


Fig. 1. Transverse sections showing differences in the position of the slow-twitch, oxidative myotomal muscle (RM) between an ectothermic scombrid (*Sarda chiliensis,* A) and a tuna (*Allothunnus fallai,* B). The RM fibers (outlined in white on the right of each section) form a lateral wedge adjacent to the skin in ectothermic scombrids, with some RM penetrating along the horizontal septum to the vertebrae in *Sarda,* and are in a more medial position in the tunas.

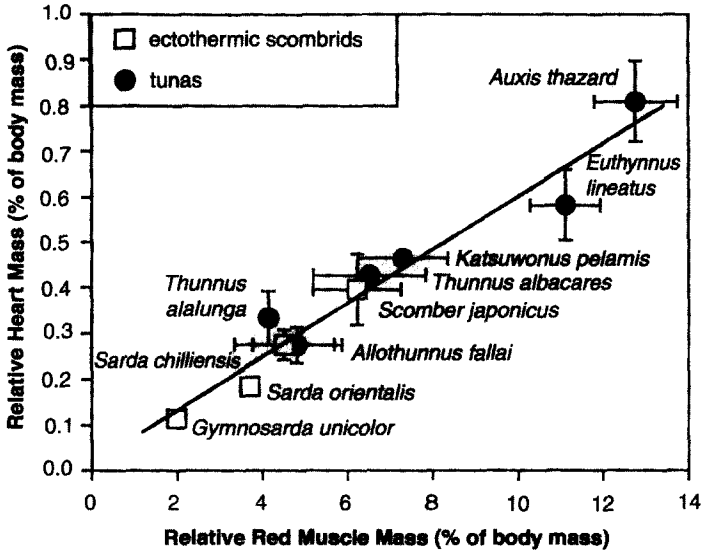


Fig. 2. Relationship between relative heart mass and relative red muscle mass in 10 scombrid species: Relative Heart Mass (%) = 0.059[Relative Red Muscle Mass (%)] + 0.018, $r^2 = 0.95$. Error bars represent 95% confidence intervals of mean values for species when $n \geq 3$. Data are from Graham *et al.* (1983) and Graham and Dickson (2000); graph is from Graham and Dickson (2000).

all other cruise-adapted bony fishes, including the ectothermic scombrids, RM occurs along the horizontal midline near the lateral edge of the body, just beneath the skin. Tuna RM is both more anterior and nearer to the vertebral column and is completely surrounded by white muscle (WM; Kishinouye, 1923; Graham *et al.*, 1983). This RM position and its specialized connective-tissue linkage to the caudal fin affects swimming mechanics and results in the unique tuna swimming mode which is termed "thunniform locomotion." Features of the thunniform locomotion pattern include minimal lateral body flexion and changes in the relationships between muscle activation and the strain cycle (Graham *et al.*, 1983; Westneat *et al.*, 1993; Block and Finnerty, 1994; Shadwick *et al.*, 1999; Ellerby *et al.*, 2000). The relative amount of RM varies among tuna species. In *Auxis thazard* and *Euthynnus lineatus,* for example, RM composes more than 10% of total body mass. However, in other tuna species, relative RM amounts range from 4.1 to 8.4% of total mass, which is similar to amounts in ectothermic scombrids (reviewed by Dickson, 1995). Another difference in tuna RM is a lower scaling coefficient for RM mass with respect to body mass than is found in the ectothermic scombrids *Sarda chiliensis* and *Scomber japonicus* (Graham *et al.*, 1983). Among the scom-

brids that have been examined, a significant positive relationship exists between mean relative RM mass and mean relative heart mass (Figure 2). This is expected because of the role of RM in powering sustained swimming and that of the heart in providing O_2 and metabolic fuels to RM. This relationship also suggests that, in view of the allometric scaling of RM mass in tunas, the relative size of the tuna heart may also decrease with body size, as has been found for some tuna species (Graham *et al.*, 1983).

B. Metabolic Heat Conservation in RM

1. *Retia Mirabilia*

Oxidative heat production by continuously active RM occurs in all fishes. What distinguishes tunas is that circulation to and from the RM is by way of countercurrent heat exchangers, termed *retia mirabilia* (wonderful nets), which conserve heat and establish a stable thermal gradient or thermal excess ($T_x = T_m - T_w$). The RM *retia mirabilia* are vascular bundles composed of sheets of parallel arterial and venous blood vessels that are intimately juxtaposed (Figure 3). To distinguish heat-exchanging *retia* from other countercurrent exchange vasculatures such as those associated with teleost gas bladders, previous workers emphasized that heat-exchanging *retia* were composed of small arterial and venous vessels rather than capillaries (Carey and Teal, 1966; Stevens *et al.*, 1974;

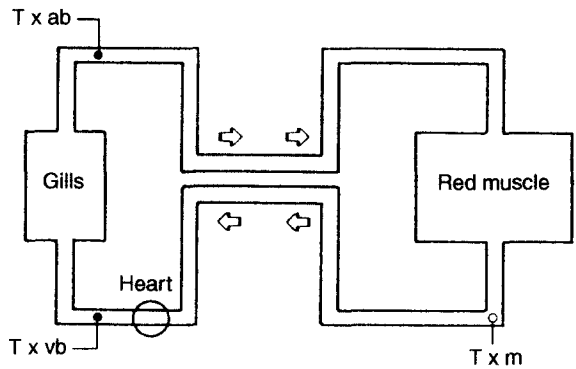


Fig. 3. Schematic showing the position of the central *retial* heat exchanger on the major systemic blood supply (the dorsal aorta and postcardinal vein) of the skipjack, *Katsuwonus pelamis*. Arrows indicate flow direction: arterial inflow is from the gills and venous outflow is to the heart. The three T_x positions illustrate thermistor positions for determination of temperatures in the RM (m), the ventral aorta (vb), and the dorsal aorta (ab) during the heat-pulse experiments of Stevens and Neill (1978; also see Figure 5). (From Brill *et al.*, 1994.)

Graham and Diener, 1978). New structural evidence shows that these vessels are, in fact, arterioles and venules; the diameters of the vessels fall within the ranges for vertebrate arterioles and venules, and the vessel wall ultrastructure resembles these types of vessels (Moore, 1998). Venules exiting the RM carry heat generated by aerobic metabolism and, as this venous blood passes in close proximity to the oppositely flowing cool arterial blood, thermal equilibration occurs. Because thermal diffusion occurs rapidly and the vessel walls are several cell layers thick, only heat is transferred within the *retia.* The RM *retia* of tunas contain more arterioles than venules (Table I) but, because the venules are larger, they compose a greater volume of the structure (Graham and Diener, 1978; Graham, 1983).

In the four species that have been examined (*Euthynnus lineatus, Katsuwonus pelamis, Thunnus albacares,* and *Thunnus alalunga*), the *rete* arterial vessel walls contain two or three layers of smooth muscle while the venule walls have a single layer (Figure 4). Varying the contractile state of the vascular smooth muscle provides a possible mechanism whereby vessel diameter and thus blood-flow and heat-exchange effectiveness may be adjusted *in vivo.* Although *rete* blood-flow characteristics have not been examined, preliminary data from restrained kawakawa (*Euthynnus affinis*) suggest that the intravenous administration of catecholamines affects *retial* heat-exchange efficiency (Brill *et al.,* 1994), which may be mediated by alterations in *rete* vessel diameter.

2. *Retia* Disrupt the Balance between Heat Production and Heat Loss in RM

As originally emphasized by Carey and Teal (1966), the importance of heat-conserving *retia* to tuna endothermy cannot be overstated. Fish lacking *retia* cannot block the convective transfer of heat to the gills. Because the heat capacity of water (1 cal g^{-1} $°C^{-1}$) is four times greater than that of air and because thermal diffusion occurs about 10 times faster than molecular diffusion, blood residing in the gills for the time required for respiratory gas exchange would also reach thermal equilibrium with the water (Graham, 1983).

The critical need for RM heat conservation is illustrated by the relationship between its heat production (HP_{RM}) and the potential branchial heat loss rate (HL_{GILLS}) in a steadily swimming fish that lacks heat-conserving *retia.* Heat production depends upon O_2 delivered by the blood to the aerobically powered RM fibers,

$$HP_{RM} = Q \cdot d[O_2]_{a-v} \cdot O_2 \text{ cal}, \qquad (1)$$

where Q (ml min^{-1}) is the blood-flow rate to RM, $d[O_2]_{a-v}$ is the quantity of O_2 consumed by RM [i.e., arterial − venous O_2 content (ml O_2 min^{-1})], and O_2 cal is the oxycalorific equivalent [the quantity of heat produced per unit of O_2 consumed (cal ml^{-1} O_2)]. [Note that the units for HP_{RM} in Equation (1) are cal $time^{-1}$.]

Blood also has a high heat capacity, which means that heat formed in the RM

Table I

Summary of Published Data on Some Characteristics of the Arterial (A) and Venous (V) Blood Vessels of Tunas' Central *Retia*, Countercurrent Heat Exchangers Serving the Red Myotomal Muscle

Species	Fish fork length (cm)	Mean ratio A:V	Inside diameter arteriole (μm)[a]	Inside diameter venule (μm)[a]	Reference
Euthynnus lineatus	49.2	1.04	53.9 ± 4.6 (20)	109.5 ± 6.2 (20)	Graham & Diener, 1978
	12.9	1.11	No data	No data	Dickson, 1994
Katsuwonus pelamis	42.7	1.11	35.7 ± 1.3 (706)	83.8 ± 4.5 (637)	Stevens *et al.*, 1974
	49.7	No data	36.6 ± 7.9 (10)	79.0 ± 3.9 (11)	Graham & Diener, 1978
Thunnus albacares	55.5	1.48	33.5 ± 2.2	71.0 ± 3.6	Koehrn, 1980
	66.5	1.44	43.5 ± 2.0	115.9 ± 2.2	Koehrn, 1980

[a] Values are ±SD (number of vessels measured).

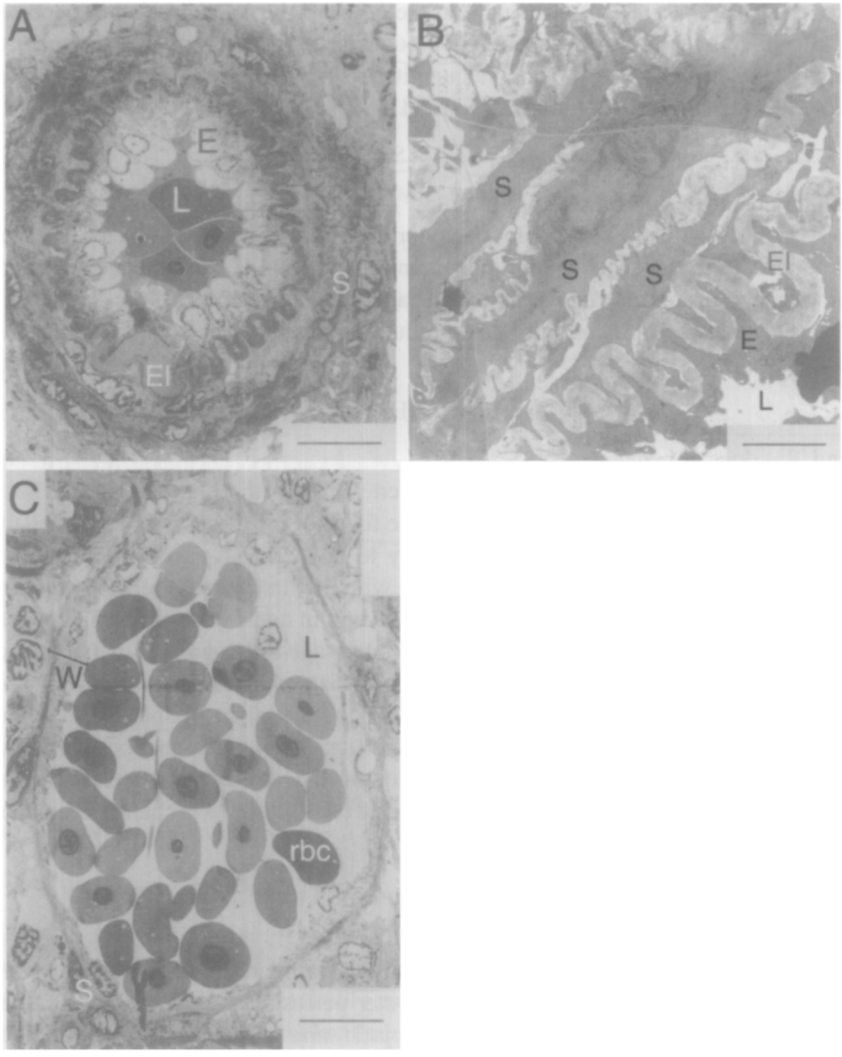


Fig. 4. Transverse sections of (A) a lateral *rete* arteriole from the skipjack tuna *Katsuwonus pelamis*, (B) a portion of the wall of a *rete* arteriole from albacore, *Thunnus alalunga*, and (C) a central *rete* venule from *K. pelamis*. The scale bar represents 10 μm in A and C and 2.5 μm in B. E, endothelial cells; EI, elastica interna; L, vessel lumen; rbc, red blood cell; S, smooth muscle cell; and W indicates the wall thickness of the venule. All images are from 1-μm-thick sections cut on an ultramicrotome from plastic-embedded, glutaraldehyde-fixed rete specimens, and viewed at low power on a Hitachi H7000 transmission electron microscope. (Photo montages prepared by S. Karl and J. Moore.)

has a high probability of diffusing into the capillary blood and being transported to the gills. In fact, the heat capacity of blood plasma meets or exceeds the quantity of heat that can be formed from the quantity of O_2 transported. Thus, HL_{GILLS} (cal $time^{-1}$) is also described in terms of blood flow,

$$HL_{GILLS} = Q \cdot S_{blood} \cdot T_{x\ RM}, \tag{2}$$

where Q is RM blood-flow rate (ml min^{-1}), S_{blood} is blood heat capacity (cal ml^{-1} $°C^{-1}$), and $T_{x\,RM}$ is the rise in blood temperature caused by the release of RM heat produced from the O_2 consumption. Equations (1) and (2) show that the rate of blood flow through RM governs both heat production and heat loss. If flow increases, more O_2 is provided for heat production but there is also more convective heat loss. Thus,

$$HP_{RM} = HL_{GILLS} \tag{3}$$

and T_{RM} does not change.

Discussion to this point has considered HP_{RM} in the absence of any heat-conserving capacity. Also, RM has been the focus of the discussion. However, the principles that have been developed apply to any aerobic tissue (i.e., which is generating metabolic heat in conformance with the first law of thermodynamics) and, as will be discussed below, other tissues within tunas generate sufficient heat to raise regional temperature. The important message at this point is that, irrespective of where the tissue heat source is placed, it is a physical impossibility for an active fish lacking a vascular heat exchanger to maintain a T_b that is more than 1°C warmer than T_w under steady state conditions (i.e., when heat production = heat loss; Brill *et al.,* 1994). It is the retention of RM heat by the *retia* that enables tunas to be endothermic, and several studies of *retial* heat-exchange efficiency have been done.

3. *Retial* Exchange Efficiency: The Key to Tuna Endothermy

Retial efficiency in heat exchange was first estimated by Stevens and Neill (1978), who applied a heat pulse to the water perfusing the gills of a restrained (ventilated and slightly anesthetized) skipjack tuna (*Katsuwonus pelamis,* Figure 5). Thermistors monitored temperatures in the gills, ventral aorta, brain, RM, and venous blood, and heart rate (HR) was also recorded. A square-wave heat pulse was applied by switching to 5°C warmer perfusion water for 15 s. Figure 5 shows the immediate rise in gill temperature as well as the appearance of the heat pulse in the ventral aorta within 10–15 s after it was given. This is about three times faster than if the pulse had transited the entire circulation. Because the heated aortic blood traversed various routes through the systemic circulation, warmed blood continued to return to the ventral aorta for about 2 min.

The heart of all tunas operates at or very near to T_w (Graham, 1983), even in

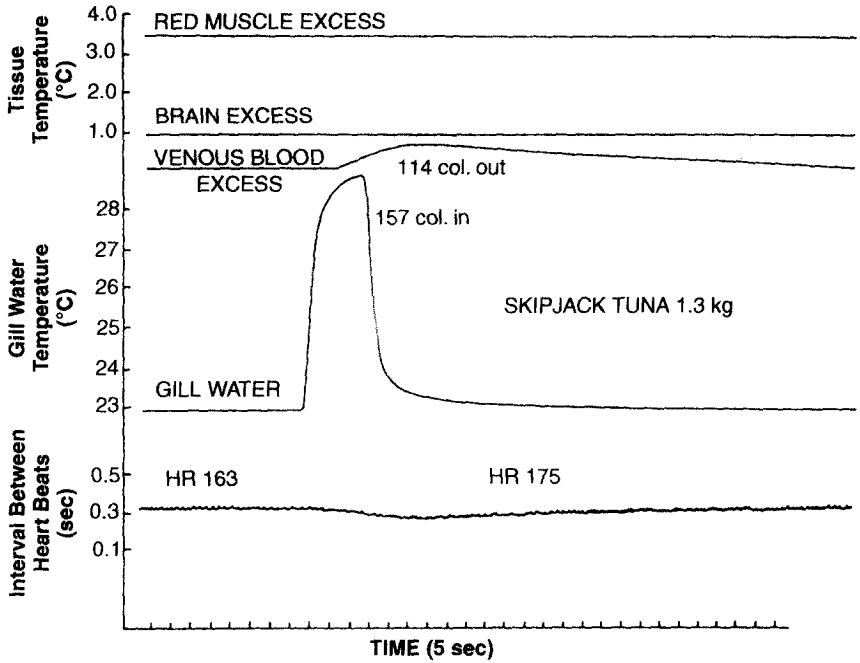


Fig. 5. Effects of a heat-pulse application to the ventilatory stream of a restrained skipjack tuna. See text for details. Refer to Figure 3 for the general circulation scheme and to see placement sites of the venous blood and RM muscle thermistors. Note that neither the RM nor the brain registered increases in T_x, but that a rise in venous blood T_x occurred shortly after pulse delivery. (From Stevens and Neill, 1978.)

fish with a high T_x (Carey *et al.*, 1971). The skipjack's initial heart rate of 163 bpm increased to 175 bpm late in the heat-pulse delivery, indicating that some warming of the heart had occurred, probably as a result of thermal conduction (defined as the diffusion of heat from molecule to molecule down the thermal gradient in a solid object) from the branchial to the pericardial cavity, and the return of warmed venous blood to the heart (Stevens and Neill, 1978). However, Figure 5 shows that the heat pulse did not arrive at the RM or the brain because it was transferred from the arterial to venous circulation by the skipjack's heat exchangers.

By assuming that gill blood came into complete thermal equilibrium with the heat pulse, Stevens and Neill (1978) estimated the quantity of heat added to dorsal aortic blood to be about 150 cal and the amount of heat returning in the venous circulation to be about 110 cal. Thus, the skipjack *retial* system was at least 75% efficient.

While this level of efficiency seems impressive, the estimate of Stevens and Neill may be low for several reasons (reviewed in Brill *et al.*, 1994). These workers did not know the percentage of cardiac output going to the RM (and thus reflected by the central *rete*) but reasoned that, because over 50% of the heat return occurred within 40 s, about 50% of the cardiac output went into the *retia* serving RM. Using radioactive microspheres and working at sea aboard the *R/V David Starr Jordan,* White and co-workers (1988) determined that about 36% of the cardiac output flowed to the RM of the albacore (*Thunnus alalunga*). Because the albacore has a smaller RM mass than the skipjack (4.1 vs. 7.5%; Magnuson, 1973; Graham *et al.*, 1983), the proportionally larger Stevens and Neill estimate of 50% of cardiac output to RM in skipjack seems reasonable.

With additional data such as cardiac output to RM, better estimates of *retial* exchange efficiency became possible (Graham, 1983; Brill *et al.*, 1994). These reveal the interdependence of O_2 delivery, heat production rate, and blood flow in determining the level of *retial* exchange efficiency needed to sustain a specified T_x. Figure 6 illustrates this for a 10-kg albacore, with 410 g of RM that receives about 36% (White *et al.*, 1988) of the cardiac output (which is 108 ml min^{-1}). Because each milliliter of arterial blood contains nearly 0.2 ml O_2 (Stevens and Neill, 1978), oxygen delivery is about 0.053 ml O_2 min^{-1} g^{-1} [i.e., 108(0.2)/410]. Assuming a RM metabolism of 0.124 cal min^{-1} g^{-1} (Stevens and Neill, 1978) and an oxycalorific equivalent of 4.7 cal ml^{-1} O_2, 0.026 ml O_2 min^{-1} g^{-1} is required at low swimming speeds, which is about 50% of the O_2 quantity being delivered. If total RM heat production is 50.8 cal min^{-1} (0.124 × 410), a metabolic heat increment of 0.47 cal ml^{-1} will be applied to capillary blood (50.8 cal min^{-1}/108 ml min^{-1}). Assuming 50% of this heat is conducted into the surrounding WM (Figure 1) and a T_x of 10°C, a 97% efficiency is needed to maintain a stable T_x (Figure 6A). Figure 6 also shows how efficiency requirements change with T_x and with O_2 utilization. If 85% of the available O_2 is consumed (Figure 6B), RM heat production rises to 81.2 cal min^{-1} and the thermal increment increases (81.2/108 = 0.75 cal ml^{-1}); however, and allowing for 50% conductance to the WM, a *retial* efficiency of 96.3% is still required to maintain a 10°C T_x. Even if blood-flow rate and RM O_2 consumption were dramatically elevated (Figure 6C), a 96% efficiency is required to maintain a 10°C T_x. Thus, O_2 delivery and RM heat production are tightly linked to blood flow, which has the potential to carry heat away as fast as it is produced. High *retial* exchange efficiencies are required to prevent this (Figure 6D); the minimum efficiency needed to defend a steady state T_x of 2°C is about 75%, the level measured by Stevens and Neill (1978).

4. Interspecific Differences in the Structure of RM *Retia*

Retia occur adjacent to the RM in all tuna species, but there are interspecific differences in *rete* size, complexity, and position (Graham, 1975; Stevens and Neill, 1978; Bushnell *et al.*, 1992). Many tunas have a central *rete* [*Auxis* spp.,

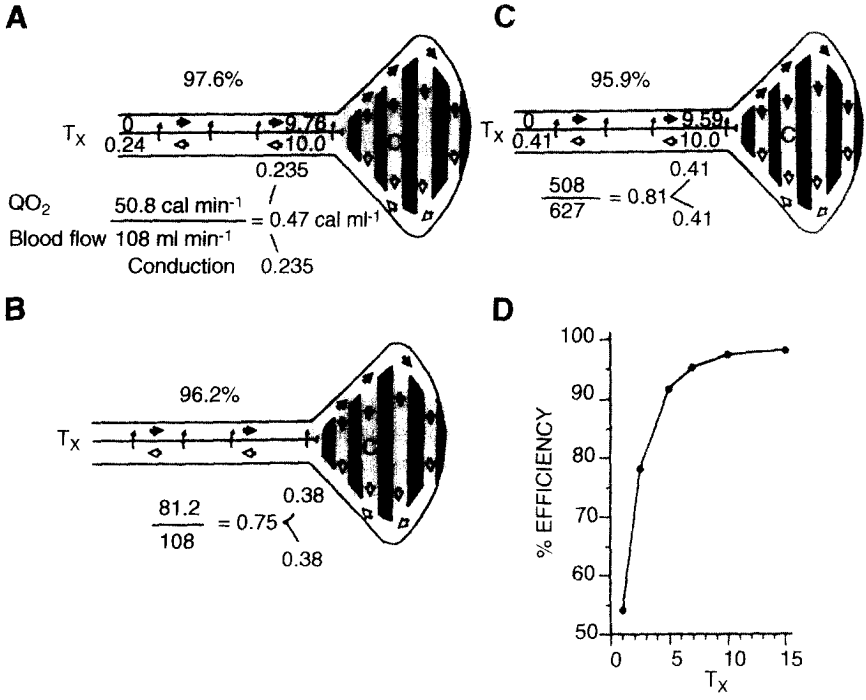


Fig. 6. Effects of RM O_2 utilization (heat production) on the level of *retial* heat-conservation efficiency required to maintain a constant temperature in the RM. The model is for a 10-kg albacore having 410 g of RM that receives 36% of cardiac output, or 108 ml min^{-1}. Comparison of A and B shows that to conserve T_x, a rise in the consumption rate from 50 to 85% of the O_2 arriving in the RM must be accompanied by a slight drop in exchange efficiency (assuming no change in blood flow). C shows that a 10-fold increase in O_2 uptake, when accompanied by a sixfold increase in blood flow, does not alter the requisite efficiency. D illustrates how, under conditions in A, *retial* exchange efficiency is affected by T_x. (From Graham in *Fish Biomechanics*, P. W. Webb and D. Weihs, Eds. Copyright © 1983 by Praeger Publishers. Reproduced with permission of Greenwood Publishing Group, Inc., Westport, CT.)

Euthynnus spp., *Katsuwonus pelamis, Thunnus tonggol, Thunnus atlanticus,* and *Thunnus albacares* (Graham, 1975; reviewed by Bushnell *et al.,* 1992), and *Allothunnus fallai* (Graham and Dickson, 2000)] supplied by the dorsal aorta and postcardinal vein. All tunas except *A. fallai* (Graham and Dickson, 2000) have lateral *retia,* which are supplied via the lateral arteries and veins. Among teleosts, these lateral blood vessels (which have also been termed cutaneous or subcutaneous vessels) are found only in the tunas.

C. Maintenance of Elevated Temperatures in Other Tissues

Some tunas have the capacity to warm other body regions and, in all such cases, *retia* positioned at critical sites are required to conserve this heat and main-

tain elevated temperatures (Linthicum and Carey, 1972; Bushnell *et al.*, 1992). *Euthynnus* spp., *Katsuwonus pelamis,* and *Thunnus* spp. have warm brains and possess *retia* on each carotid artery to warm blood entering the brain. The heat source for brain warming in tunas is unknown. It may arrive by thermal conduction through myotomal muscle via the frontoparietal fenestrae that are found in the skulls of all tuna species that can maintain elevated brain temperatures (Graham and Dickson, 2000), or metabolism within the central nervous system or the extraocular muscles may be the heat source (Linthicum and Carey, 1972).

Retia also conserve heat in the viscera of several *Thunnus* species (*T. albacares, T. obesus, T. maccoyii, T. alalunga,* and *T. thynnus;* see Table II). Facultative heating of the stomach occurs after feeding in the bluefin, *T. thynnus* (Carey *et al.*, 1984). Digestion, absorption, and anabolic processes within the stomach and particularly the caecal mass, the warmest visceral organ in *T. thynnus*, are most likely the primary source of heat for visceral warming in tunas (Carey *et al.*, 1984).

The rates of heat production by these tissues are not as well quantified as the rates for RM. Visceral heating, for example, occurs only after feeding and may therefore be largely intermittent. Nevertheless, and regardless of the rate and site of heat production, it is important to emphasize that, if cool arterial blood destined for either the warm brain or warm visceral cavity was not warmed (by venous blood draining these tissues) prior to entering these regions, an elevated regional temperature could not be maintained (Carey *et al.*, 1971; Graham, 1983).

III. A HISTORY OF DISCOVERY AND THE DEVELOPMENT OF IDEAS ABOUT TUNA ENDOTHERMY

The first principles for heat conservation provide the basis for reviewing the history of laboratory studies of tuna endothermy. Historical accounts of discoveries related to tuna T_b are contained in Stevens (1978), Stevens and Neill (1978), Dizon and Brill (1979a,b), Graham (1983), Brill *et al.* (1994), and Fudge and Stevens (1996). The purpose of this section is to integrate the chronology of primarily laboratory discoveries about endothermy with the evolution of the diverse ideas suggested about the advantages, limitations, biological significance, and evolutionary origins of endothermy.

A. Early Observations

British physician John Davy (1835) was the first to document the warmth of tunas. He observed that skipjack (*Katsuwonus pelamis*) in waters near Ceylon had a "temperature of 99°F when the surrounding medium was 80°F, and it constituted an exception to the generally received rule that fishes are universally cold

Table II

Probable Importance for Endothermy Proposed by Graham (1975) of Some of the Taxonomic Characters Used by Gibbs and Collette (1967) to Distinguish the Species of the Genus *Thunnus*

Probable importance for endothermy	Character	*T. alalunga*	*T. thynnus*	*T. maccoyii*	*T. obesus*	*T. albacares*	*T. atlanticus*	*T. tonggol*
Index of body shape and the extent of anterior-lateral RM position	Cutaneous artery branch-point from the dorsal aorta (vertebra number)	3–4	3–4	3–4	6–8	6–8	6–8	6–8
Index of relative lateral *retial* surface area	Number of arteriole rows branching from the cutaneous artery	1	2	2	2	1	1	1
Presence/absence of postcardinal vein indicates whether or not there is complete central circulation	Postcardinal vein[a]	Absent	Absent	Absent	Present[b]	Present	Present	Present
Position of articulating surface indicates quantity of haemal arch open space for central circulation	Position of the haemal prezygapophyses on anterior vertebrae	On centrum	Near centrum	Near centrum	Near centrum	Well ventrad	Well ventrad	Well ventrad
Another indication of greater haemal arch open space	Length of the haemal postzygapophyses on the anterior vertebrae	Short	Short	Short	Short	Long	Long	Long
Indicates a large lateral aperture for *rete* vessels supplying RM	Ventrolateral foramina size	Small	Small	Small	Small	Large	Large	Large
Indicates capacity for facultative heating of viscera	Liver striations and vascular *retia*	Present	Present	Present	Present	Absent[c]	Absent	Absent

[a] Incomplete central circulation necessitates greater reliance upon lateral circulation for RM and WM perfusion.

[b] *T. obesus* has a postcardinal vein but not a central *rete*.

[c] *T. albacares* has a caecal *rete* (Block, personal communication).

blooded." [An annotated copy of Davy (1835) and another of his papers on tuna temperature (Davy, 1844) are contained in Fudge and Stevens (1996).]

At the time of Davy's work, the role of the respiratory organs and blood, in particular the erythrocytes, in supplying O_2 to the body was not understood. The concept of metabolic heat did not exist and it was thought that, while some animals (endotherms) produced heat, cold-blooded animals (ectotherms) did not. Linnaeus, for example, had distinguished animals on the basis of temperature and used the phrase "sanguine frigido" to describe ectotherms. The generality of fish "cold bloodedness" had been proclaimed by Georges Cuvier in the *Historie Naturelle des Poissons:* "Ne respirant que par l'interméde de l'eau, c'est-à-dire, ne profitant pour rendre à leur sang les qualité d'oxigene contenu dans l'air melé à l'eau, leur sang a dû rester froid" (Cuvier and Valenciennes, 1828, 275). Volume VIII of that same work (Cuvier and Valenciennes, 1831, 64–65) detailed features of the specialized lateral circulatory anatomy of tunas. Cuvier and Valenciennes did not interpret the function of this structure, nor did their descriptions of the tuna viscera indicate that they had observed the visceral *retia.* Eschricht and Müller (1835) made the first descriptions of the visceral *retia* of the bluefin tuna and, knowing of Davy's findings, they made the link between the arrangement of arteries and veins in the "Wundernetze" (*retia mirabilia*) of this organ with the warmth of tunas. However, they did not articulate the principle of countercurrent exchange, and neither the source nor the mechanism of heat generation was known.

The link between tuna vascular anatomy, activity level, and an elevated body temperature was suggested by Kamakichi Kishinouye, who in 1923 published a remarkable treatise on the autecology of tunas and other scombrids, "Contributions to the Comparative Study of the So-called Scombroid Fishes." This work, the single most comprehensive treatment of scombrid biology ever written, focused mainly on species in Japanese waters. Kishinouye provided information about most aspects of tuna and scombrid biology, including feeding, development and growth, distribution, locomotion, migration, predators, and parasites. He also compared their skeletal, muscular, nervous, sensory, digestive, renal, reproductive, respiratory, and vascular systems. An especially valuable feature of Kishinouye's monograph was that it was published in English. Another was that it contained large color plates and line drawings of tuna vascular anatomy that were accompanied by written descriptions of other structural details. The illustrations have appeared in several volumes on tunas (Sharp and Dizon, 1978; Fudge and Stevens, 1996) and the *Traite de Zoologie* (Bertin, 1958). Kishinouye also provided numerous comparative details about RM (*chiai*) structure in different scombrids, illustrated its different positions in tunas and bonitos (*Sarda*), and showed the intimate relationship between RM and the special vascular complex adjacent to it [*kurochiai* (= *retia*)] in tunas.

Based on the unique circulatory features of tunas, especially the prominent lateral vessels, Kishinouye (1923) proposed placing the tunas in their own order,

the Plecostei, to distinguish them from all of the other modern teleost fishes. Although this proposal for a major revision of fish systematics was not adopted, Kishinouye's monograph was unprecedented at the time for its synthesis of tuna biology. As modern interest in the anatomical and physiological bases of tuna endothermy developed in the mid-1960s, comparative physiologists and anatomists rediscovered this work and, some 75 years after its publication, Kishinouye (1923) remains a fundamental contribution.

B. The Carey and Teal Era

The mid-1960s saw the beginnings of the explosive growth in the rate of discovery and insight in most areas of science, and the biology of tunas was no exception. Very little tuna T_b data were obtained in the interval from Davy's first report to the early 1900s [reviewed by Carey and Teal (1966) and Stevens (1978)]. Barrett and Hester (1964), who used electronic thermometers, began the modern era of tuna T_b measurements. Working with freshly caught skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*), these workers demonstrated one physiological feature of tuna endothermy, the tendency for the T_x ($= T_b - T_w$) to be lower for fish caught in warmer waters, particularly in the skipjack.

However, it was the publication of "Heat Conservation in Tuna Fish Muscle" by Francis Carey and John Teal (1966) that ignited this field. This paper presented new T_b data, provided the first illustrations of thermal profiles, and detailed the anatomical and physiological bases for tuna thermoconservation, including the direct dependence of metabolic heat production on the delivery of oxygen. Further, this work also elucidated the biophysical and biochemical principles underlying the physical challenges for, and biological advantages afforded to, a warm fish.

Over the next 25 years, Carey and co-workers added many details about fish endothermy, including documentation of elevated brain, eye, and stomach temperatures in certain tunas (Carey *et al.*, 1971; Linthicum and Carey, 1972; Stevens and Carey, 1981); evidence of the bluefin tuna's capacity to thermoregulate (Carey and Teal, 1969a; Carey and Lawson, 1973); demonstration of endothermy and elevated visceral temperatures in the lamnid sharks (Carey and Teal, 1969b; Carey *et al.*, 1981; Block and Carey, 1985); and description of the structural and biochemical modifications in swordfish eye muscles that permit elevated brain and eye temperatures (Carey, 1982; Block, 1986). These works more than any others have set the pace for this field and, while the scope of the fish endothermy problem has evolved considerably since Carey and Teal (1966), this work remains a frequently cited reference and is noteworthy because of its breadth of coverage and concise elucidation of first principles.

While Carey and Teal's 1966 paper established the field of tuna thermal biology, it made little reference to the evolution of tunas or to how interspecific differences in body form or circulation might affect swimming performance or

heat conservation capacity. Two other important papers on tuna biology that appeared about the same time as Carey and Teal (1966) were "Comparative Anatomy and Systematics of the Tunas, Genus *Thunnus*" (Gibbs and Collette, 1967), and "Studies in Locomotion and Anatomy of Scombroid Fishes" (Fierstine and Walters, 1968). Most tuna biologists would agree that these papers, along with Carey and Teal (1966), form the foundation of our current understanding of tuna endothermy.

However, as important as these papers were, they did not make reference to one another. When these works appeared there was not a large critical mass of tuna biologists, and most of the work being done focused on fisheries questions. A unified understanding of the systematics, distribution, and movements of these widely distributed, commercially important species was a critical issue for stock assessment and management. The treatise on the taxonomy and biology of the seven species of *Thunnus* by Gibbs and Collette (1967) clarified and standardized what had been an arcane and provincial nomenclature. It also compared the morphologies, natural histories, and depth distributions of the *Thunnus* species and detailed many of the comparative differences in the skeletal and vascular systems that were used by Gibbs and Collette to distinguish between members of the genus (Table II). While Gibbs and Collette did not specifically discuss what role "heat conservation" might have played in the evolution, radiation, and geographical distribution of *Thunnus* species, the vascular and vertebral skeletal differences they noted for the two subgenera are now regarded as indicators of endothermic capacity that correlate with the penetration of *T. alalunga, T. maccoyii, T. thynnus,* and *T. obesus* into deeper and cooler waters (Graham, 1975). Thus, what was important for the comparative physiologists and anatomists interested in tuna endothermy was that, in addition to providing important morphological information, the paper by Gibbs and Collette (1967), several other works by Collette and coworkers (Collette and Chao, 1975; Collette, 1978, Collette *et al.*, 1984), and some earlier studies (Godsil and Byers, 1944; Godsil, 1954) established an authoritative reference point for defining and understanding the relationships among the now five genera and 15 species of tunas and for comparing the tunas (tribe Thunnini) to their sister group, the bonitos (tribe Sardini; Graham and Dickson, 2000; Collette, Reeb, and Block, this volume).

Fierstine and Walters (1968) examined skeletal and morphological differences in bonitos and tunas that relate to the tuna's stiffer (thunniform) swimming mode, and in so doing provided the first information on scombrid swimming biomechanics. These workers described the deeply nested myotomal cones of scombrids and contrasted the myotomal structures of the tunas and bonitos, which differ in cone thickness and length as well as in the relative amount and position of RM. However, Fierstine and Walters (1968) did not consider the implications of the tuna's elevated T_{RM} for its swimming performance relative to the bonito.

Magnuson (1973) examined scombrid locomotion and compared functional

differences in tunas and other scombrids. Working with live fish at the Kewalo Basin Facility in Hawaii, he measured the swimming velocity of different scombrids and developed a hydrodynamic model predicting the basal swimming velocity (i.e., the minimum speed for hydrodynamic equilibrium) of a species based on morphological characteristics such as body shape, thickness, density, mass–length ratio, and area of the pectoral fin (and other lifting surfaces). Magnuson also found a correlation between basal speed and the relative amount of RM and blood hemoglobin (Hb) concentration, concluding that scombrid aerobic capacity had been directly influenced by requirements for sustained swimming. Magnuson did not consider the question of tuna endothermy, but his data indicated that, for tunas (*Katsuwonus, Euthynnus*) and ectothermic scombrids (*Sarda*) having about the same basal speeds, the tunas had both more RM and more Hb. This was quite intriguing to physiologists interested in endothermy because it suggested that tuna RM quantity was more than adequate to power basal swimming speed, and that tunas incurred a greater metabolic cost because they had more and warmer RM (Graham, 1975; Sharp and Pirages, 1978).

Thus, when the works of Carey and Teal, Gibbs and Collette, and Fierstine and Walters appeared, it was not expected that answers to questions that have occupied tuna physiologists for the past 30 years (viz., Why and how did endothermy evolve? How is it regulated? What is its functional significance? Why is it present in tunas but not other scombrids?) would be answered in part by the integration of information contained in these three seemingly disparate works. Comparative biologists who became interested in tuna endothermy at that time were inspired by the discoveries of Carey and his colleagues, could be confident of the foundations in tuna morphology and systematics provided by Gibbs and Collette and others, and, thanks to the contributions of Fierstine and Walters and Magnuson, could begin to see the outlines of the relationship between tuna vascular specializations, swimming activity, and an elevated T_b that had been suggested by Kishinouye. As the remainder of this chapter will show, interrelationships among mechanisms affecting heat gain and loss (principally swimming velocity and T_w), the physiological effects of elevated temperature on the physiology (including swimming performance), ecology, and evolutionary radiation of tunas, and the influences of large-scale changes in ocean ecology and thermal structure occurring over geologic time all appear to have had a major influence on the evolution of tuna swimming performance and endothermy, which in turn influenced this group's adaptive radiation (Graham and Dickson, 2000).

C. Thermocentrism: Toward a Modern Synthesis of Tuna Endothermy

The conclusion of the 1978 review of tuna thermal relations by Stevens and Neill was titled "A Thermocentric Overview of Tuna Evolution." That title was

appropriate then and it remains so now. Most investigators would agree that tuna thermal relations are as fundamental to their biology as is swimming. In the next section we describe four categories of laboratory research on tuna endothermy: (1) the capacity of tunas to regulate heat gain and loss, (2) the effects of temperature on tuna metabolic processes, (3) the combined effects of tuna endothermy and enhanced swimming performance on this group's evolutionary radiation, and (4) the ontogeny of tuna endothermy.

However, before ending this discussion of the history of research into and ideas about tuna endothermy, it is important to consider some of the factors that influenced the direction of the laboratory work. Fisheries issues such as the eastern tropical Pacific tuna–porpoise problem increased the need to develop more precise models for predicting (for commercial purposes) tuna movements, and these began to use physiological data to better define the role that ambient temperature and dissolved oxygen might play. For example, the model of Barkley *et al.* (1978) suggested that, for larger *Katsuwonus,* the intersection of limiting thermal and oxygen isopleths made large regions of the eastern tropical Pacific uninhabitable (Brill and Bushnell, 1991; Korsmeyer *et al.,* 1996a,b). To refine such predictions, experiments at Kewalo Basin tested the ability of tunas to perceive temperature gradients and determined the effects of different O_2 levels and T_w's on swimming velocities (Stevens and Neill, 1978; Dizon *et al.,* 1978; Brill, 1992). A related idea was that tunas were prisoners of their efficient thermoconserving machinery and thus vulnerable to overheating in warm waters, especially during bouts of intense activity (Sharp and Vlymen, 1978). This led to tests of tuna capacity to alter T_b by adjusting *retial* exchange efficiency (Dizon and Brill, 1979a,b; Brill *et al.,* 1994). Similarly, questions about tuna metabolic rate were logical extensions of the need to develop energetics models.

It is certainly true that conjecture about tuna metabolism was strongly tied to the generalization that tunas had a mammal-like physiology (Korsmeyer and Dewar, this volume). It was thought that, to thermoregulate in water, tunas had to have acquired mammal-like metabolic rates and that they had "beaten the fish system" in the sense of having overcome the ventilatory limitations of water (high heat capacity, low O_2 volume). Stevens and Neill (1978) wrote, "Tunas are not poikilotherms; at least one tuna, the bluefin, is in fact on the verge of homiothermy."

The bluefin studied by Carey and co-workers were very large, whereas the kawakawa, skipjack, bigeye (*T. obesus*), and yellowfin studied in the Kewalo Basin laboratory were small (1–5 kg). Studies with these smaller tunas show that they are not as warm as mammals, they can elevate the temperature of only certain tissues and are thus regional heterotherms rather than true homeotherms, the heart cannot be warmed, and they have less precise central nervous system (CNS) control over T_b (Brill *et al.,* 1994; Dewar *et al.,* 1994; Brill, 1996). As subsequent sections will show, the extent to which body size is a prevailing feature in the

physiological capacity for endothermy in some species remains a largely open question.

IV. RECENT LABORATORY STUDIES OF TUNA ENDOTHERMY

A. Control of Heat Gain and Loss

With the discovery that bluefin and quite likely other tunas could thermoregulate (Carey and Lawson, 1973), the stakes were raised for physiologists interested in tuna endothermy because they now had a model system that appeared to function like a mammal even with the limitations imposed by respiring with gills and being immersed in water. The obvious questions were the following: How efficient at heat conservation were the *retia* (see Section II.B.3)? Do tunas have circulatory shunts that bypass *retia* for purposes of regulating T_b? If so, are these regulated by the CNS? How precise is tuna thermoregulation? How much heat can RM generate?

To these ends, laboratory studies examined heat-exchanger anatomy and efficiency, measured body temperature and heat balance, and determined how swimming activity affects T_b and how T_w affects swimming. Computer modeling of the temperature changes exhibited by free-swimming, telemetered bluefin also challenged the ideas that a conventional thermoregulatory physiology occurred in tunas. Neill and Stevens (1974) suggested that large tunas had a thermal inertia and, rather than defending a specific T_b, simply had retarded heat gain and loss rates that minimized changes in T_b. The next sections show how laboratory research provided insight into the mechanisms of heat production and conservation and, by permitting the substitution of real values for assumed ones, contributed importantly to integrating tuna endothermy into fishery models.

1. Steady State Conditions

Heat-transfer principles applying to tunas have been elucidated by a number of workers (Neill *et al.*, 1976; Dizon *et al.*, 1978; Sharp and Vlymen, 1978; Dizon and Brill, 1979a; Graham, 1983; Brill *et al.*, 1994; Dewar *et al.*, 1994; and also consult the papers cited within these works). Here, we begin by defining heat balance in a tuna swimming at steady state; that is, when its rates of heat production (use of RM in swimming is the principal source of this heat production) and heat loss are equal and T_b is constant (Equation 3). Under these conditions, and assuming the gut is empty so that visceral heat generation is not contributing to the heat-balance problem, the temperature in a tuna's peripheral tissues approaches T_w, but it has a warm core insulated by *retia*. Steady state heat balance can be described by

$$dQ/dt = K\ (A/d)\ (T_b - T_w), \quad (4)$$

where dQ/dt is the rate of heat transfer for the entire body (and which is zero at steady state), A is body surface area, T_b is the temperature of the warm core which has a thickness of d, and K is the coefficient of thermal exchange, an empirically determined descriptor of heat transfer (Brill *et al.*, 1994; Dewar *et al.*, 1994).

Four aspects of this model warrant discussion. First, as emphasized in section II.B.2, visceral as well as RM heat may contribute to steady state heat balance in some tuna species. In this case "steady state" conditions would be subject to change as a function of feeding frequency and the duration of the postprandial periods required for digestion and assimilation.

Second, specification of a warm isothermal core differs from the actual tuna condition where the "core" has a temperature gradient and its shape also varies with RM position. In the more basal tunas the warm core encompasses the vertebral column and extends both horizontally and vertically. In *T. obesus, T. thynnus,* and *T. alalunga* the vertebral region is cooler than the two warm areas positioned more laterally within the RM (Carey and Teal, 1966; Carey *et al.*, 1971; Graham, 1973, 1975, 1983; Graham and Dickson, 1981). Thus, while models assume standard conditions in all tunas, many biologically interesting features exist because of these interspecific differences. For example, the thermal profiles of the above-mentioned fish might be different following a large meal. [As detailed in Graham (1983) and elsewhere, the discrepancy between the core temperature and equation assumptions is minor and resolved mathematically by defining a series of progressively cooler concentric rings around the central core and, with the Fourier equation, integrating these with respect to temperature to determine an empirically verifiable thermal gradient from the core to the skin.]

Third, as developed in Graham (1983), detailed heat-transfer models include a dimensionless term, h, describing the convective heat-transfer coefficient for water contacting the body surface. This term may also be combined with the Nusselt (Nu) and Reynolds (Re) numbers to define how body shape and boundary layer motion (velocity) affect heat transfer. These applications are beyond the scope of this review and are probably irrelevant for tunas because they are continuously in a state of high convective flow over the body surface which minimizes boundary layer thickness.

Fourth, K in Equation (4) describes all of the internal and external conductive and convective properties affecting heat transfer. This includes convective heat loss to the gills from the tuna's warm RM core as well as "non-*retial*" heat-flux avenues such as the conduction of RM (and visceral) heat from the core through the muscle and other tissues to the body surface, and conduction of heat across the core to other tissues and from there into the blood where it is convected to the gills. (Note that at steady state, T_b is not changing and the rate of heat loss via all of these routes must equal heat production rate.) Because it is not possible to

simultaneously measure these different components of K, it is important to design standardized experiments that minimize their variation, as is now discussed.

2. Non-Steady State Conditions

Non-steady state heat transfer applies when heat production and loss are not equal and T_b is changing. This commonly occurs during vigorous swimming in pursuit of prey (Figure 7) and during rapid depth changes, which can greatly increase the difference between T_b and T_w, and even reverse the direction of heat flow (Holland *et al.*, 1992; Dewar *et al.*, 1994). The non-steady state condition is described by

$$dT_b/dt = K\ (A/d)\ (T_b - T_w) + dT_{b\ MET}/dt, \tag{5}$$

where K, A, and d are as in Equation (4), dT_b/dt is rate of change of T_b (°C min^{-1}, which can be positive or negative), and $dT_{b\ MET}/dt$ is the rate of T_b change resulting from RM, visceral, and other sources of heat production. HP_{RM} is heat production (°C min^{-1}), as defined earlier. Assuming that the tuna maintains a constant swim-

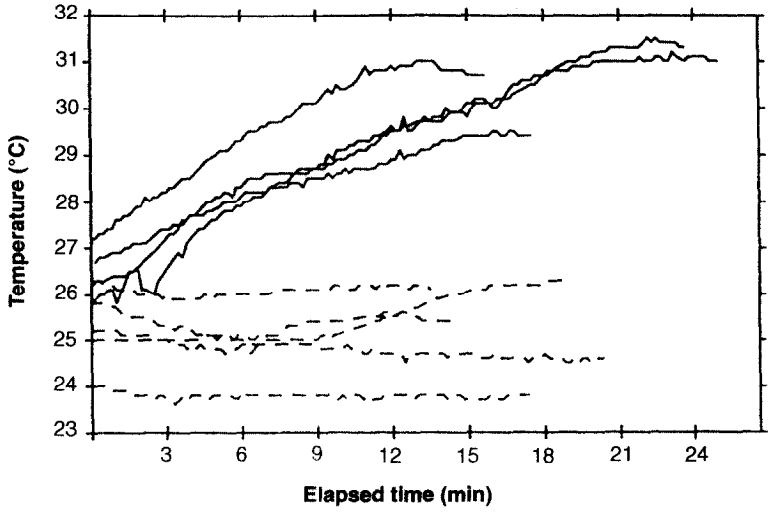


Fig. 7. Changes in RM (solid lines) and WM (dashed lines) temperatures of nine skipjack (*Katsuwonus*, 1–2 kg) during vigorous swimming induced by chasing food thrown across a large pool, away from their location. The large oceanarium tank at Kewalo Basin was used and ultrasonic pulse rate transmitters provided the temperature records. Because RM circulation is via *retia*, T_{RM} increased over the period of feeding. WM circulation is not via *retia* and T_{WM} remained about the same, although in some specimens T_{WM} was 0.5–2.0°C warmer than T_w (23.6–23.9°C), which probably reflects probe position in the body. (From Brill *et al.*, 1994, with kind permission from Kluwer Academic Publishers.)

ming speed (and use of RM for this is the largest source of metabolic heat) and that the thermal effects on other metabolic heat sources are minimal, the $dT_{b\,MET}/dt$ term can be neglected (Graham, 1983; Brill *et al.*, 1994). Also, because A/d is assumed to be constant, Equation (5) reduces to

$$dT_b/dt = K\,(T_b - T_w), \tag{6}$$

and integration with respect to t yields

$$T_b\ (at\ any\ time,\ t) = T_e - [T_e - T_b\ (at\ t = 0)\ e^{-Kt}], \tag{7}$$

where t is the elapsed time, T_e is the equilibrium T_b at the new T_w, and the other variables are as above. Studies of steady state and non-steady state heat transfer have contributed to documentation of tuna physiological thermoregulation.

3. Physiological Control of Heat Balance

The relationship between T_w and T_b (usually T_{RM} and T_{WM}) of freshly caught bluefin provided the first evidence for thermoregulation (Carey and Teal, 1966, 1969a; Carey *et al.*, 1971). Based on 162 temperature measurements, the linear regression relating T_b and T_w was

$$T_b = 25.84 + (0.206)T_w. \tag{8}$$

Thus, bluefin T_b was only slightly less in warm waters than in cool waters (Graham, 1983). Telemetric monitoring of T_b and T_w provided additional evidence for the bluefin's capacity to control T_x over a range of T_w's (Linthicum and Carey, 1972; Carey and Lawson, 1973; Gunn and Block, this volume).

However, computer analysis of the short-term changes in bluefin T_b by Neill and Stevens (1974) suggested that, rather than physiological thermoregulation, thermal inertia (i.e., a large thermal mass "cushioned from T_w" by conductance-retarding *retia*) offered a less presumptive explanation of the data. Although "thermal inertia" is involved in the reduced rate of heat loss in a tuna descending into cooler water, it does not apply to the facets of tuna endothermy that require modulation of rates of heat gain and loss in relation to T_x, T_w, and activity level, including the capacity to "reverse" conductance and rapidly elevate T_b during ascent into warmer water. Nor does thermal inertia and its assumption of a large thermal mass strictly apply to bluefin physiology; small bluefin at a T_w of 21°C have the same T_x as do giant bluefin and are warmer than either skipjack or yellowfin at similar T_w's (Linthicum and Carey, 1972, Table 1). More recent telemetry studies have shown that physiological thermoregulation and control of thermal conductance occur in bigeye tuna *in vivo* (Holland *et al.*, 1992).

Laboratory studies also demonstrated the capacity of tunas to change T_b by regulating K. Thermally telemetered yellowfin and skipjack tunas swimming in a donut tank in Kewalo Basin could, within several hours of an abrupt change in T_w, alter K and arrive at a new steady state T_x (Dizon *et al.*, 1978; Dizon and Brill,

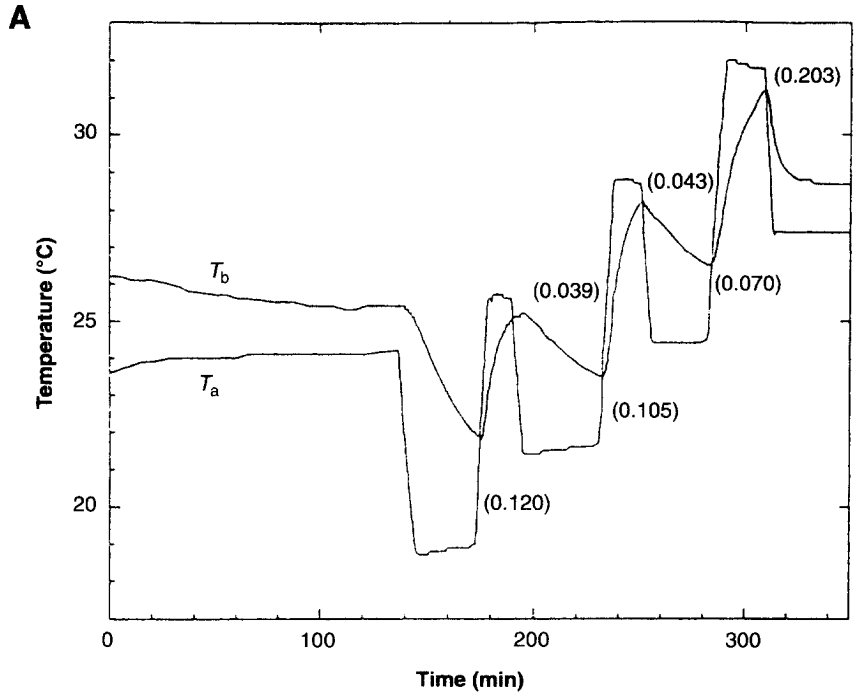
1979a,b). Because those fishes were swimming at a nearly constant velocity and thus had stable RM heat production rates, the data suggested that changes in K enabled them to alter T_x with respect to T_w. Shipboard tests also showed that lightly anesthetized albacore exposed to abrupt cooling could alter thermal conductance and reduce their cooling rate (Graham and Dickson, 1981).

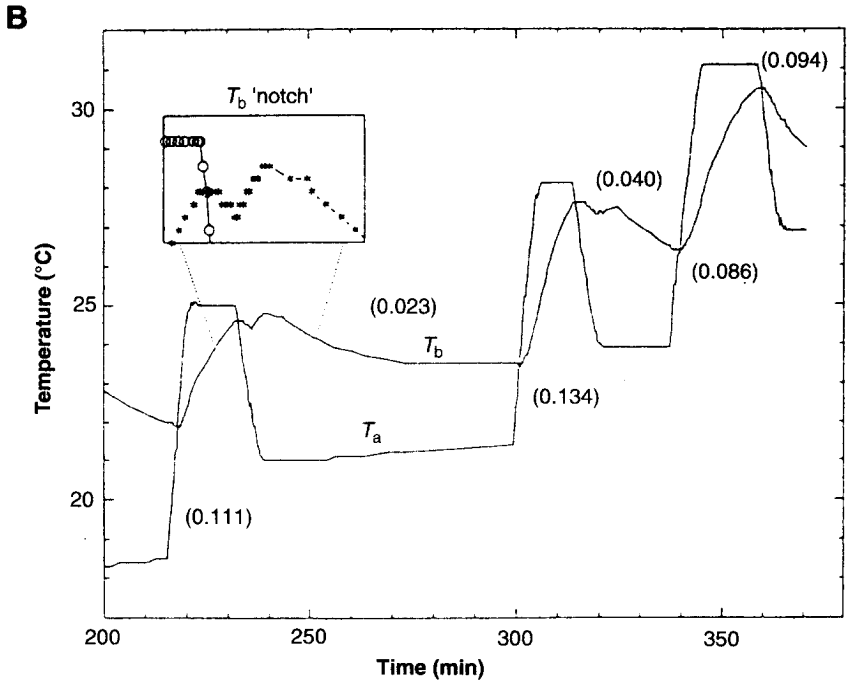
The yellowfin tuna's capacity for altering thermal conductance was demonstrated by Dewar *et al.* (1994). These tests involved imposing three successive square-wave T_w changes on steadily swimming yellowfin tuna (about 2 kg mass) in which T_{RM} was continuously monitored by percutaneously implanted thermocouples. The T_w changes mimicked the rate and range of temperature change encountered during the fish's normal vertical movements and were thus physiologically relevant. Furthermore, tests at higher than typical T_w's enabled contrasting of the impact of changes in K and temperature on T_{RM}. The experimental technique also regulated the magnitude of each T_w change so that the initial thermal gradient between T_{RM} and T_w was always the same, thus allowing the estimates of K to be made over the same range of $T_{RM} - T_w$. This also minimized the non-*retial*-regulated variables affecting K, as well as other thermal effects on physiology (Brill *et al.*, 1994; Dewar *et al.*, 1994).

The findings were that the rate of RM temperature change depends upon T_w, T_b, and the magnitude and direction of the T_w change. When swimming in 32°C water, which is warmer than normally encountered, yellowfin respond to square-wave cooling by immediately and rapidly shedding heat (Figure 8A). This rate of heat loss exceeds that observed at lower T_w's (where heat conservation would be more important). Similarly, when the yellowfin's T_b is cooler than "preferred" and cooler than T_w, a condition is modeled that normally occurs as a fish ascends into warm surface waters after an extended time in deeper, cooler water (Holland *et al.*, 1992); it heats more rapidly than if it had the approximately steady state T_x of a near-surface swimming fish exposed to a square wave of heating.

That the CNS regulates heat gain and loss is suggested by the experimental induction of "thermal notches." Figure 8B shows that, during the warming phase (i.e., $T_{RM} < T_w$, and T_x is negative), heat transfer was increased to allow the influx of heat to augment warming. Then, when T_w was dropped (T_x became positive), the fish was momentarily trapped in a "high K mode" which led to the rapid but short-lived fall in T_{RM}. To prevent continued heat loss at the lower T_W in cycles 1 and 2, heat flux was abruptly curtailed, leading to the leveling off and subsequent increase in T_{RM}.

The most parsimonious explanation for the rise in T_{RM} in the "thermal notch" is that the rapid induction of thermoconservation curtailed convective heat loss sufficiently to elevate T_{RM}. Also, with the heat exchangers "turned off" during the warming phase, the abrupt onset of cool water may have channeled unheated blood directly into the yellowfin's RM to cause localized convective cooling. Because the adjacent WM is also warm but receives less blood flow, its temperature


A
30
25
20
Temperature (°C)
T_b
T_a
(0.203)
(0.043)
(0.039)
(0.070)
(0.105)
(0.120)
0
100
200
300
Time (min)


B
30
25
20
Temperature (°C)
T_b 'notch'
(0.094)
(0.040)
(0.086)
(0.023)
T_b
(0.134)
T_a
(0.111)
200
250
300
350
Time (min)

would not decline as rapidly. Thus, if T_{RM} was less than T_{WM}, conductive heat flux from the WM to the RM may have also contributed to the rise in T_{RM}.

In summary, tunas do not precisely regulate T_b and thus do not thermoregulate in the same way as mammals. Even the most refined data for large free-swimming bluefin tunas show that they lack the thermoregulatory precision of mammals (Carey and Lawson, 1973; Gunn and Block, this volume). Tunas do, nevertheless, have the ability to regulate heat gain and loss and modulate K, and they do this in concert with "thermal-gradient-altering behaviors" [e.g., changing depth (= T_w), swimming speed (= HP_{RM}), or both]. Thus, tunas appear capable of using physiological mechanisms to minimize changes in T_{RM} and other deep tissues, and they are not prisoners of their own thermoconserving devices (see Brill *et al.*, 1994).

The suite of physiological mechanisms underlying this remains largely unknown. As summarized here, laboratory studies by Dewar *et al.* (1994), Brill *et al.* (1994), and others have demonstrated that tunas do alter K, probably by adjusting *retial* heat-exchange efficiency. The anatomical studies of *retia* summarized above (Section II.B.1) suggest that tunas may alter K by vasodilation or vasoconstriction of the *rete* blood vessels, thereby modulating blood flow through the *retia* and affecting heat-exchange effectiveness. It also appears that the *Thunnus* species that lack both a postcardinal vein and a central *rete* (Table II) may be able to adjust T_{RM} by altering the relative blood flow via the dorsal aorta (carrying cool blood to the RM) and the lateral arteries. Vascular casts of the bluefin's central and lateral circulations (Funakoshi *et al.*, 1983) show that arterial branches from the dorsal aorta penetrate into the same RM regions as do *retia* from the lateral vessels.

Species having both central and lateral *retia,* in which all blood flow to the RM presumably passes through *retia,* might be able to adjust K by changing the relative flow through the two *rete* types, assuming these have different heat-exchange efficiencies. For example, *Euthynnus lineatus* has two small lateral *retia* with relatively little surface area contact between arterial and venous vessels for heat exchange, but a much larger central *rete* with a large surface area for heat exchange (Graham and Diener, 1978; Dickson *et al.*, 2000). However, there are precious few details about *retial* geometry, vessel fine structure, and microcirculation in the different tuna species, and nothing is known of how *rete* vessel diameter is controlled physiologically (Brill *et al.*, 1994). There are several observations of nerves occurring near or within the *retia* (Eschricht and Müller, 1835; Kishinouye, 1923; Stevens *et al.*, 1974; Moore, 1998), but it is not known if they innervate the *rete* vessel smooth muscle cells, or even if they are autonomic motor

Fig. 8. (A) Traces of T_w and T_{RM} over time in a yellowfin tuna swimming at a constant velocity. Beginning at 120 min the fish was exposed to a series of "square-wave" changes in T_w, and the effect of these on T_{RM} and K (parenthetic values) were calculated. (B) Traces of T_w and T_{RM} during square-wave changes in T_w. K values are in parentheses. Note that the rapid drop in T_w while the fish is still warming results in the thermal notch (see text for details). (From Dewar *et al.*, 1994, with permission from Company of Biologists, Ltd.)

nerves. Stevens *et al.* (1974) reported unsuccessful attempts to locate nerves within the walls of central *rete* vessels in *Katsuwonus pelamis.* Apart from the apparent capacity of bluefin to perfuse the same RM region with either warm or cool blood (Funakoshi *et al.,* 1983), anatomical studies have failed to show any circulatory shunts around *retia* (Carey *et al.,* 1971; Gibbs and Collette, 1967; Graham, 1973, 1975) which would provide another mechanism for controlling K.

B. Metabolic Performance

The enhancing effect of temperature on most biological rate processes was emphasized by Carey and Teal (1966), and subsequent research has documented this (Carey *et al.,* 1971; Graham, 1975; Neill *et al.,* 1976; Stevens and Neill, 1978; Dizon and Brill, 1979a,b; Johnston and Brill, 1984; Block *et al.,* 1993). Korsmeyer *et al.* (1996a) provided an integrated energy budget analysis for tuna metabolism in which the "enhancing effect of elevated temperature" was factored into estimates of the different components of total metabolic rate.

First principles (Rome, 1995) dictate that elevation of T_{RM} results in greater RM contraction velocity, force, and power output, and a positive thermal effect for muscle has been demonstrated at several levels. Johnston and Brill (1984) demonstrated the positive effect of temperature on the *in vitro* contraction rate of isolated skipjack tuna RM fibers. Altringham and Block (1997) showed that a 10°C temperature increase doubled the muscle contractile power output of isolated blocks of RM from yellowfin tuna. Dickson (1995, 1996) found that while the activity of the RM aerobic enzyme citrate synthase (CS) at a given temperature did not differ significantly between tunas and their closest scombrid relatives [the ectothermic bonitos (*Sarda*), mackerels (*Scomber*), and Spanish mackerels (*Scomberomorus*)], the Q_{10} for tuna RM CS activity ranged between 1.77 and 2.08. Thus, when adjusted to *in vivo* temperatures, tuna RM has a much greater potential for supplying energy for sustainable swimming. That temperature may also affect scombrid swimming performance is suggested by the findings that maximal sustainable swimming speed, O_2 consumption rate, and net cost of transport of the chub mackerel (*Scomber japonicus,* an ectothermic scombrid) are all higher at 24°C than at 18°C (Sepulveda and Dickson, 1998). However, what is needed to test if endothermy enhances the swimming performance of tunas is a comparison of an endothermic tuna with a member of its ectothermic sister taxa. A recent comparison of swimming performance in juvenile kawakawa tuna (*Euthynnus affinis*) and size-matched chub mackerel showed no interspecific difference in maximum sustainable speed or net cost of transport (Sepulveda and Dickson, 2000). However, the kawakawa in that study had a T_{RM} that was at most only 2.3°C warmer than T_w. Similar work on larger individuals and on bonitos is clearly needed.

Another dimension of heat conservation for tuna muscle function is that a large percentage of the WM is also warm (Carey and Teal, 1966, 1969a; Graham,

1973). Tuna WM has higher activities of aerobic and anaerobic metabolic enzymes than that of ectothermic scombrids (Dickson, 1995, 1996). As with RM, an elevated T_{WM} would positively affect contraction velocity, force, and power production. Thus, endothermy may also have a positive effect on burst swimming and acceleration (Graham, 1975; Dizon *et al.*, 1978; Brill, 1996). However, no data exist to test this hypothesis due to the difficulty of measuring burst swimming in tunas and other scombrids. An elevated T_{WM} and this tissue's high aerobic activity may also increase the rate of lactate clearance following burst swimming (Dickson, 1995; Korsmeyer *et al.*, 1996a; Brill, 1996). The skipjack tuna (*Katsuwonus pelamis*) has the fastest rate of lactate clearance known for any fish (Arthur *et al.*, 1992), but no comparisons with ectothermic scombrids have been made.

The visceral cavity of four tuna species and the brains of most tunas are warm, and this must also positively affect thermally dependent rate processes such as digestion, gastric evacuation, assimilation, and sensory perception, although there are no data for thermal effects on sensory perception or on assimilation (reviewed in Korsmeyer *et al.*, 1996a). Carey *et al.* (1984) documented the facultative heating of the bluefin stomach with feeding, and Stevens and McLeese (1984) found that the bluefin's elevated visceral temperatures resulted in a threefold increase in the activity of digestive peptidases. It is also known that the gastric evacuation rates of tunas (*Thunnus albacares, Euthynnus lineatus*) exceed those of most other species (Schaefer, 1984; Olson and Boggs, 1986), but neither of these species has been shown to maintain elevated $T_{viscera}$. Moreover, because there are no data for ectothermic scombrids, it is not known if the rapid gastric evacuation rates of tunas are a consequence of endothermy. More information on the role of elevated brain and visceral temperatures in tunas is needed.

Thus, as predicted by Carey and Teal (1966), the enhancing effect of temperature on various rate processes in tunas has been confirmed, primarily in laboratory studies of isolated tissues. Future research to determine if such thermal enhancements affect whole-animal performance, and additional data on digestion, assimilation, growth, and sensory perception in tunas and their ectothermic relatives, is needed (Brill, 1996; Korsmeyer *et al.*, 1996a; Korsmeyer and Dewar, this volume).

C. Tuna Locomotion, Endothermy, and Evolution

A larger issue concerning endothermy is the role it may have played in tuna evolutionary ecology (Block *et al.*, 1993; Graham and Dickson, 2000). Whereas elevated temperature enhances tuna performance, the evolutionary impact of endothermy may have been to expand the thermal range, both vertically and latitudinally, of tunas relative to ectothermic scombrids. Because the early radiation of tunas coincided with the geological time span in which major changes in ocean surface currents, thermal structure, and productivity patterns were taking place,

selection that enhanced sustained swimming performance (for migration to reach distantly located food resources) may have been important in the evolution of both a more efficient swimming mode and endothermy (Graham and Dickson, 2000).

The paleontological record indicates that tunas diverged from a tuna–bonito ancestor during the early Tertiary (Bannikov, 1985). At that time a number of the physical characteristics of the modern oceans (e.g., basin geography, wind-driven gyre circulation, thermal structure, and upwelling) were first appearing. Changing paleoceanographic conditions may have led to the radiation of tunas from a coastal distribution to a more open-ocean existence involving long-distance migrations. With the cooling of ocean temperatures beginning in the Tertiary and a reduction in the ancestral tunas' habitat (the warm Tethys Sea), endothermy may have enabled the early tunas to extend their foraging to below the thermocline without acclimating or adapting to a cold environment, in order to maintain or expand the volume of water available for exploitation (Graham and Dickson, 2000).

We have proposed a sequence of character-state acquisitions leading to efficient, high-performance swimming and endothermy in the tunas (Figure 9). This sequence is based on the discovery that the slender tuna, *Allothunnus fallai,* has its RM in the anterior and internal position that is a synapomorphy of the tunas, and which differs from the RM distribution in the bonitos *Sarda* spp. and *Gymnosarda unicolor* (Graham and Dickson, 2000). We also found that the central circulation of *Allothunnus* is elaborated to form a *rete*-like structure composed of numerous arterial and venous vessels to and from the RM. However, *Allothunnus* lacks the lateral countercurrent heat-exchanging blood vessels perfusing the RM that are present in all other tunas. Based on these characters and ancestral character-state reconstructions done in MacClade (Maddison and Maddison, 1992), we have proposed that the anterior, internalized RM position preceded the evolution of endothermy (Figure 9). Block and Finnerty (1994) also proposed this evolutionary sequence, based on some degree of RM internalization in *Sarda.*

Our view is that it was the selection for more efficient swimming that led to the derived RM position of tunas. The most recent studies support this hypothesis, because it appears that only the tunas, with a distinctly different RM distribution in which parts of the anterior-pointing myotomal cones are composed of RM fibers, swim in the thunniform mode. Recent studies of swimming yellowfin tuna (Shadwick *et al.,* 1999; Altringham and Shadwick, this volume) have shown that internally placed RM produces greater strain, thus providing a selective advantage related to swimming performance for the derived RM position. That work provides a mechanism to explain the first step in the evolutionary progression revealed by our studies of *Allothunnus* (Figure 9). We theorized that, once RM was internalized, elaboration of blood vessels to perfuse the RM led first to the central *rete* and then to the lateral *retia,* which conserved enough metabolic heat for the fish to maintain elevated muscle temperatures (Graham and Dickson, 2000). The acquisition of endothermic capabilities would have further enhanced swimming performance and allowed thermal niche expansion in the more derived tunas. With

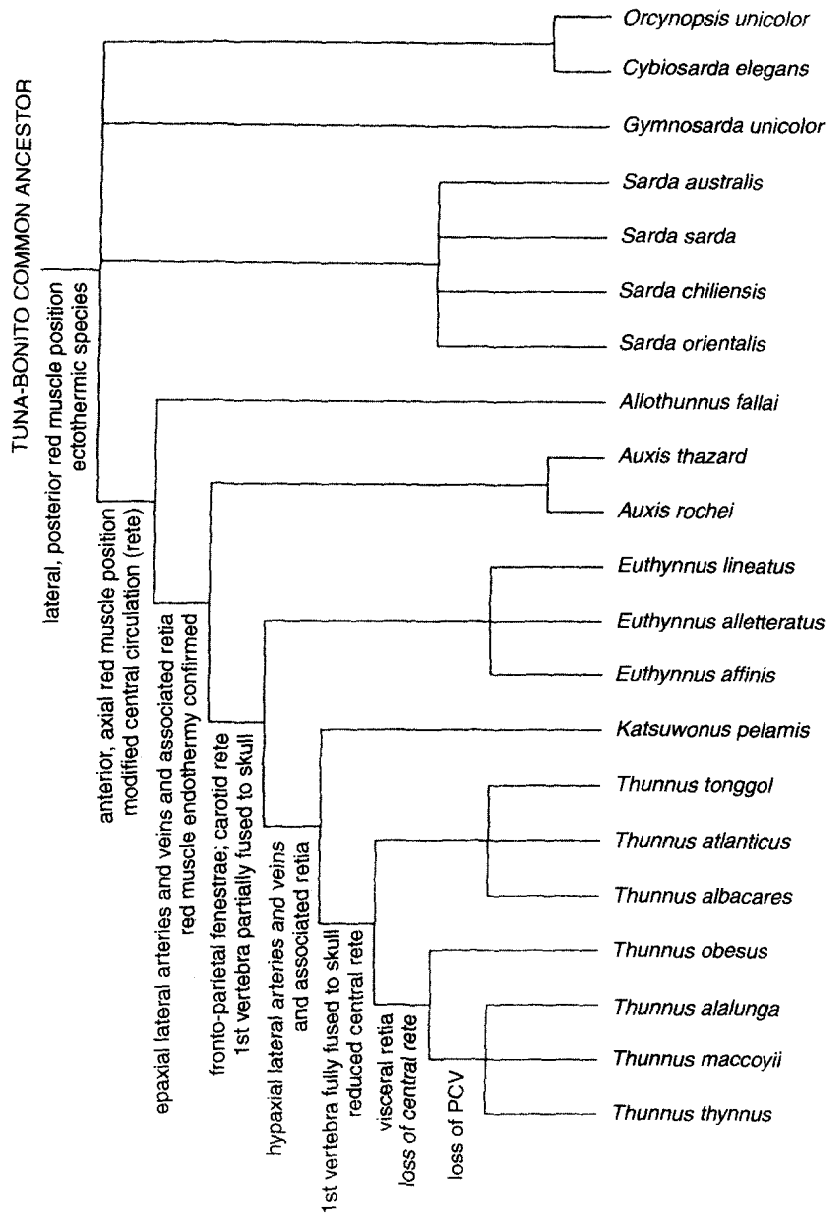


Fig. 9. Pylogeny for all species in the clade composed of the bonitos and tunas, based on morphological characteristics (Collette and Chao, 1975; Carpenter *et al.*, 1995) and new data for the slender tuna, *Allothunnus fallai* (Graham and Dickson, 2000). Mapped onto this phylogeny are the characteristics related to endothermy and thunniform locomotion, showing the hypothesized sequence of character changes reflecting a co-evolutionary progression of locomotor (red muscle) and heat conservation (circulation) specializations in the tuna species. (From Graham and Dickson, 2000.)

the Tertiary cooling of the oceans, selection for endothermy would have been very important, and we postulate that this drove the subsequent evolution of mechanisms to maintain elevated temperatures of the locomotor muscle, brain and eyes, and viscera (Figure 9).

It is emphasized that the phylogeny shown in Figure 9 differs from the one in Figure 2 of Collette, Reeb, and Block (this volume), which is based on cytochrome *b* gene sequences of many of the scombrid species. If that cladogram is supported by additional data, then the evolutionary sequence of character changes would differ from the one we have proposed in Figure 9. Specifically, the Collette, Reeb, and Block phylogeny requires the assumption that characters such as the loss of a post cardinal vein and the presence of visceral *retia* evolved independently in at least two clades of *Thunnus.* Also, because the Collette, Reeb, and Block phylogeny does not indicate *Allothunnus fallai* as the sister group to the rest of the Thunnini, this would require the assumption that both changes in RM position and a modified central circulation evolved independently in *A. fallai* and the tunas or that these two characters were lost in *Sarda.* It should also be noted that the position of *A. fallai* shown in Figure 2 of Collette, Reeb, and Block is not

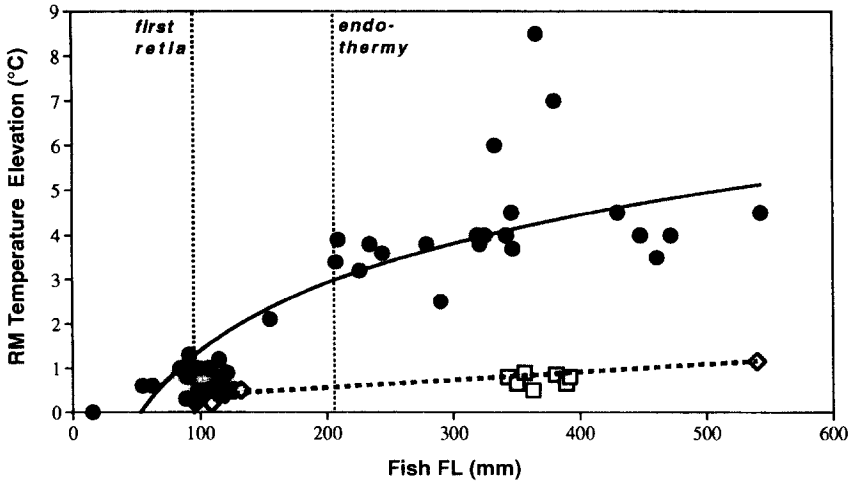


Fig. 10. Relationship between T_{RM} elevation (T_x) and fork length (FL) in *Euthynnus lineatus* (solid circles) and two ectothermic scombrid species, the chub mackerel, *Scomber japonicus* (squares; Roberts and Graham, 1979), and the sierra mackerel, *Scomberomorus sierra* (diamonds; Lindsey, 1968; Dickson, 1994). A 3°C or greater T_x can be generated by all *E. lineatus* ≥ 207 mm FL, the hypothesized minimum size for endothermy (vertical dashed line). The first appearance of *retia* at 95.9 mm FL (dashed line) in this species coincides with the point at which the tuna and ectotherm curves diverge. (From Dickson *et al.*, 2000.)

strongly supported statistically (bootstrap values are < 50%), and moreover differs from the position shown in Figure 3 of the same paper. As was reported in Graham and Dickson (2000), an analysis of cytochrome *b* gene sequences from *A. fallai, Gymnosarda unicolor,* and *Sarda orientalis* (unpublished data of Blaise Eitner and Carol Kimbrell), combined with sequences from Block *et al.* (1993) and Finnerty and Block (1995), could not resolve this node of the phylogeny. Thus, until the problems with the molecular phylogenetic data for the Scombridae that are discussed in Collette, Reeb, and Block (this volume) are overcome, it will be difficult to test our hypothesis for the evolution of tuna specializations.

D. The Ontogeny of Tuna Endothermy

Juvenile tunas ranging in length from 20 to 30 mm fork length are rarely collected and it has only recently been possible to study the ontogeny of endothermy. Neither the small pelagic eggs nor the larvae of tunas have a T_x; endothermy is acquired during the juvenile stage (Dickson, 1994). The transition to endothermy is accompanied by increases in the ability to both produce and retain metabolic heat, and also correlates with changes in body shape (declining ratio of surface area to volume and an increase in girth).

The studies summarized here were conducted on juvenile black skipjack tuna, *Euthynnus lineatus,* raised from postflexion larvae and early juvenile stages (10–20 mm fork length, FL) at the Inter-American Tropical Tuna Commission Laboratory in Panama. Dickson (1994) showed that juvenile *E. lineatus* as small as 207 mm FL can elevate $T_{RM} \geq 3°C$ above T_w (Figure 10). Because all acute temperature measurements from fishes incapable of elevating T_{RM} at any size are $\leq 2.7°C$, Dickson (1994) hypothesized that the minimum size for endothermy in tunas is approximately 207 mm FL.

Subsequent studies (Dickson *et al.,* 2000) have tracked the development of characteristics required for endothermy across this critical size. Central *rete* vessels are first evident in *E. lineatus* at 95.9 mm FL, and lateral *rete* vessels first appear at 125 mm FL (Dickson *et al.,* 2000). As fish girth and mass increase, both central and lateral *retia* become longer (a greater distance to the RM), and additional vessel rows are added to them (Dickson, 1994; Dickson *et al.,* 2000). Increases in both *rete* vessel length and number augment heat retention within a RM mass that is also increasing with fish FL (Figure 11).

Internal RM occurs in all juvenile tunas that have been examined, down to 14 mm FL (Dickson *et al.,* 2000); black skipjack juveniles of this size are approximately 16 days posthatch (Wexler, 1993). The ontogeny of the unique interior–anterior RM position of tunas has not been detailed but undoubtedly must involve a change in fiber-type expression in the cells within the anterior-pointing cones of the myotomes. As juvenile *E. lineatus* grow, total RM heat production potential increases due primarily to increases in total RM mass (RM–body mass scaling

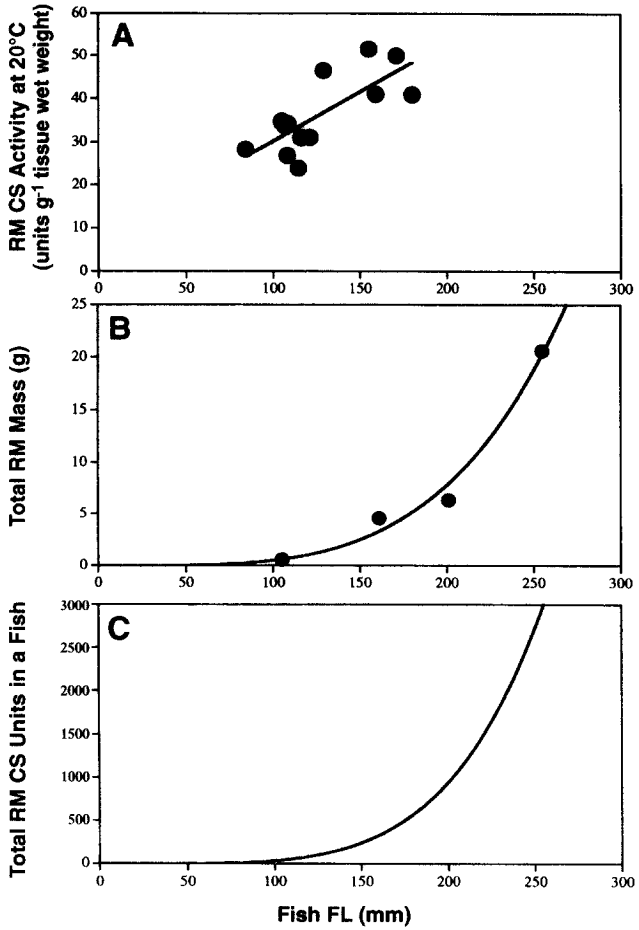


Fig. 11. Estimated total heat production potential [total activity of the mitochondrial marker enzyme, citrate synthase (CS), in RM] versus fish fork length (FL) in juvenile black skipjack, *Euthynnus lineatus*. (A) The relationship between RM CS specific activity [international units (μmol substrate converted to product min^{-1}) g^{-1} tissue wet weight] at 20°C and fish FL. (B) Relationship between total RM mass and FL. (C) The product of A and B is the total units of CS in the RM as a function of FL.

coefficient is 1.17) and also to a rise in the specific activity of RM CS (Figure 11). Both of these increases with fish FL are greater than they are in the ectothermic scombrid *Scomberomorus sierra* (Dickson *et al.*, 2000).

The size or age at which each tuna species transitions to endothermy and thus gains some independence from the thermal environment has implications for the

early life history and ecology of the species. All tuna species spawn in warm waters (Nakamura, 1969; Bayliff, 1980) and the juveniles may require warm waters for optimal growth and feeding, and might also not be able to exploit cooler waters until they become endothermic. To test this idea, we need to know more about the distribution and behavior of young tunas to determine if they must be able to maintain a certain T_x before they move into cooler waters below the thermocline or at higher latitudes.

E. Endothermy in Large Tunas

Most of the laboratory studies completed to date on live tunas have used small individuals. With the exception of at-sea studies of restrained albacore (Graham and Dickson, 1981; White *et al.*, 1988), these have all been done with tropical species (*Euthynnus* spp., *K. pelamis*, and *T. albacares*). Thus, a major question resulting from laboratory investigations of thermal physiology is whether the small tunas that have been studied provide any insight into the suite of endothermic properties likely to be present in larger tunas. The answer is an unqualified yes.

First, the initial concept held by many workers, that smaller tunas do not normally encounter the same thermal environmental range as larger individuals, has changed somewhat because recent tracking data for small tunas (e.g., 3- to 5-kg bigeye) show that they make excursions into very cool water (Holland *et al.*, 1992; Lowe *et al.*, 2000; Gunn and Block, this volume). Field telemetry data show that large tunas can control T_b fairly well (Gunn and Block, this volume). Laboratory telemetry studies indicate that 1- to 2-kg tunas can also generate a large T_x during activity and maintain this for a relatively long period (Brill *et al.*, 1994). Although there are few data for large tunas, T_b measurements on freshly decked, large tunas suggest that they do not necessarily have a higher T_b than do smaller individuals, but more extensive regions of the body are warm compared with smaller tunas (Carey *et al.*, 1971, 1984; Linthicum and Carey, 1972). This is also suggested by field telemetry (Gunn and Block, this volume).

While there are no metabolic data for large tunas, basic principles do suggest properties of their thermal physiology. First, because of the allometric scaling of metabolism and because the metabolic cost of transport diminishes with increased body size (Schmidt-Nielsen, 1984), relative heat production should be lower in large tunas. Also, larger tunas have lower relative amounts of RM and lower relative minimum swimming speeds (Magnuson, 1973, 1978; Graham *et al.*, 1983). Although these facts indicate a lower relative rate of RM heat production with increasing size, a larger tuna has both a thicker body and a larger thermal mass. This means that once a T_x is attained, a larger tuna would take much longer to reach thermal equilibrium at a new T_w than would a small tuna. In addition, large tunas have a more remote RM position relative to the body surface with longer

retial vessels connecting RM to the lateral arteries and veins, a lower surface area to volume ratio, and more insulation (subcutaneous fat)—all of which would favor a more stable T_b. Thus, although the relative size and activity of the heat generator are smaller in a large tuna, its remoteness from the body surface and the thermal inertia of a large body mass may lead to an expansion of the warm region as well as a more precise regulation of T_b through a finer scale control of the balance between heat production and heat loss (see Brill *et al.*, 1994).

V. EFFECTS OF ENDOTHERMY ON SOME CARDIOVASCULAR CHARACTERISTICS

This section discusses how variations in T_w and T_x may potentially affect two critical elements of tuna physiology related to endothermy, cardiac performance and the binding and transport of oxygen by Hb.

A. Endothermy and Heart Function

An account of tuna cardiovascular physiology is found in this volume's chapter by Brill and Bushnell. Tunas differ from most other fishes in having higher heart rates and by modulating cardiac output mainly through changes in heart rate as opposed to stroke volume. Additional research is needed to determine how heart activity is modulated with respect to endothermy and the metabolic requirements of the RM. The tuna heart is essential for endothermy, but it is not warm [i.e., it is seldom warmer than 0.1°C above T_w (Carey *et al.*, 1971; Graham, 1983)] and there are no known excitation-contraction coupling specializations to mitigate the effect of acute temperature change on heart rate.

Korsmeyer *et al.* (1997a) documented a rapid and strong effect of T_w on the heart rate of steadily swimming yellowfin. A T_w decrease from 28 to 18°C reduced heart rate by about 50%, and even though the stroke volume of the slowed heart increased, cardiac output declined by about 30%. Rapid depth changes expose tunas to abrupt T_w changes (as great as 8–14°C in a few minutes for *T. obesus;* Holland *et al.*, 1992). The Korsmeyer *et al.* data indicate how such a change would affect the heart: as T_w declines so does T_{HEART} and cardiac output. However, as detailed in Section IV.A.3, T_{RM} would "be defended," and RM would cool at a much lower rate. Thus, cardiac output to RM would drop abruptly while RM O_2 demand (a function of velocity and T_{RM}) would remain relatively constant (Korsmeyer *et al.*, 1997a,b).

The mismatch between blood-perfusion rate and RM O_2 requirements resulting from a rapid T_w change might limit the capacity of a tuna to remain in cool water. On the other hand, slowing of the heart could actually favor maintenance of T_{RM} and thus lengthen the tuna's time limit in cool water. The key issue in the perfusion reduction is how tissue O_2 delivery is impacted. Korsmeyer *et al.*

(1997b) reported that yellowfin tuna swimming in a water tunnel (normoxic water at 25°C) had a mean venous O_2 content of about 50% of arterial concentration. Thus, a sizable venous O_2 reserve is available to the tissues. As the rate of blood flow through RM capillaries falls in cooler water, the RM and other warm tissues could obtain their required O_2 by utilizing the venous reserve. This means that, provided cardiac output is adequate to sustain the O_2 reserve, tissue aerobic metabolism could be maintained. In fact, it might even be the case that under such conditions the potential for heat retention within RM increases (i.e., K is reduced). If a greater quantity of O_2 is used (and more heat is produced) per unit volume of blood flow, the ratio of heat removal to heat production is reduced, thus lowering convective heat transport from the RM. A lower perfusion rate also means that blood residence time within the *retia* increases, and this favors countercurrent heat transfer. A calculation could, for example, be made to determine the extent to which the heart-rate changes observed by Korsmeyer *et al.* (1997a) could account for the reduced K values observed for cooling yellowfin by Dewar *et al.* (1994).

Endothermy is critically dependent upon blood flow and, because T_w changes have a direct and immediate effect on the heart, cardiac output makes an important contribution to heat balance. This, however, does not mean that the T_w effect on the heart is the only or principal mechanism underlying the modulation of K. While thermal disequilibrium resulting from changes in T_w can result in blood-flow changes that appear to augment heat balance (i.e., slowing the heart in cool water, and accelerating it in warm water), changes in heat-balance requirements also occur independently of T_w. For example, increased swimming speed will require an elevated cardiac output, mediated by either catecholamines or sympathetic stimulation, and T_b usually increases (Dewar *et al.*, 1994; Brill *et al.*, 1994). It is unknown how increased velocity in cooler water would affect heart action and, in some environments, a deep-swimming tuna will also come in contact with hypoxic water. It can be expected that, whereas cardiac function may be responsive to T_b, control of the heart for purposes of O_2 delivery will prove of greater importance than heat balance.

B. Endothermy and Hb–O_2 Affinity

Endothermy also has implications for the kinetics of O_2 binding by Hb. Studies with a diversity of tuna species have documented the temperature independence of tuna Hb–O_2 binding (Carey and Gibson, 1983; Brill and Bushnell, 1991; Lowe *et al.*, 2000), an adaptation that permits rapid changes in T_w without impacting O_2 transport.

However, circulation through the countercurrent heat exchangers poses another potential problem for tuna Hb. Blood reaching thermal equilibrium with water in the gills may be transported to tissues having the same temperature as T_w or a higher temperature. In the latter case, the blood undergoes a relatively large temperature increase and remains warm until it passes back through the *retia.*

Blood heated within the *retia* cannot equilibrate with the atmosphere (i.e., it is a closed system) and, although its total O_2 and CO_2 content does not change, heating affects the pH and the gas solubility of the plasma, which results in changes in PO_2, PCO_2, and pH.

There has been considerable uncertainty over what adaptive scenario best applies to the closed-system temperature changes imposed on tuna Hb. The normal response to heating is for the Hb–O_2 binding curve to shift to the right (i.e., Hb–O_2 binding affinity is reduced, which raises the PO_2 and thus the O_2 diffusion gradient). After the first discovery of temperature-independent O_2 binding for bluefin tuna Hb solutions (Rossi-Fanelli and Antonini, 1960), it was argued that no effect or a negative effect of temperature on Hb–O_2 affinity was necessary to prevent the premature off-loading of O_2 within the *retia* (which would raise the trans-*retial* PO_2 gradient), and that a reduction in Hb–O_2 affinity within the *rete* would not favor tissue gas exchange (Graham, 1973; Carey and Gibson, 1983; Cech *et al.,* 1984). It was further assumed that because Hb insensitivity to temperature was critically important for tissue metabolism, the conditions for gas transfer in the gills (high surface area, short diffusion distance, high perfusion and ventilation) and in the RM (a strong Bohr effect) would ensure efficient gas exchange (Graham, 1973; Cech *et al.,* 1984).

When exposed to closed-system heating, the Hb of both bluefin and albacore tunas undergoes a reversed temperature effect (i.e., affinity increases; Carey and Gibson, 1983; Cech *et al.,* 1984), whereas the Hb of the skipjack tuna is unaffected by closed-system heating (Brill and Bushnell, 1991). On the other hand, normal (right-shift) responses to closed-system heating have been shown for yellowfin and kawakawa tunas (Jones *et al.,* 1986; Brill and Bushnell, 1991) and for the bigeye tuna (Lowe *et al.,* 2000). If a Hb molecule leaving the gills does not enter a part of the tuna body where temperature increases, there is no need for an intrinsic Hb property that compensates for closed-system heating. Taken together, these findings suggest no correlation between endothermy and closed-system temperature changes, and the topic needs further study.

VI. SUMMARY, CONCLUSIONS, AND FUTURE DIRECTIONS FOR LABORATORY STUDIES

Temperature is a critical ecological factor, particularly for aquatic organisms. That fishes are in general ectothermic (i.e., $T_b = T_w$) has been recognized from the time of Linnaeus. That tunas are warmer than T_w and the anatomical basis for heat conservation were both discovered over 160 years ago, which qualifies tuna endothermy as one of the oldest subject areas within the field of comparative physiology. In the mid-1960s, when comparative physiology was gaining momentum, publication of the first electronic measurements of tuna T_b and Carey and

Teal's (1966) elucidation of the biophysical, anatomical, physiological, biochemical, and biological problems inherent in tuna endothermy established this subject's core importance. New initiatives in the study of tuna endothermy were aided by the timely completion of a robust classification system for the tunas and for the entire scombrid family. These works also documented important comparative features of the tuna vascular heat-exchange system and provided details about the distribution and natural history of different species. Novel information about scombrid morphology and locomotion biomechanics provided the link between the warm temperatures of tunas, their vascular anatomy, and high activity rates. Thus, works by Kishinouye, Carey and Teal, Gibbs and Collette, Fierstine and Walters, and others have become keystones for understanding the evolutionary history of these specializations and the functional significance of tuna endothermy. Added momentum for laboratory studies of tuna thermal biology at Kewalo Basin came from theoretical models suggesting that the distribution and abundance of tunas could be predicted from ambient temperature and oxygen conditions and that tuna T_b and metabolic O_2 requirements might limit their occurrence in certain waters.

In the last two decades, many advances in our understanding of endothermy in tunas have occurred as a result of laboratory studies, but there is still much to be learned:

1. It has been established that tunas do, indeed, control their thermal conductance and alter heating and cooling rates, depending on environmental temperature and swimming speed. What we still do not know, however, is how this control is achieved. It is hypothesized to be due to physiological control of heat-exchanger effectiveness, by contracting or relaxing the smooth muscle in the countercurrent heat exchanger blood vessel walls, but how this is mediated remains unknown.
2. The enhancing effects of increased T_{RM} on RM contraction rate and power output and of increased $T_{VISCERA}$ on digestive enzyme activities have been demonstrated. However, how or if these thermal effects translate into increases in whole-fish performance as a result of endothermy has not been substantiated, due to the difficulties of testing such hypotheses with live tunas in the laboratory. The role of visceral heat production clearly impacts both steady and non-steady state models of heat transfer, and data are needed in order to estimate this effect. Also, we need data on how velocity changes, whether spontaneous or induced by T_w or other factors, alter heat balance. Finally we lack comparative data for similarly sized specimens of the tuna sister taxa, the bonitos and mackerels, with which to make valid comparisons for performance enhancements actually associated with endothermy.
3. Recent laboratory studies, combined with modern methods of phylogenetic analysis and reconstruction, have resulted in the mapping of characters re-

lated to locomotion and endothermy onto phylogenies of the family Scombridae. These have led to a hypothesized series of character-state acquisitions in the ancestral tunas that led to the evolution of endothermy, which will guide and focus future research into this question. We have only a limited understanding of the significance of interspecific differences among the tunas, and future studies should seek to elucidate the diversity of adaptations and endothermic capabilities of these fishes and their closest relatives.

4. The first studies of the development of endothermy in tunas have been conducted, but these have been based almost exclusively on individuals raised in captivity. There is a need to repeat these studies with wild-caught juvenile tunas, if they can be found. Future study of species such as bluefin and albacore that are known to inhabit cool waters as adults will be important in determining how the ontogeny of endothermy impacts tuna ecology and life history.
5. Specific effects and consequences of endothermy on the cardiovascular system have been described. Additional studies are needed to explain interspecific differences in the effects of temperature on $Hb-O_2$ binding. It is also important to understand more fully the consequences of regional heterothermy for tunas, given that the heart's temperature cannot be maintained above T_w.

The past decades have seen a great deal of activity and progress in the field of tuna physiology and endothermy. Future integrated laboratory and field studies designed to complement one another will lead to a broader understanding of size effects, of the consequences of the many interspecific differences among the 15 species of tunas, and of the evolutionary radiation of tunas.

ACKNOWLEDGMENTS

Research leading to this review has been supported by grants from the U.S. National Science Foundation (IBN 93-18065 to K.A.D, and IBN 93-16621 and 96-04699 to J.B.G). Support was provided by the intramural grant program at California State University, Fullerton (K.A.D), by the Academic Senate, University of California, San Diego (J.B.G.), and by the Japanese Society for the promotion of Science (J.B.G.). We thank B. Block, E. D. Stevens, and one anonymous reviewer for their comments on the manuscript.

REFERENCES

Altringham, J. D., and Block, B. A. (1997). Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200,** 2617–2627.

Arthur, P. G., West, T. G., Brill, R. W., Schulte, P. M., and Hochachka, P. W. (1992). Recovery metabolism of skipjack tuna (*Katsuwonus pelamis*) white muscle; rapid and parallel changes in lactate and phosphocreatine after exercise. *Can. J. Zool.* **70,** 1230–1239.

Bannikov, A. F. (1985). "Iskopaemye skumbrievye SSSR" (Fossil Scombrids of the USSR). Nauka, Moscow.

Barkley, R. A., Neill, W. H., and Gooding, R. M. (1978). Skipjack tuna, *Katsuwonus pelamis*, habitat based on temperature and oxygen requirements. *Fish. Bull. U.S.* **76,** 653–662.

Barrett, I., and Hester, F. J. (1964). Body temperature of the yellowfin and skipjack tunas in relation to sea surface temperatures. *Nature* **203,** 96–97.

Bayliff, W. H., Ed. (1980). Synopses of biological data on eight species of scombrids. Inter-American Tropical Tuna Commission Special Report no. 2. IATTC, La Jolla, CA.

Bertin, L. (1958). Appareil Circulatoire. *In* "Traite de Zoologie" (Grassé, P., Ed.), pp. 1399–1458. Masson, Paris.

Block, B. A. (1986). Structure of the brain and eye heater tissue in marlins, sailfish, and spearfishes. *J. Morphol.* **190,** 169–189.

Block, B. A., and Carey, F. G. (1985). Warm brain and eye temperatures in sharks. *J. Comp. Physiol.* **156,** 229–236.

Block, B. A., and Finnerty, J. R. (1994). Endothermy in fishes: A phylogenetic analysis of constraints, predispositions, and selection pressures. *Environ. Biol. Fish.* **40,** 283–302.

Block, B. A., Finnerty, J. R. Stewart, A. F. R., and Kidd, J. (1993). Evolution of endothermy in fish: Mapping physiological traits on a molecular phylogeny. *Science* **260,** 210–214.

Brill, R. W. (1992). The Kewalo Research Facility, 1958–92: Over 30 years of progress. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-171.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. *Comp. Biochem. Physiol.* **113A,** 3–15.

Brill, R. W., and Bushnell, P. G. (1991). Effects of open- and closed-system temperature changes on blood oxygen dissociation curves of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*. *Can. J. Zool.* **69,** 1814–1821.

Brill, R. W., Dewar, H., and Graham, J. B. (1994). Basic concepts relevant to heat transfer in fishes, and their use in measuring the physiological thermoregulatory abilities of tunas. *Environ. Biol. Fishes* **40,** 109–124.

Bushnell, P. G., Jones, D. R., and Farrell, A. P. (1992). The arterial system. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Farrell, A. P., Eds.), pp. 89–139. Academic Press, San Diego.

Carey, F. G. (1982). A brain heater in swordfish. *Science* **216,** 1327–1329.

Carey, F. G., and Gibson, Q. F. (1983). Heat and oxygen exchange in the *rete mirabile* of the bluefin tuna, *Thunnus thynnus*. *Comp. Biochem. Physiol.* **74A,** 333–342.

Carey, F. G., and Lawson, K. D. (1973). Temperature regulation in free-swimming bluefin tuna. *Comp. Biochem. Physiol.* **44A,** 375–392.

Carey, F. G., and Teal, J. M. (1966). Heat conservation in tuna fish muscle. *Proc. Natl. Acad. Sci. U.S.A.* **56,** 1464–1469.

Carey, F. G., and Teal, J. M. (1969a). Regulation of body temperature by the bluefin tuna. *Comp. Biochem. Physiol.* **28A,** 205–213.

Carey, F. G., and Teal, J. M. (1969b). Mako and porbeagle: Warm bodied sharks. *Comp. Biochem. Physiol.* **28A,** 199–204.

Carey, F. G., Teal, J. M., Kanwisher, J. W., Lawson, K. D., and Beckett, J. S. (1971). Warm-bodied fish. *Am. Zool.* **11,** 137–145.

Carey, F. G., Teal, J. M., and Kanwisher, J. W. (1981). The visceral temperatures of mackerel sharks (Lamnidae). *Physiol. Zool.* **54,** 334–344.

Carey, F. G., Kanwisher, J. W., and Stevens, E. D. (1984). Bluefin tuna warm their viscera during digestion. *J. Exp. Biol.* **109,** 1–20.

Carpenter, K. E., Collette, B. B., and Russo, J. L. (1995). Unstable and stable classifications of scombroid fishes. *Bull. Mar. Sci.* **56,** 379–405.

Cech, J. J., Jr., Laurs, R. M., and Graham, J. B. (1984). Temperature-induced changes in blood gas equilibria in the albacore (*Thunnus alalunga*), a warm-bodied tuna. *J. Exp. Biol.* **109,** 21–34.

Collette, B. B. (1978). Adaptations and systematics of the mackerels and tunas. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 7–39. Academic Press, San Diego.

Collette, B. B., and Chao, L. N. (1975). Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). *Fish. Bull. U.S.* **73,** 516–625.

Collette, B. B., Potthoff, T., Richards, W. J., Ueyangi, S., Russo, J. L., and Nishikawa, Y. (1984). Scombroidei: Development and relationships. *In* "Ontogeny and Systematics of Fishes" (Moser, G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, A. W., and Richardson, S. L., Eds.), Special Publication 1, pp. 591–620. Am. Soc. Ichthyol. Herpetol.

Cuvier, G., and Valenciennes, A. (1828/1969). "Histoire Naturelle des Poissons," Vol. I. Asher and Co., Amersterdam.

Cuvier, G., and Valenciennes, A. (1831/1969). "Histoire Naturelle des Poissons," Vol. VIII. Asher and Co., Amersterdam.

Davy, J. (1835). On the temperature of some fishes of the genus *Thynnus*. *Edinburgh N. Philos. J.* **19,** 325–330.

Davy, J. (1844). Miscellaneous observations on animal heat. *Philos. Trans. R. Soc. London* **134,** 57–64.

Dewar, H., and Graham, J. B. (1994). Studies of tropical tuna swimming performance in a large water tunnel. I. Energetics. *J. Exp. Biol.* **192,** 13–31.

Dewar, H., Graham, J. B., and Brill, R. W. (1994). Studies of tropical tuna swimming performance in a large water tunnel. II. Thermoregulation. *J. Exp. Biol.* **192,** 33–44.

Dickson, K. A. (1994). Tunas as small as 207 mm fork length can elevate muscle temperatures significantly above ambient temperature. *J. Exp. Biol.* **190,** 79–93.

Dickson, K. A. (1995). Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environ. Biol. Fishes* **42,** 65–97.

Dickson, K. A. (1996). Locomotor muscle of high-performance fishes: What do comparisons of tunas and ectothermic sister taxa reveal? *Comp. Biochem. Physiol.* **113A,** 39–49.

Dickson, K. A., Johnson, N., Donley, J. M., Hoskinson, J. A., Hansen, M. W., and Tessier, J. D. (2000). Ontogenetic changes in characteristics required for endothermy in juvenile black skipjack tuna (*Euthynnus lineatus*) *J. Exp. Biol.*, **203,** 3077–3087.

Dizon, A. E., and Brill, R. W. (1979a). Thermoregulation in tunas. *Am. Zool.* **19,** 249–265.

Dizon, A. E., and Brill, R. W. (1979b). Thermoregulation in the yellowfin tuna. *Thunnus albacares*. *Physiol. Zool.* **52,** 581–593.

Dizon, A. E., Brill, R. W., and Yuen, H. S. H. (1978). Correlations between environment, physiology, and activity and the effects on thermoregulation in skipjack tuna. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 233–259. Academic Press, San Diego.

Ellerby, D. J., Altringham, J. D., Williams, T., and Block, B. A. (2000). Slow muscle function of Pacific bonito (*Sarda chiliensis*) during steady swimming. *J. Exp. Biol.* **203,** 2001–2013

Eschricht, D. F., and Müller, J. (1835). Uber die arteriösen und venösen Wundernetz an der leber und einen merkwürdigen bau dieses Organes beim thunfische. *Abh. Dtsch. Akad. Wiss.*, 1–30.

Fierstine, H. L., and Walters, V. (1968). Studies in locomotion and anatomy of scombroid fishes. *Mem. S. Calif. Acad. Sci.* **6,** 1–31.

Finnerty, J. R., and Block, B. A. (1995). Evolution of cytochrome b in the scombroidei (Teleostei): Molecular insights into billfish (Istiophoridae and Xiphiidae) relationships. *Fish. Bull. U.S.* **93,** 78–96.

Fudge, D. S., and Stevens, E. D. (1996). The visceral *retia mirabilia* of tunas and sharks: An annotated translation and discussion of the 1835 paper and related papers. *Guelph Ichthyol. Rev.* **4,** 1–54.

Funakoshi, S., Suzuki, T., and Wada, K. (1983). Anatomical observations on the rete mirabile of young bluefin tuna, *Thunnus thynnus*. *Natl. Res. Inst. Aquaculture* **4,** 87–97.

Gibbs, R. H., and Collette, B. B. (1967). Comparative anatomy and systematics of the tunas, genus *Thunnus*. *Fish. Bull. U.S.* **66,** 65–130.

Godsil, H. C. (1954). A descriptive study of certain tuna-like fishes. *Calif. Dept. Fish Game, Fish Bull.* **97,** 1–188.

Godsil, H. C., and Byers, R. D. (1944). A systematic study of the Pacific tunas. *Calif. Dept. Fish Game, Fish Bull.* **60,** 1–131.

Graham, J. B. (1973). Heat exchange in the black skipjack, and the blood-gas relationship of warm-bodied fishes. *Proc. Natl. Acad. Sci. U.S.A.* **70,** 1964–1967.

Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares,* and skipjack tuna, *Katsuwonus pelamis,* and the adaptive significance of elevated body temperatures in scombrid fishes. *Fish. Bull. U.S.* **73,** 219–229.

Graham, J. B. (1983). Heat transfer. *In* "Fish Biomechanics" (Webb, P. W., and Weihs, D., Eds.), pp. 248–278. Praeger, New York.

Graham, J. B., and Dickson, K. A. (1981). Physiological thermoregulation in the albacore *Thunnus alalunga. Physiol. Zool.* **54,** 470–486.

Graham, J. B., and Dickson, K. A. (2000). The evolution of thunniform locomotion and heat conservation in scombrid fishes: New insights based on the morphology of *Allothunnus fallai. Zool. J. Linn. Soc.* **129.**

Graham, J. B., and Diener, D. R. (1978). Comparative morphology of the central heat exchangers in the skipjacks *Katsuwonus* and *Euthynnus. In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 113–133. Academic Press, San Diego.

Graham, J. B., Koehrn, F. J., and Dickson, K. A. (1983). Distribution and relative proportions of red muscle in scombrid fishes: Consequences for body size and relationships to locomotion and endothermy. *Can. J. Zool.* **61,** 2087–2096.

Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R., and Fournier, D. A. (1992). Physiological and behavioral thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358,** 110–112.

Johnston, I., and Brill, R. W. (1984). Thermal dependence of contractile properties of single skinned muscle fibres from Antarctic and various warm water marine fishes including skipjack tuna (*Katsuwonus pelamis*) and kawakawa (*Euthynnus affinis*). *J. Comp. Physiol.* **114,** 203–216.

Jones, D. R., Brill, R. W., and Mense, D. C. (1986). The influence of blood gas properties on gas tensions and pH of ventral and dorsal aortic blood in free-swimming tuna, *Euthynnus affinis. J. Exp. Biol.* **120,** 201–213.

Joseph, J., Klawe, W., and Murphy, P. (1988). "Tuna and Billfish—Fish without a Country." IATTC, La Jolla, CA.

Kishinouye, K. (1923). Contributions to the comparative study of the so-called scombroid fishes. *J. Coll. Agric. Imp. Univ. Tokyo* **8,** 293–475.

Koehrn, F. J. (1980). Comparative vascular anatomy of the counter-current heat exchangers of albacore and yellowfin tunas. Masters Thesis, San Diego State University, San Diego.

Korsmeyer, K. E., Dewar, H., Lai, N. C., and Graham, J. B. (1996a). The aerobic capacity of tunas: Adaptations for multiple metabolic demands. *Comp. Biochem. Physiol.* **113A,** 17–24.

Korsmeyer, K. E., Dewar, H., Lai, N. C., and Graham, J. B. (1996b). Tuna aerobic swimming performance: Physiological environmental limits based on oxygen supply and demand. *Comp. Biochem. Physiol.* **113B,** 45–56.

Korsmeyer, K. E., Lai, N. C., Shadwick, R. E., and Graham, J. B. (1997a). Heart rate and stroke volume contributions to cardiac output in swimming yellowfin: Responses to exercise and temperature. *J. Exp. Biol.* **200,** 1975–1986.

Korsmeyer, K. E., Lai, N. C., Shadwick, R. E., and Graham, J. B. (1997b). Oxygen transport and cardiovascular responses to exercise in the yellowfin tuna *Thunnus albacares. J. Exp. Biol.* **200,** 1987–1997.

Laurs, R. M., Yuen, H. S. H., and Johnson, J. H. (1977). Small-scale movements of albacore, *Thunnus alalunga,* in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fish. Bull. U.S.* 75, 347–357.

Lindsey, C. C. (1968). Temperatures of red and white muscle in recently caught marlin and other large tropical fish. *J. Fish. Res. Bd. Canada* **25,** 1987–1992.

Linthicum, D. S., and Carey, F. G. (1972). Regulation of brain and eye temperatures by the bluefin tuna. *Comp. Biochem. Physiol.* 43A, 425–433.

Lowe, T. E., Brill, R. W., and Cousins, K. L. (2000). Blook oxygen-binding characteristics of bigeye tuna (*Thunnus obesus*), a high-energy demand teleost that is tolerant of low ambient oxygen. *Mar. Biol.* **136,** 1087–1098.

Maddison, W. P., and Maddison, D. R. (1992). "MacClade: Analysis of Phylogeny and Character Evolution, Version 3.0." Sinauer Associates, Sutherland, MA.

Magnuson, J. J. (1973). Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. *Fish. Bull. U.S.* **71,** 337–356.

Magnuson, J. J. (1978). Locomotion by scombrid fishes: Hydromechanics, morphology, and behavior. *In* "Fish Physiology" (Hoar, W., and Randall, D. J., Eds.), Vol. 7, pp. 239–313. Academic Press, New York.

Moore, J. A. (1998). Possible nervous innervation and characterization of the blood vessels of the counter-current heat exchangers in three species of tuna. Masters Thesis, California State University Fullerton, Fullerton.

Nakamura, H. (1969). "Tuna Distribution and Migration." Fishing News, London.

Neill, W. H., and Stevens, E. D. (1974). Thermal inertia versus thermoregulation in "warm" turtles and tunas. *Science* **184,** 1008–1010.

Neill, W. H., Chang, R. K. C., and Dizon, A. E. (1976). Magnitude and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). *Environ. Biol. Fishes* **1,** 61–80.

Olson, R. J., and Boggs, C. H. (1986). Apex predation by yellowfin tuna (*Thunnus albacares*): Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Can. J. Fish. Aquat. Sci.* **43,** 1760–1775.

Olson, R. J., and Scholey, V. P. (1990). Captive tunas in a tropical marine research laboratory: Growth of later-larval and early juvenile black skipjack *Euthynnus lineatus*. *Fish. Bull. U.S.* **88,** 821–828.

Roberts, J. L. (1978). Ram gill ventilation in fish. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 83–88. Academic Press, San Diego.

Roberts, J. L., and Graham, J. B. (1979). Effect of swimming speed on the excess temperatures and activities of heart and red and white muscles in the mackerel, *Scomber japonicus*. *Fish. Bull. U.S.* **76,** 861–867.

Rome, L. C. (1995). Influence of temperature on muscle properties in relation to swimming performance. *In* "Biochemistry and Molecular Biology of Fishes" (Hochachka, P. W., and Mommsen, T. P., Eds.), pp. 74–95. Elsevier Science, Amsterdam.

Rossi-Fanelli, A., and Antonini, E. (1960). Oxygen equilibrium of hemoglobin from *Thunnus thynnus*. *Nature* **186,** 895–896.

Schaefer, K. M. (1984). Swimming performance, body temperatures, and gastric evacuation times of the black skipjack, *Euthynnus lineatus*. *Copeia* **1984,** 1001–1004.

Schmidt-Nielsen, K. (1984). "Scaling: Why Is Animal Size So Important?" Cambridge Univ. Press, Cambridge.

Sepulveda, C., and Dickson, K. A. (1998). Are tunas faster or more efficient swimmers as a result of endothermy? *Am. Zool.* **38,** 45A.

Sepulveda, C., and Dickson, K. A. (2000). Maximum sustainable speeds and cost of swimming in juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J. Exp. Biol.* **203,** 3089–3101.

Shadwick, R. E., Katz, S. L., Korsmeyer, K. E., Knower, T., and Covell, J. W. (1999). Muscle dynamics in skipjack tuna: Timing of red muscle shortening in relation to activation and body curvature during steady swimming. *J. Exp. Biol.* **202,** 2139–2150.

Sharp, G. D., and Dizon, A. E. (1978). "The Physiological Ecology of Tunas." Academic Press, San Diego.

Sharp, G. D., and Pirages, S. W. (1978). The distribution of red and white swimming muscles, their biochemistry, and the biochemical phylogeny of selected scombrid fishes. *In* "The Physiological

Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 41–78. Academic Press, San Diego.

Sharp, G. D., and Vlymen, W. J. (1978). The relation between heat generation, conservation, and the swimming energetics of tunas. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 213–232. Academic Press, San Diego.

Stevens, E. D. (1978). A historical introduction to the study of warm-bodied tuna. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 209–211. Academic Press, San Diego.

Stevens, E. D., and Carey, F. G. (1981). One why of the warmth of warm-bodied fish. *Am. J. Physiol.* **240,** R151–R155.

Stevens, E. D., and McLeese, J. M. (1984). Why bluefin tuna have warm tummies: Temperature effect on trypsin and chymotrypsin. *Am. J. Physiol.* **246,** R487–R494.

Stevens, E. D., and Neill, W. H. (1978). Body temperature relations of tunas especially skipjack. *In* "Fish Physiology" (Hoar, W., and Randall, D. J., Eds.). Vol. 7, pp. 316–356. Academic Press, New York.

Stevens, E. D., Lam, H. M., and Kendall, J. (1974). Vascular anatomy of the countercurrent heat exchanger of skipjack tuna. *J. Exp. Biol.* **61,** 145–153.

Sund, P. N., Blackburn, M., and Williams, F. (1981). Tunas and their environment in the Pacific Ocean: A review. *Oceanogr. Mar. Biol. Annu. Rev.* **19,** 443–512.

Westneat, M. W., Hoese, W., Pell, C. A., and Wainwright, S. A. (1993). The horizontal septum: Mechanisms of force transfer in locomotion of scombrid fishes (Scombridae, Perciformes). *J. Morphol.* **217,** 183–204.

Wexler, J. B. (1993). Validation of daily growth increments and estimation of growth rates of larval and early-juvenile black skipjack, *Euthynnus lineatus*, using otoliths. *Inter-Am. Tropic. Tuna Commission Bull.* **20,** 401–440.

White, F. C., Kelly, R., Kemper, S., Schumacker, P. T., Gallagher, K. R., and Laurs, R. M. (1988). Organ blood flow haemodynamics and metabolism of the albacore tuna *Thunnus alalunga* (Bonnaterre). *Exp. Biol.* **47,** 161–169.

5

ADVANCES IN ACOUSTIC, ARCHIVAL, AND SATELLITE TAGGING OF TUNAS

JOHN GUNN
BARBARA BLOCK

I. Introduction
II. Acoustic Tagging
  A. Technology and Methods
  B. Tracking Studies of Tuna
  C. Summary
III. Archival Tags
  A. Technology and Methods
  B. Archival Tagging of Tunas
  C. Summary
IV. Pop-Up Satellite Tags
  A. Technology and Methods
  B. Application of Pop-Up Satellite Tags on Tunas
  C. Summary
V. The Problem of Attachment
VI. The Future of Acoustic, Archival, and Pop-Up Satellite Tagging
  A. Technology
  B. The Future Application of Electronic Tags and Integration of Data into Spatial Dynamics Models

I. INTRODUCTION

In the scientific and popular literature, tunas are most often described as highly migratory fishes—"wanderers" of the world's oceans. Their "highly charged lifestyles as apex predators in the oceanic pelagic environment" (Dickson, 1995) are facilitated by a number of anatomical, biological, and physiological specializations (Brill, 1996; Bushnell and Jones, 1994; Sharp and Dizon, 1978).

While considerable time has been spent in the laboratory examining the physiological attributes of tunas, relatively little attention has been paid to critical shortcomings in our understanding of what tuna do in their open ocean environ-

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

ment. For example, although most species of tuna are capable of long-distance movements, there is growing evidence that for some species or populations large-distance migrations are more the exception than the rule (Hampton and Gunn, 1998; Hilborn and Sibert, 1988).

Hunter *et al.*'s 1986 review of tuna movement dynamics concluded that for many of the tuna species major uncertainties regarding the nature and extent of movement constrained stock assessments and the management of resources that are often shared by many countries. The most serious of these uncertainties were the:

1. Timing, extent, directionality, and seasonality of movement
2. Rates of exchange of exploited adults among different management jurisdictions
3. Rates of exchange among vertical and horizontal habitats fished by different gears
4. The distribution of adults
5. Residence times and probability of return
6. Links between environmental factors, movements, and distribution

Since Hunter *et al.*'s review, the world's tuna catch has increased by almost 30% (FAO, 1998), and populations of albacore, bigeye, southern bluefin, and Atlantic bluefin tuna in various ocean basins have been listed by the IUCN in their Red List of endangered species (Hilton-Taylor, 2000) under categories ranging from vulnerable to critically endangered. Increased exploitation and scrutiny of stock assessments has resulted in increased pressure on fishery scientists and managers to reduce uncertainty in stock assessments and reduce the risks of overexploitation of tuna populations. However, despite their very significant commercial value, and the status of some tuna populations, many of the uncertainties identified by Hunter *et al.* (1986) remain as unresolved today as they were 15 years ago.

Hunter *et al.* (1986) made recommendations on "actions needed to improve the knowledge of tuna movements." These were to:

1. Establish international arrangements whereby data on tuna movement could be shared
2. Increase the number and kinds of observations of tuna movement in the vertical plane
3. Develop and use technology for tracing the actual paths followed by tuna over extended periods and for measuring movements independent of fisheries
4. Conduct intensive studies on tuna movement dynamics which combine old and new technologies

How have we progressed since 1986?

Regional tuna management agencies are now established, or are in the final stages of being established, to conserve most of the world's tuna resources. This

is an important advance that provides a good basis for sharing data on tuna movement.

Research into tuna movement and migration has also benefited immensely from the development of new technologies—including a suite of electronic tags, satellite communication and remote sensing, and faster computers. As a result, there has been significant progress in Hunter *et al.*'s second and third "actions."

The focus of this chapter is to review the advances in tagging technology since 1986, and the ways in which these new technologies in combination with recent acoustic tracking have provided exciting new insights into tuna movement, behavior, and physiology in the open ocean.

For some species, we are finally beginning to understand where tuna go and what they do in their open ocean, pelagic environment. The rapid advances made over the last 5 years suggest it may not be too long before integration of three-dimensional movement data into spatial dynamics models is actively pursued.

As many of the new tagging technologies are still under development or in early stages of application, we have integrated a review of the recent literature with a broad range of observations from our unpublished data. In so doing we hope to provide a benchmark and assist in the optimal use of the many exciting new technologies available.

II. ACOUSTIC TAGGING

The first published account of the acoustic tracking of tuna is that of Yuen (1970), who used acoustic tags to study the movement and behavior of skipjack off Hawaii in August 1969. Twenty days earlier Carey and Lawson (1973) had apparently been the first to track tunas when they began their pioneering work on Atlantic bluefin off the coast of Nova Scotia. Yuen (1970) used 8-cm-long, 50 kHz transmitters, weighing 62 g in air, in conjunction with a frequency-modulated sonar on board the research vessel *Townsend Cromwell.* His technology, crude as it was in comparison to many of today's systems, provided signals at ranges of up to 2.3 km and allowed him to examine diel shifts in the position of his fish relative to topographic features. Carey and Lawson (1973) used acoustic telemetry to study the physiology of giant bluefin, and by the time Hunter *et al.* (1986) wrote their review, acoustic or sonar tags had been used successfully to study the fine-scale movement, thermal physiology, and behavior of individuals of a number of species of tuna [skipjack (Dizon *et al.,* 1978), albacore (Laurs *et al.,* 1977), yellowfin (Yonimori, 1982; Carey and Olson, 1982), and Atlantic bluefin (Carey and Lawson, 1973)].

In the early tracking work a key issue was whether the behavior of a tracked animal was normal, or whether it was affected by stress caused by handling and/or capture. The labor-intensive nature of tracking had also meant that observations were generally from a relatively narrow size range and thus it was unclear whether

the promising results could be extrapolated to either larger and more mature fish in the case of yellowfin and bigeye, or smaller fish in the case of Atlantic bluefin. Considerable effort has been placed into acoustic tracking over the last decade, and to some extent these uncertainties have been addressed and some of the gaps filled.

A. Technology and Methods

The design concept for ultrasonic acoustic tags has changed little since the work conducted by Yuen (1970) and Carey and Lawson (1973)—ultrasonic frequencies are generated by driving an annular ceramic transducer at its resonant frequency, and the frequency of the signal transmitted is determined by the transducer diameter. However, acoustic tag technology has progressed significantly throughout the last decade. As electronic circuitry controlling tag function has been miniaturized with surface mounting and then integrated circuit technology, tags have become smaller. The constraints of transducer size and battery volume remain when long range or extended transmission life is required. A number of new sensor options have been introduced that enhance the ability of researchers to study movement of tunas in three dimensions, physiology, and behavior. For example, Vemco Pty., Ltd., of Nova Scotia Canada supplies tags with sensors that collect data on depth, temperature, heart rate, and swimming speed (paddle wheel sensor). Used in combination with real-time measurements of the physical and biological environment, acoustic tags have become a powerful tool in examining environmental preferences of tuna (Block *et al.*, 1997; Brill *et al.*, 1999; Dagorn *et al.*, 2000). Acoustic studies primarily focus on collecting data from a single fish equipped with the ultrasonic tag. The tag encodes the data as a series of ultrasonic pulses transmitted through the water column to a hydrophone and receiver on the ship. Few studies on tuna have been designed to acquire data from more than one sensor at a time. To record two types of data from a single fish simultaneously requires using two tags of different frequencies, or a multiplex acoustic tag such as a pressure and temperature device, or a pressure, ambient temperature, and swimming speed tag (Block *et al.*, 1992).

The recent development of multidirectional hydrophone arrays coupled with independent acoustic receivers and computers has improved estimation of direction and range of fish relative to the tracking vessel (Block *et al.*, 1997), and perhaps just as importantly have made the very labor-intensive task of following fish for hours to days much easier on the researcher.

"Listening stations" are an exciting new acoustic technology. They are acoustic receivers that are moored at set locations, and are able to communicate with and log details of tags that come within range over very extended periods of time. Although listening stations have yet to be fully evaluated for tunas and other oceanic pelagics, a recent study on yellowfin tuna (Klimley and Holloway, 1999) demonstrated their use in examining school fidelity and the residency of fish around Fish Aggregating Devices (FADs). To date, the most extensive work with

listening stations has been on salmonids (Lacroix and Knox, 2000) have used arrays of listening stations in enclosed embayments to examine migratory behavior and residency of fish.

The success of listening stations has spawned the development of "chat tags," which combine many of the features of archival tags (see below) with acoustic transmission of data when a fish comes near enough to a receiver. The receiver used with chat tags regularly sends signals out to search for and identify tags within its range. Having received a positive response from a tagged fish, it sends a command enabling the tag to download data via an acoustic signal (VEMCO, 2000). Although "chat tags" have yet to be used on tuna, they have great potential in areas where fish are likely to return regularly to topographical or aggregating features.

B. Tracking Studies of Tuna

Six species of *Thunnus* have been acoustically tracked since Yuen's (1970) early work on skipjack—Atlantic bluefin (*T. thynnus*), Pacific bluefin (*T. orientalis*), southern bluefin (*T. maccoyii*), yellowfin (*T. albacares*), albacore (*T. alalunga*), and bigeye (*T. obesus*). Recent efforts have been directed toward broadening the size range of fish on which observations are being made to include adults, for example, Brill *et al.* (1999) in yellowfin, and Dagorn *et al.* (2000) in bigeye, and significant work has been undertaken on simultaneous measurement of environmental variables while tracking (Block *et al.*, 1997; Josse *et al.*, 1998; Brill *et al.*, 1999; Dagorn *et al.*, 2000; Marcinek *et al.*, 2001).

1. Yellowfin

Yellowfin tuna (*T. albacares*) have been tracked more than any other tuna species. The literature describes tracks of 23 fish, ranging in size from 54 to 167 cm fork length (FL). The duration of these tracks ranged from 4 to 86 h, and in total 631 hours (approximately 26 days) have been observed.

All tracking data suggest that yellowfin, in coastal and open ocean habitats, are primarily inhabitants of the mixed layer. Although they are obviously capable of swimming to great depths—Carey and Olsen (1982) followed one fish that descended to 464 m—yellowfin spend most of their time in the upper 100 m above the thermocline. The most likely explanation for their limited depth distribution appears to be an inability to cope physiologically with temperatures below the thermocline. The same factor would explain their geographical distribution within tropical and subtropical latitudes. Even at large sizes, where surface area to body mass ratios and a vascular countercurrent heat exchanger allow maintenance of elevated body temperatures, it appears that water temperature limits the cardiac muscle function and hence restricts vertical movement (Brill *et al.*, 1999). Brill *et al.* (1999) found that in Hawaiian waters, where sea surface temperatures

(SSTs) were 24°C, the maximum dives of large yellowfin appeared to be limited by a temperature differential of 8°C below sea surface temperature. In these fish the maximum dives were to 250 m. At the northern extent of their range in the eastern Pacific, yellowfin occupy waters with SSTs of 19–20°C, and in this habitat small yellowfin are primarily restricted to waters above the upper thermocline (18–45 m) and temperatures of >17.5°C (Block *et al.*, 1997).

In many cases, the objective of tracking has been to understand the behavior of yellowfin around fish aggregating devices and topographic features (Yonimori, 1982; Holland *et al.*, 1990; Cayré, 1991; Cayré and Marsac, 1993; Klimley and Holloway, 1999). Very similar patterns of behavior have been observed for small yellowfin (40–100 cm FL) associated with FADs in the Pacific (Hawaii) and Indian oceans (Seychelles; Holland *et al.*, 1990; Cayré, 1991). In both locations, fish have shown very close associations with FADs and other topographic features such as sea mounts and continental shelf edges, and there has been clear diurnal variation in their position relative to these features and their depth preferences. Holland *et al.* (1990) were able to show that yellowfin off Hawaii stayed close to FADs or the continental shelf drop-off during the day, while during the night they tended to move away from these features. Klimley and Holloway (1999), using fixed listening stations in the same area, found that individuals tended to revisit FADs regularly, and often remained in the same school in which they had been tagged days to months previously. Their data, showing an allegiance to a school, a tendency for fish to return to the site at which they were tagged, and a set temporal pattern for revisiting sites, led Klimley and Holloway (1999) to hypothesize that their yellowfin had migratory pathways, consisting of "waypoints," that were visited regularly. The hypothesis is intriguing, and serves to emphasize the value of data collected over long periods. It would have been extremely difficult to make the observations on which the hypothesis is based on tracking data alone.

Oscillatory diving is a behavior observed frequently in yellowfin tracking studies (Carey and Olsen, 1982; Holland *et al.*, 1990; Block *et al.*, 1997). In this mode of swimming, ascent rates are higher than descent rates. Several authors have suggested that the tuna glide during the descent, a behavior that would result in significant energy savings (Weihs, 1973). Although gliding has yet to be confirmed in the open ocean, recent success with acoustic electromyogram tags on captive tuna (Dewar *et al.*, 1999) suggests that it should be possible to examine muscle activity in wild fish. If it could be demonstrated that swimming muscle activity decreased significantly during descent, the hypotheses based on tracking data could be validated.

2. Bigeye

Twelve bigeye tuna tracks are reported in the literature for fish ranging in size from 57 to 160 cm [length estimated from the weight of approximately 70 kg given by Carey and Lawson (1973)]. The tracks range in duration from 6 to 29 h

(average = 19 h), and in total 228.5 hours have been observed. Carey and Lawson (1973) were the first to track bigeye when they double tagged a large adult off the New England coast of the USA with both stomach and water temperature tags, and followed it for 17 h. On the basis of their limited observations, and comparisons with tracks of Atlantic bluefin made with similar equipment, they concluded that bigeye did not appear to control their body temperature. In the late 1980s Holland began his important research into bigeye movement and thermoregulation, based on tracking data. He demonstrated the very different depth distribution of yellowfin and bigeye (Holland *et al.*, 1990). Of particular interest were the observations that although the geographic ranges of these species overlap significantly, and that they share an association with FADs and floating objects, tracked bigeye differed from yellowfin in that they regularly made extensive and prolonged excursions below the thermocline as part of diel vertical migrations. Tracking data suggest that bigeye are generally found in the mixed layer during the night, while during the day they regularly dive to depths in excess of 200 m. Small (3–5 kg) bigeye appear to be restricted to depths above the 15°C isotherm (Holland *et al.*, 1990), whereas adults are capable of much deeper diving, and regularly make prolonged excursions to 500+ m during the daytime as they follow the deep scattering layer (Holland *et al.*, 1992; Josse *et al.*, 1998; Dagorn *et al.*, 2000). At these depths, bigeye spend significant time in water temperatures as low as 7°C, and tracking data have revealed the species' unique behavioral and physiological adaptations to thermoregulation in these temperatures (Holland *et al.*, 1992; Holland and Sibert, 1994). Although based on very few observations, tracking has demonstrated how bigeye are able to take advantage of a much broader foraging space than yellowfin. They have the ability to forage in both the warm mixed layers of tropical and subtropical latitude and the cooler waters well below the thermocline at subtropical and warm temperate latitudes.

3. Bluefins

There has been relatively little tracking of the three bluefin tuna species since the pioneering work on the thermal biology of Atlantic bluefin by Carey and Lawson (1973), Carey *et al.* (1984), and Stevens *et al.* (2000; based on data collected by Carey in 1978). Carey's research, using acoustic tags fabricated in his laboratory, demonstrated the capacity of giant Atlantic bluefin to thermoregulate through significant ranges in ambient temperature. At water temperatures varying between 9 and 17°C, the muscle temperature of giant bluefin held in large pens remained at about 24°C (Stevens *et al.*, 2000). Using acoustic tags placed in the stomach, Carey *et al.* (1984) also made the first observations of significant visceral warming following a meal, and based on these data suggested that the elevated temperatures would serve to speed digestion and allow the tuna to feed frequently when food is abundant.

Lutcavage *et al.* (2000a) tracked 12 adult Atlantic bluefin (136–340 kg)

in the Gulf of Maine off the northeast coast of the USA to obtain information on surfacing behavior for use in interpretation of fishery-independent aerial surveys of abundance. During tracks of 3.5–48 h (average 28 h) the bluefin remained largely in the upper mixed layer (mean swimming depth was 14 m). However, less than 8% of this time was spent on the surface. Although mean swimming speed over the ground was 5.9 km h^{-1}, speeds of 20–31 km h^{-1} were observed for brief periods. Perhaps the most significant feature of the data collected by Lutcavage *et al.* (2000a) was the fact that the tagged fish remained in schools throughout the tracking periods, allowing the study to infer the behavior of schools rather than just individual fish (as is usually the case in tuna tracking data). The association of tagged fish with their school was achieved by attaching transmitters to free-swimming fish using a harpoon attachment technique (Chaprales *et al.*, 1998).

Davis and Stanley (in press) have recently reported on tracking studies of the vertical and horizontal movement of juvenile southern bluefin tuna (SBT) in the Great Australian Bight. They tracked 16 SBT ranging in size from 67 to 103 cm (FL), for periods of between 1 and 49 h (average 16.5 h). Like Lutcavage *et al.* (2000a,b,c), the objective of their work was to examine the surfacing behavior of fish to determine the probability of sighting SBT schools during aerial surveys. Davis and Stanley (in press) found that in the continental shelf waters of the Great Australian Bight, juvenile SBT spent long periods throughout the day on the surface, and horizontal movements were commonly between topographic features such as reefs, islands, and the shelf break.

Recent work on Pacific bluefin tuna (Marcinek *et al.*, 2001) provides tracking and physiological data on 2- and 3-year-old fish in the eastern Pacific. Six Pacific bluefin tuna were tracked for a period of 46–86 h with both depth and temperature transmitters. These data suggest they are similar in many ways to their very close relative, the Atlantic bluefin. Figure 1 shows 4 days in the life of a Pacific bluefin (9801) equipped with two acoustic tags transmitting pressure and deep slow-oxidative muscle temperature information. The data are shown in relationship to the thermal stratification of the water column as determined with a CTD. Pacific bluefin as well as Atlantic bluefin examined with similar acoustic techniques (Carey and Lawson, 1973; Lutcavage *et al.*, 2000) show a preference for the surface and mixed layer. On several occasions Pacific bluefin 9801 spent extended periods at depth in cooler waters, as well as periods during the afternoon at the surface. The acoustic tracking data indicate that Pacific bluefin tuna spent the majority of the time in the warmest parts of the water column in the region of the eastern Pacific where the study was conducted. Direct observation of the internal muscle temperatures of the Pacific bluefin tuna revealed a relatively constant muscle temperature with a range from 23 to 26°C. These values are similar to data from muscle temperature data obtained from Atlantic bluefin tuna by Carey and Lawson (1973).

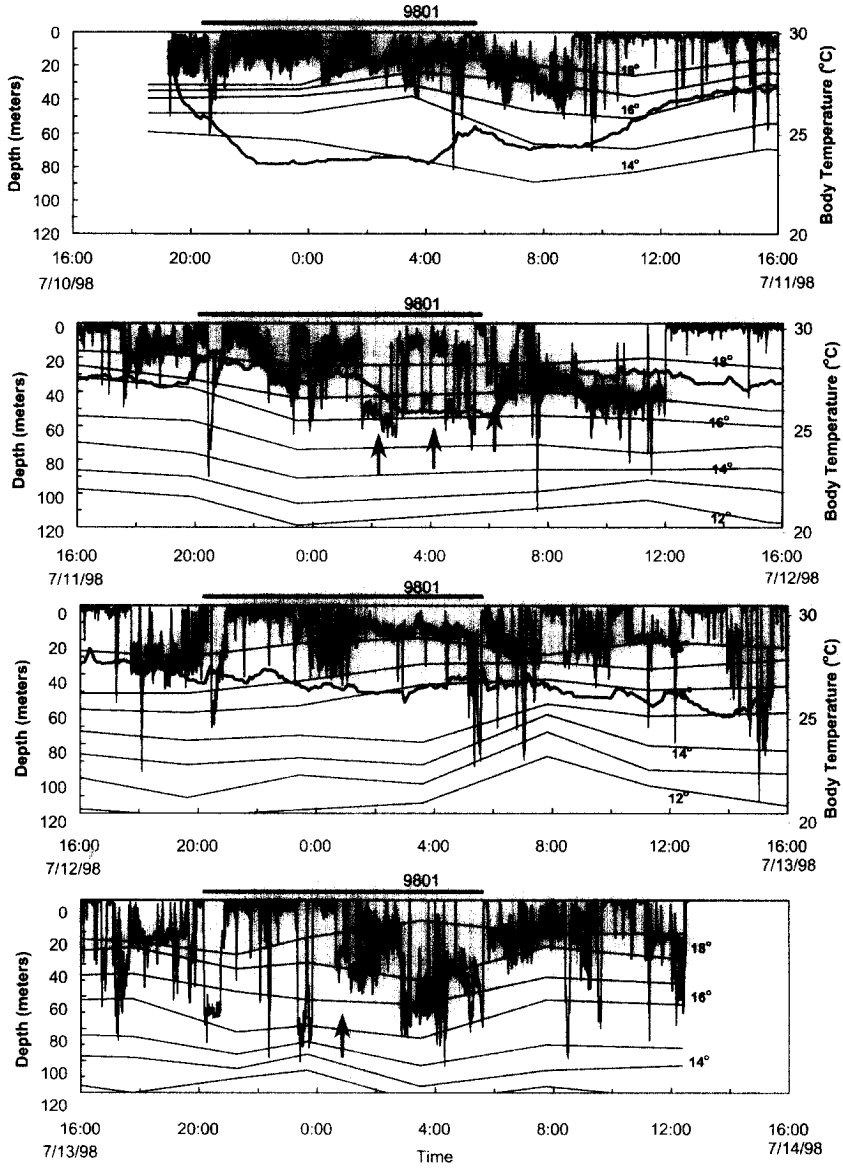


Fig. 1. Four days in the life of a Pacific bluefin tuna, *Thunnus orientalis*, equipped with two acoustic tags measuring pressure and muscle temperature. These data are overlaid on data showing the thermal structure of the water in which the fish was swimming obtained with a Conductivity, Temperature, Depth Recorder (CTD). Marcinek *et al.*, 2001).

4. Albacore

Laurs *et al.* (1977) tracked albacore in the North Pacific, and found they undertook frequent vertical migrations during both day and night. Their study was also important as it was one of the first to demonstrate the importance of frontal systems in the movement patterns of tunas—similar observations were later to be made for yellowfin (Holland *et al.*, 1990; Block *et al.*, 1997; Brill *et al.*, 1999) and Atlantic bluefin (Lutcavage *et al.*, 2000a). In the case of albacore, tracking data showed they tended to aggregate and move along the warm side of fronts, predominantly in waters above 15°C. Recent albacore tracking data indicate that they have a conspicuous presence at the thermocline, and appear to remain out of the mixed layer much of the time (B. Block, unpublished data).

C. Summary

Acoustic tracking has provided significant contributions to our understanding of the behavior, localized movement, and physiology of six *Thunnus* species. Specifically,

- Tracking has been instrumental in providing the first examination of fine-scale horizontal and vertical movement patterns of tunas in a range of habitats, and in particular oceanographic frontal zones.
- Tracking data have provided baseline information on the thermal and depth habitat preferences for at least a few individuals of all six species of *Thunnus*. For yellowfin and bigeye the data are extensive enough to examine changes in these parameters with body mass.
- Acoustic tags have been used to acquire thermal physiology of muscle temperature on Atlantic bluefin, Pacific bluefin, and bigeye tuna; visceral temperatures of Atlantic bluefin; and swimming speeds of albacore, yellowfin, bigeye, Atlantic bluefin, Pacific bluefin, and southern bluefin.
- Tracking data have also provided descriptions of the nature and extent of association of yellowfin, bigeye, and southern bluefin tuna with FADs and/or topographic features.

Unfortunately, we do not have enough tracking data for any species to define lunar, seasonal, interannual, ontogenetic, or regional differences in their behavior, habitat preferences, and physiology. If acoustic tracking data are to be a useful input into movement and spatial dynamics models developed as components of stock assessments, then understanding the nature and extent of temporal variation in patterns of behavior and movement is a very important goal for future research. In the spatial context, we are limited somewhat in our ability to extrapolate from the existing acoustic tracking data as the majority of these have been collected from fish swimming close to islands or continental land masses. Without comparable data

for fishes in open ocean habitats, it is not possible to objectively determine whether the behavioral observations made to date are representative of the species or are habitat-specific.

Quite simply, the requirement to continually follow a fish with a research vessel is the major limitation of acoustic telemetry. Acoustic tracking also requires intensive effort on behalf of the researchers and ship crew to stay with the fish on a 24-h basis, and often can be limited by human endurance. The costs involved in tracking have limited the sample sizes and meant that most observations have been short term—1 to 4 days. Although there are undoubtedly unpublished tracking data we have not covered here, the total number of tuna tracked since Yuen's (1970) first work with skipjack is less than 60, and there have been less than 120 days of behavior observed.

Most acoustic tracking has involved the release of a single fish caught on hook and line, and there is some question whether the behavior observed represents school-associated behavior. However, more recent work has focused on tagging a single fish while in a school (Lutcavage *et al.*, 2000a; Davis and Stanley, in press) or releasing a school of fish simultaneously with the individual tuna equipped with tags (Marcinek *et al.*, 2001).

The maximum distance between the vessel and the fish that has been reliably achieved for tracking is 0.7 NM (nautical mile), and most often the distance is 0.25–0.5 NM. Thus, the question of how the close proximity of a tracking vessel may affect behavior of tuna has been a concern for tuna researchers for many years. For example, Davis and Stanley (in press) found some fish were attracted to their vessel and to other fishing vessels in the area. To objectively answer the attraction/repulsion and stress questions simply through further tracking seems circular, although tracking for longer periods—perhaps 5–7 days—may allow resolution of whether behavior changes over time. Some experienced trackers note that it is reassuring to observe that fish of a particular species have very similar diving behavior in different oceans, conditions, and studies (K. Holland, personal communications). Some of the most compelling arguments for the representativeness of tracking data come from recent comparisons of acoustic and archival records, as well as acoustic and pop-up satellite records (Boustany *et al.*, 2001; Marcinek *et al.*, 2001). These studies have revealed a good correlation between key parameters (e.g., mean swimming depth, mean water temperature) despite the fact that data are acquired at very different sampling rates (seconds for acoustic data, minutes for archival and pop-up tags). Comparisons of acoustic and archival or pop-up satellite data for the same species (Atlantic bluefin tuna), and in the same area, indicate that in some cases, but not all, the first day or two of an acoustic track are poor indicators of the behavior of the fish (Boustany *et al.*, 2001). This seems most likely to be a problem if fish are caught on a hook and line, and suggests that in some cases a recovery period is required (Block *et al.*, 1992). However, it is clear that individual fish have distinctly different abilities

to recover from the tagging events and not all fish are equally affected by the experience.

With this caution in interpretation of short acoustic tracking records, it is interesting to note that for most of the *Thunnus* species examined, the published acoustic tracks provide a good record of the median depth distribution and ambient temperature preferences of the species. Acoustic data on the depth and ambient temperature preferences of yellowfin tuna are the most extensive (approximately 60 days of records from 23 fish have been obtained). Comparing the results in the literature with a larger data set from pop-up satellite archival tags indicates similar information on yellowfin depth distribution (B. Block, unpublished data). Thus, while in some cases the behaviors in the early portions of acoustic tracks are clearly aberrant, due to the handling or the presence of the tracking vessel, in most tracks the fish settle down and exhibit movement patterns that are typical of individuals tracked with archival and pop-up satellite archival tags (PATs) (Marcinek *et al.*, 2001). The great advantage of acoustic tagging is it puts the researcher in the field close to the fish where interactions with prey species and associations with other organisms can be noted.

III. ARCHIVAL TAGS

Following their successful use to study marine mammal movement and behavior (Delong *et al.*, 1992), archival or data storage tags were described as a "potential tagging technology" for studying tuna movement and behavior by Hunter *et al.* (1986). The concept was a tag that would allow collection and storage of data from a number of environmental sensors for a year. If this could be achieved, it would fill in the gaps that existed between the very short-term and detailed data collected by acoustic tracking studies and the single points of release and recapture provided by conventional tagging experiments. Archival tags were seen as a means of understanding residency and long-term variations in movement and behavior. Also, being fishery independent, they would provide much-needed information of the movements of tuna into areas where there were no fisheries (and thus where there had been no conventional tag returns).

A U.S. company, Northwest Marine Technology of Shaw Island, Washington, completed a feasibility design for an archival tag in the mid 1980s. However, the technology was not used on tuna until 1993 (southern bluefin tuna; Gunn *et al.*, 1994). Block *et al.* (1998a), inspired by the southern bluefin work, began archival tagging Atlantic bluefin tuna in 1996. At much the same time, data storage tags without light sensors were also first used on plaice in the North Sea (Metcalfe and Arnold, 1997), and Tsuji *et al.* (1999) began archival tagging Pacific bluefin tuna in pens and in the wild. The success of these independent studies has led to the

use of archival tags on bigeye (Boggs *et al.*, 1999; J. Gunn and J. Hampton, personal communication; K. Schaefer, personal communication).

A. Technology and Methods

Archival tags are basically miniature computers, incorporating microprocessors, memory, and a suite of environmental and physiological sensors. They have very low power budgets, allowing data to be collected over many years. Specifications vary among manufacturers (Klimley *et al.*, 1994). However, the most advanced tags available as of this writing have light sensors capable of measuring variation in moon light at depths of 100 m, 1–4 megabytes of flash (nonvolatile) RAM memory, depth sensors providing accuracy of <1 m over a range of 1000 m, and thermistors capable of measuring temperature to within 0.1°C over a range of 40°C+. They use 8- or 16-bit microprocessor technology and allow data to be collected from 3–4 sensors every few minutes for periods of up to 5 years. The nonvolatile memory allows data to be retrieved even after the tag's battery has run down.

Perhaps the most critical feature of an archival tag is the collection of data that can be used in estimating the position of the tagged animal. Over the last 5 years, researchers have used light, water temperature, and depth data collected by archival tags in estimating position.

Estimating position from variation in light levels involves relatively simple concepts and algorithms (Wilson *et al.*, 1992; Hill, 1994; Hill and Braun, 2001). If tunas remained on the surface and did not migrate long distances in short periods, estimating their position from archival tag data would be relatively straightforward. Unfortunately, most tunas tend to make very rapid dives, often at sunrise and sunset—the times most critical for estimating latitude with light—and all are capable of rapid movement over large geographic scales. Thus, when using archival tags to estimate the position of tunas we can expect systematic and random errors resulting from equinoxes, light attenuation, water clarity, weather patterns, precision of astronomical algorithms, clock errors, resolution of light sensor, and behavior of the animal (Musyl *et al.*, 2001).

Welch and Eveson (1999) and Musyl *et al.* (2001) estimated the accuracy of geoposition estimates based on light data from archival tags by comparing the known and estimated positions of tags attached at various depths to fixed oceanographic moorings. They used tags from different manufacturers, and employed a number of different analytical methods. Although there was variation in performance between tags, and some methods performed better than others under particular conditions, the scales of error in longitude and latitude estimates were similar in the two studies. Briefly, longitude consistently varied less than latitude, regardless of the analytical method used or the depth at which tags were moored. The standard deviation of errors in longitude estimates using the Welch and Eve-

son (1999) method was ±0.9°, or approximately 60 km, while that of latitude estimates was ±1.2°, or 130 km. Musyl *et al.* (2001) used a slightly different method of presenting their data; the absolute mean errors (i.e., true position − estimate) in longitude estimates for three methods ranged from 0.15° ± 0.12 (SD) to 0.29° ± 0.83, and in latitude estimates from 1.49° ± 2.72 to 4.36° ± 5.78.

As Welch and Eveson (1999) and Musyl *et al.* (2001) used tags that were essentially stationary in both the horizontal and vertical planes, their estimates provide minimum errors only. The only attempt to estimate the accuracy of position estimates from data collected by tags on fish (Gunn *et al.*, 1994) found mean errors on the order of 1.52° [±0.22 (SD)] in latitude and 0.54° (±0.09) in longitude. However, as the fish used by Gunn *et al.* (1994) were held in cages less than 20 m deep, and the study was conducted in early January, when errors in latitude are at their lowest (Hill, 1994), these estimates are again likely to be conservative for animals in the wild.

There are few published accounts of tuna movements or migrations based on archival tag geoposition estimates. However, experiences with large data sets collected by archival tagging programs on southern bluefin (SBT; J. Gunn, unpublished data), bigeye (J. Gunn and J. Hampton, unpublished data), Atlantic bluefin (B. Block *et al.*, 2001), and Pacific bluefin tuna (Kitagawa *et al.*, 2000) suggest that to get an estimate of position it is often necessary to use a combination of light, surface water temperature, and diving behavior data. The latter two data sources are used primarily to estimate latitude when light data do not allow accurate resolution of the times of sunrise and/or sunset. In SBT, the proportion of days in which light data can be used to estimate latitude varies throughout the year, largely as a result of changes in diving behavior associated with their annual migration cycle (see below). From late spring to early autumn, juvenile SBT live on or close to the southern Australian continental shelf. During this period they spend most of their time in the upper 100 m of the water column. In these depths, light data are generally good enough to make estimates of longitude and latitude, although the latter suffer from large interdaily variation (and thus presumably error) if fish consistently dive at sunrise and/or sunset. Errors in latitude estimates are also high during the summer and winter solstices (Hill, 1994). During winter, juvenile SBT migrate into oceanic waters where they make diel migrations from the surface (night) to depths over 400 m (day). Current generation archival tags, with their highly sensitive light sensors, allow longitude to be estimated from light data even during these times of extreme diving. However, as the most active vertical migration occurs close to times of sunrise and sunset, latitude estimates are rarely reliable. On these days, latitude is best estimated by comparing the records of sea surface temperature collected by the archival tag external temperature sensor with those provided by satellite SST data. If light data allow an estimate of longitude, this can be used to examine the match between tag and satellite-estimated SST to derive an estimate of latitude (Smith and Goodman, 1986).

Although it is possible to derive an estimate of position for most days using a combination of light, environmental, and behavioral data, objective measurement of the errors or reliability of these estimates is very difficult. For example, over the course of a month, geoposition estimates based on light often show movements that are simply impossible—either because they have fish "swimming" across land, or they involve movements of many hundreds of miles over 24-h periods. It is not always obvious from the light curves why one estimate is likely to be correct while another may be spurious.

By combining light and SST data one can objectively exclude position estimates on land. However, it is often more difficult to exclude positions in the ocean. For example, when fish are close to a large-scale eddy, or are within extensive areas of isothermal water (such as in the equatorial regions of most of the world's oceans), there will be a number of equally plausible latitudes for a given SST.

Several suggestions have been made on how to "objectively reject" unlikely or spurious position estimates. Among these are:

- Limiting daily movement to a sensible maximum distance, perhaps based on the maximum daily movements observed in tracked fish. This may be satisfactory for fish not actively migrating. However, as we describe below, bluefin tunas can move significant distances in one day when making directed migrations.
- Limiting analysis of position to days where diving behavior at the times of sunrise and sunset do not involve vertical movements over a defined limit.
- Using trend analysis, statistically remove outliers further than a set deviation from a trend line in a series of position estimates. This approach is based on the assumption that fish are unlikely to make random movements of scales greater than some arbitrary threshold.

Whatever the approach, showing both the raw and smoothed or reduced data is advisable, at least until more rigorous approaches have been developed to estimate error of position estimates.

B. Archival Tagging of Tunas

1. Southern Bluefin

The first tuna to be archival tagged were southern bluefin. The species has a wide and continuous distribution across the southern oceans of the world—from the southwest Atlantic to the southeastern Pacific, and one known spawning area south of Java. It has been heavily fished by Japan and Australia for over 40 years (Caton, 1991) and the estimated parental biomass in 1998 was less than 12% of that in 1960, and considered to be at historically low levels (Anonymous, 1998). Despite the heavy exploitation over many decades, little is known about the species' spatial dynamics. Recent contractions in the size and number of fishing

grounds have prompted debate over whether there has been a significant contraction in the geographic distribution of the stock, or simply a shift in the operations of fisheries targeting the species.

Much of what was known about SBT migration derives from extensive conventional tagging programs over the last 40 years. Since the 1960s over 132,000 SBT have been tagged and approximately 20,000 recaptured (Polacheck *et al.*, 1998). From conventional tagging data, catch records, anecdotal accounts of fishermen, and, we suspect, in part also the imagination of fisheries scientists, a hypothetical model of the migration of juvenile SBT was developed in the 1960s (Hynd, 1969) and later refined by Murphy and Majkowski (1981). The weakness of the SBT conventional tagging data set, as with many conventional tagging experiments, is that the vast majority of tags have been released in a few locations—mostly along the southern and eastern coastlines of Australia—and all of the recaptures have been made in locations where commercial fisheries operate. Thus, after 20,000 recaptures we know a great deal about the extent of mixing among Australian fisheries and, for fleets where reporting rates allow, between these and high seas fisheries. However, little is known of the residence times of fish in the different locations, whether a significant proportion of the populations spends time away from areas targeted by commercial fisheries, or how and when the fish moved between the points of release and recapture. Without these critical inputs, the models we have developed of SBT movement are seriously flawed.

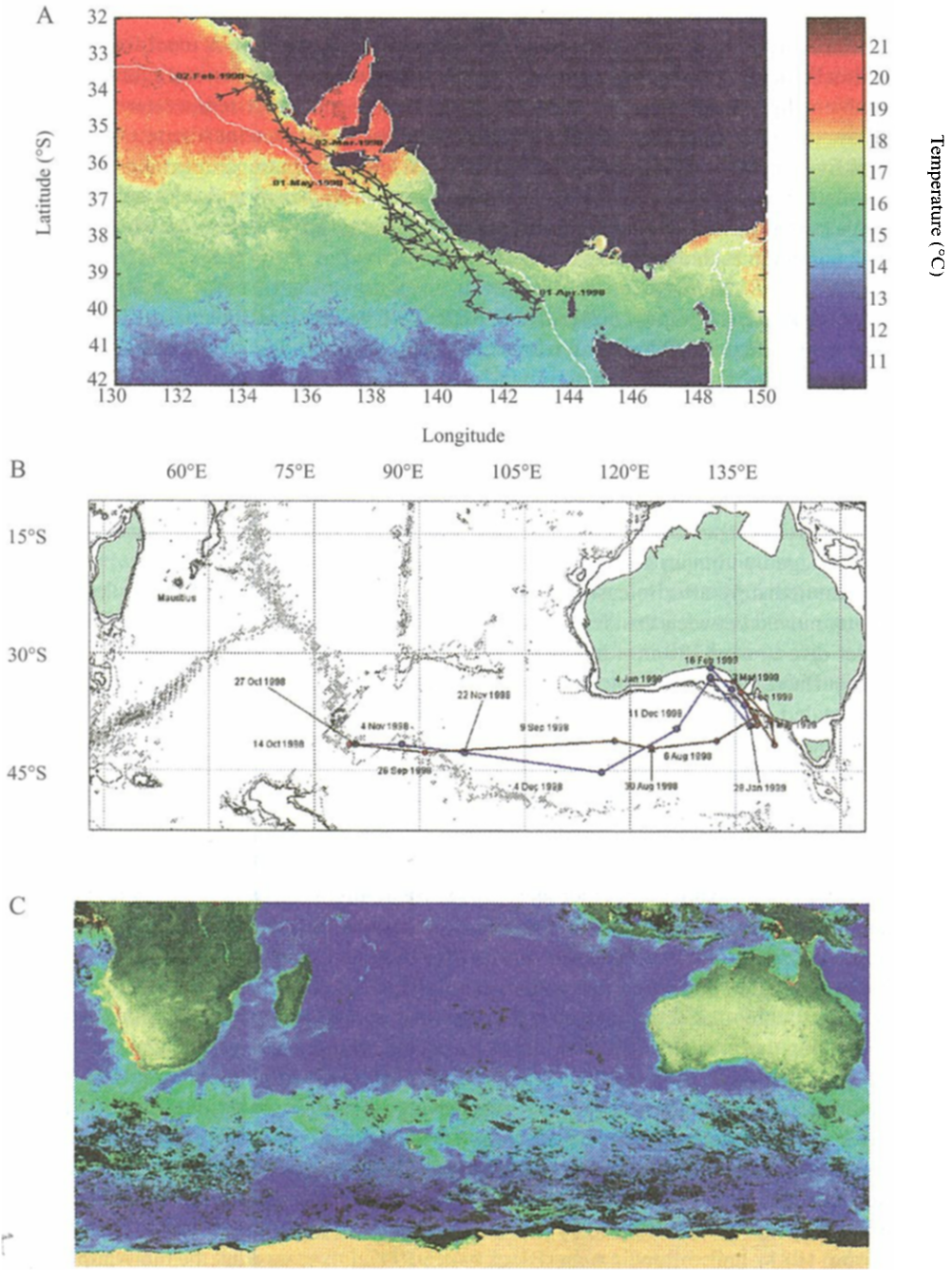
To address the inadequacies in our understanding of migrations and short-term movements of S.B.T. within the Great Australian Bight (GAB), the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Australia began to tag juvenile SBT with archival tags in 1993 (Gunn *et al.*, 1994). Five hundred and fifteen tags have been released, and 100 reported recaptured after times at liberty ranging from 10 to 1500 days. The tags have now collected over 15,000 days of data, which have challenged many of the previous views of the movements of juvenile SBT and provided a wealth of information on their behavior and physiology (Gunn *et al.*, 2001). We now know these fish make annual, cyclic migrations over ocean-basin scales. Summer is spent in the warm continental shelf waters of the GAB, while in winter they range widely over the oceanic waters of the southern Indian, Atlantic, Southern, and southwestern Pacific oceans. We have used the archival tag data to define residence times in the summer and winter feeding grounds and to examine the routes taken by fish as they migrate between these grounds. The data have also provided a unique insight into the behavior of fish in their different feeding grounds and as they migrate.

The volumes of data collected by archival tags provide an immediate challenge of how best to summarize the complex behavior of individual fish, while drawing out similarities across age classes, or groups of fish tagged at the same time. To illustrate the nature and extent of the data collected, we describe below the movements and behavior of one 3-year-old SBT between its release on 24 January 1998

and recapture 14 months later. For the time-at-liberty, we have a record of the animal's depth, its visceral temperature, the ambient water temperature, and the ambient light level, every 4 min. The light, depth, and water temperature data allow us to estimate the animal's position for most of the time at liberty (Welch and Eveson, 1999; Hill, 1994; Musyl *et al.*, 2001). Ambient temperature and depth data allow us to examine habitat preferences over daily, lunar, and seasonal time scales, and the visceral temperature provides a record of whether and when the fish has eaten each day (Gunn *et al.*, 2001).

a. A Year in the Life of a 3-Year-Old SBT. SBT 98-007 was 100 cm fork length and approximately 22 kg when it was caught by pole and line on the continental shelf edge of the Great Australian Bight (Lat. 33°17′S, Long. 131°26′E) on 24 January 1998. Within a few seconds of taking the live bait, the fish was lying on a tagging cradle having a Wildlife Computers Mk 7 archival tag surgically implanted into its body cavity, approximately 10 cm anterior to the anal vent. The surgery took 1 min and after a suture to close the wound, the fish was released back into the school from which it came. Twenty other fish from the same school were tagged within an hour, and all were released back into their school.

Immediately after release, 98-007 dived to 30 m and for the next couple of hours moved between this depth and the surface (Figure 3A). At sunset, it made a brief dive to over 120 m—below the mixed layer—and returned immediately to the surface. Shortly afterward, however, it returned to 120 m and as the night proceeded, gradually ascended and then descended, presumably in association with the vertical migration of the scattering layer. At sunrise, the fish made another short dive to 110 m and returned to the surface. These short, "spike" dives occurred almost every day throughout its 15 months at liberty, at exactly the same time relative to sunrise and sunset, whether the fish was on the continental shelf or in the open ocean. Spike dives are a common feature to all SBT archival tag data sets. Why fish would undertake short vertical migrations almost every day at sunrise and sunset is unknown. Possible explanations include locating the mixed layer (as seems to have been the case in 98-007); surveying prey fields at times when prey are silhouetted rather than camouflaged against the background; surveying the geomagnetic field on a regular basis as a means of geolocating; and surveying thermal/physical structure of the water column. Whatever the reason, it is clear that the behavior of SBT is precisely linked to variation in light levels. Sunrise and sunset are times when light is changing most rapidly, so the ability of SBT to synchronize ascent and descent to within a minute or two each day suggests they are very sensitive to these changes. As spike dives have been reported (or are obvious in figures included in publications) for a wide range of pelagic animals [e.g., blue shark (Carey and Scharold, 1990), swordfish (Carey and Robison, 1981), and yellowfin tuna (Block *et al.*, 1997)], it seems that the motivation for this behavior is common to many animals living in the open ocean.


A
Latitude (°S)
32
33
34
35
36
37
38
39
40
41
42
130
132
134
136
138
140
142
144
146
148
150
Longitude
01 Apr 1998
21
20
19
18
17
16
15
14
13
12
11
Temperature (°C)
B
60°E
75°E
90°E
105°E
120°E
135°E
15°S
30°S
45°S
Mauritius
27 Oct 1998
14 Oct 1998
4 Nov 1998
22 Nov 1998
26 Sep 1998
9 Sep 1998
4 Dec 1998
11 Dec 1998
4 Jan 1999
16 Feb 1999
6 Aug 1998
30 Aug 1998
28 Jan 1999
C

SBT 98-007's diving patterns (frequency of ascents/descents, diving depth range, diel variation) on the first day at liberty were very similar to those for the rest of the time it spent in the Great Australian Bight. From this we could conclude the stress of tagging did not to adversely affect the fish's behavior. However, it is interesting that although diving behavior seemed "normal," the fish either did not eat, or took only very small meals, for the first 29 days at liberty (Figure 4A). During this period, the lack of feeding activity can be identified by the temperature differential between ambient and the viscera remaining more-or-less stable at 1.6–2°C.

Going without food for periods of weeks to a month following tagging is common among the 100 SBT recaptured after archival tagging, and suggests that the fish take a significant time to fully recover from the stress of handling and surgery. In some fish, diving behavior during the first 2–4 days also appears abnormal with ascent/descent rates and intervals between dives during the first few days being much higher that normal, and indicative of frenetic activity.

As we discussed above, a major uncertainty in the interpretation of ultrasonic tracking data is whether the behavior observed is truly "normal." As tracks rarely last more than 2 days, the concern is that the stress of handling and attachment of the tag may cause abnormal behavior. The long-term nature of archival tag records provides a yardstick by which to measure "normal" behavior. Our data suggest that the stress of handling can have a range of expressions in the diving and feeding behavior of SBT and that these should at least be acknowledged and looked for when analyzing tracking behavior. However, we offer one caveat —as implantation of archival tags into SBT involves surgery, extrapolation of our observations to tracking studies where tags are attached externally is problematic.

On the 5 March, 98-007 took its first substantial meal (as indicated by the +5°C differential in Figure 4B). Based on the relative magnitude of temperature differentials, which are closely related to the amount of food consumed (Gunn *et al.*, 2001), the size of meals increased in the weeks following this first meal. Between 5 and 31 March, when the fish left the GAB, the fish fed every day.

While in the GAB (Figure 2), 98-007 spent the majority of its time on the continental shelf in depths less than 100 m (Figure 5A), in ambient water temperatures of 18 to 21°C (Figure 5B). On the shelf, the fish spent a high proportion of the daylight hours in the upper few meters of the water column, and from time

Fig. 2. (A) Fine-scale movements of SBT 98-007 between 24 January and 1 May 1998 determined from light and SST data collected by an archival tag. The movements along the eastern margin of the Great Australian Bight are overlaid on an SST image taken 20 May 1998. (B) Movements of SBT 98-007 between 24 January 1998 and 3 March 1999 determined from light and SST data collected by an archival tag. (C) Composite SeaWiFs ocean color satellite image for the Indian and Southern oceans for the first week of October 1998, showing the area in which 98-007 had foraged during September and October.

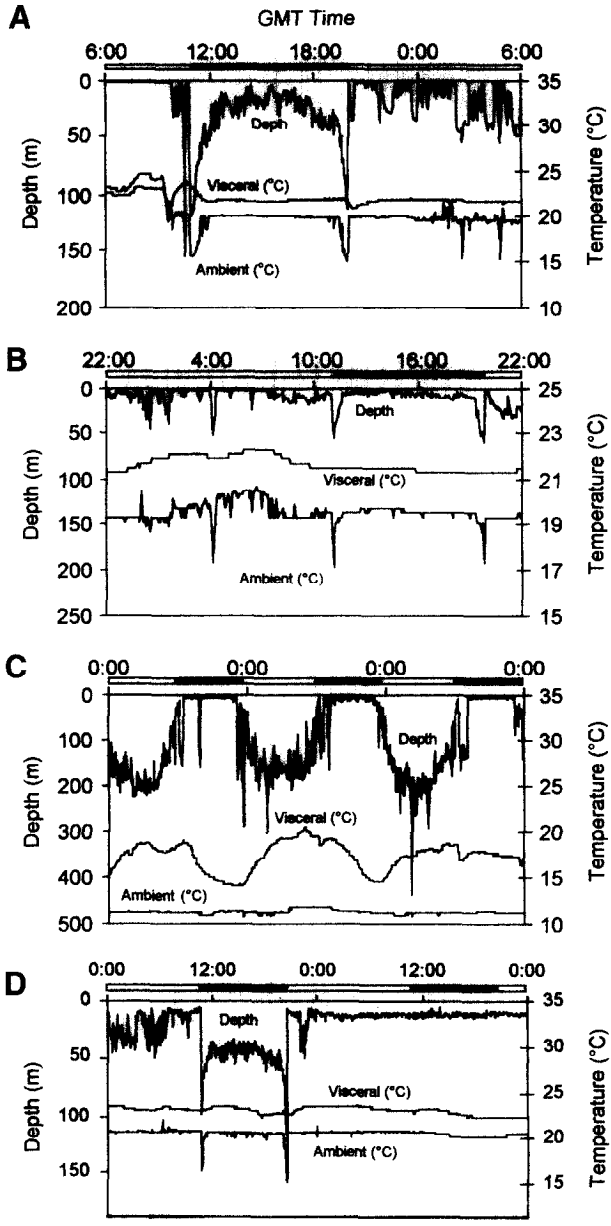


Fig. 3. Archival tag ambient water temperature (°C), visceral temperature (°C), and depth (m) data for SBT 98-007. (A) The first 24 h post release in the GAB. (B) Basking in the GAB on a summer afternoon (local time is GMT + 10.5 h) in the upper water column, and showing progressive warming of the water and associated warming of the viscera. (C) Deep diving and diel vertical migrations. Note the increases in visceral temperature indicating feeding in the early morning. (D) Capture by purse seine at around 2300 GMT (0830 local time), followed by the transfer into a cage limiting maximum diving to less than 20 m. Dark bars indicate night.

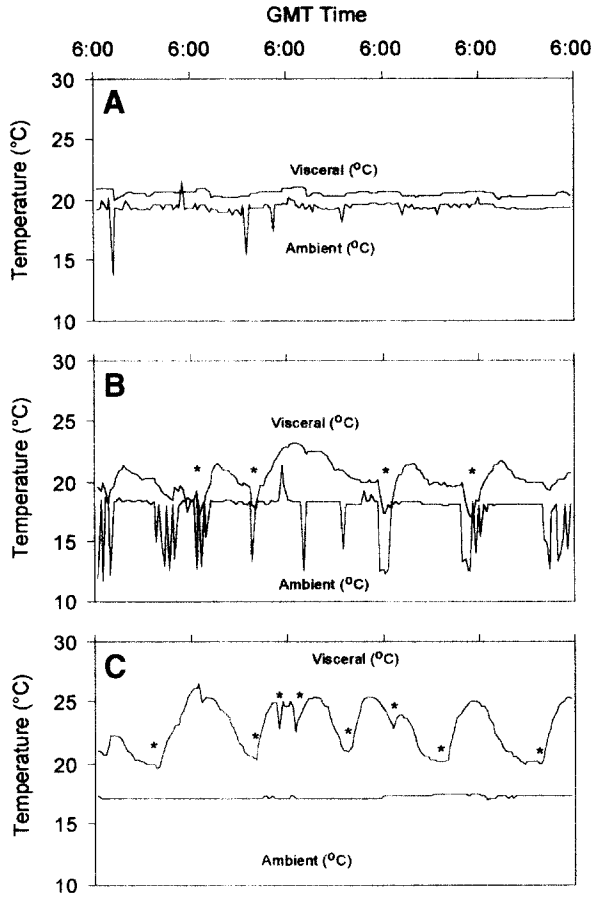
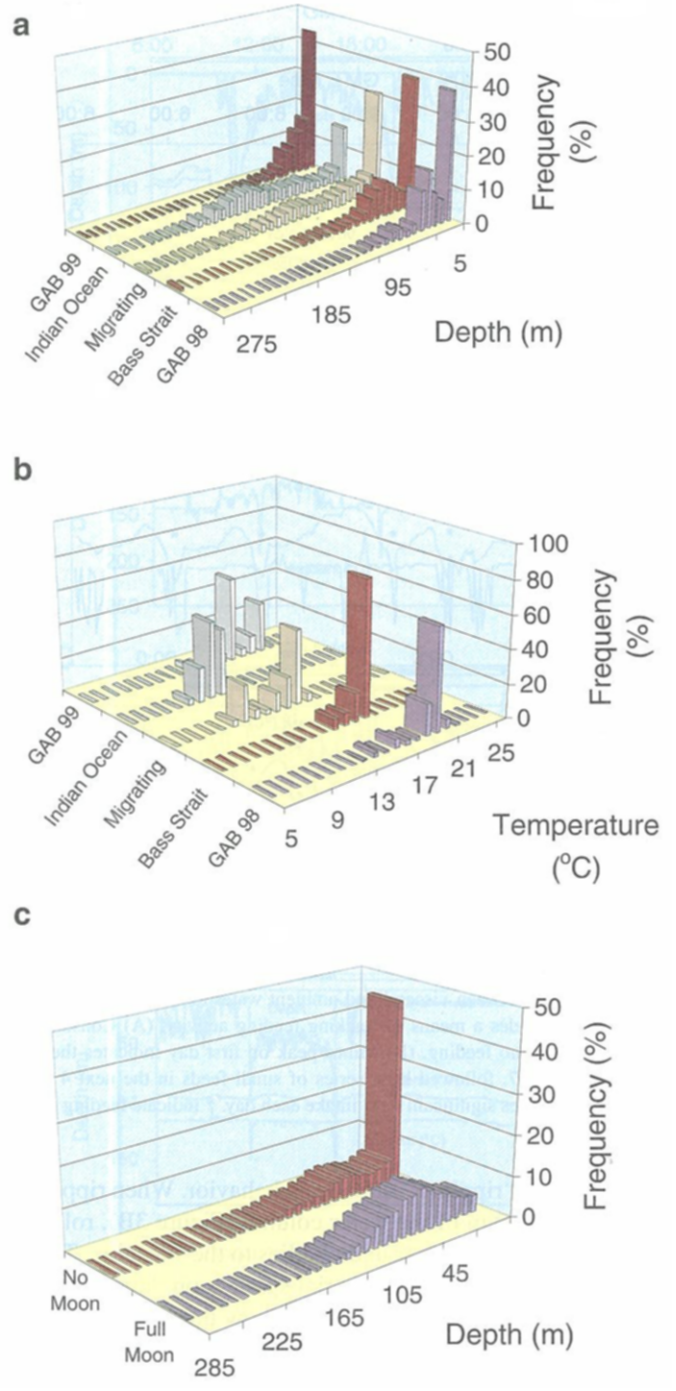


Fig. 4. The differential between visceral and ambient water temperatures recorded by archival tags over 5-day periods provides a means of tracking feeding activity. (A) Constant differential of approximately 2°C indicates no feeding. (B) Minor peak on first day indicates the first significant intake of food by SBT 98-007, followed by a series of small feeds in the next 4 days. (C) Large differential (up to 9°C) indicates significant food intake each day. * indicate feeding events.

to time the data indicate "rippling" or basking behavior. When rippling, individuals swim in the upper 1–3 m of the water column (Figure 3B), rolling from side to side thereby exposing their silver underbellies to the sunshine. The behavior is commonly observed by fishermen and aerial spotters on days when air temperatures are high (>30°C). The archival tag data show that extended periods on the surface are correlated with increased ambient temperatures as high levels of solar insolation warm the surface layers of the GAB. Increases in ambient temperature in turn result in significant warming of the viscera (and presumably the rest of the


a
50
40
30
20
10
0
Frequency (%)
GAB 99
Indian Ocean
Migrating
Bass Strait
GAB 98
275
185
95
5
Depth (m)
b
100
80
60
40
20
0
Frequency (%)
GAB 99
Indian Ocean
Migrating
Bass Strait
GAB 98
5
9
13
17
21
25
Temperature (°C)
c
50
40
30
20
10
0
Frequency (%)
No Moon
Full Moon
285
225
165
105
45
Depth (m)

body) over periods of many hours. Although this behavior has not been reported for other species of tunas, it is analogous to the behavior that sees many tunas using warm core eddies or the mixed layer as thermal refugia while making foraging excursions into colder water. Maintenance of elevated temperatures should increase aerobic performance (Dickson, 1995) and speed digestion of food (Carey *et al.*, 1984; Stevens and McLeese, 1984). We know that 3-year-old SBT accrue 80% of their annual growth while in the GAB over the summer months (Leigh and Hearn, 2000), and thus it seems likely that the energy derived from heating associated with long periods of rippling and surface schooling could contribute significantly toward increasing the energy available for growth during this period.

SBT 98-007 migrated out of the eastern GAB in late March 1998 (Figure 2A), and moved slowly in a southeasterly direction along the continental shelf. At this time of year, a narrow shelf-break current jet flows southeast from the GAB on the outside the continental shelf in this area, and it appears the fish followed this warm water as it flowed out of the GAB. Although the jet pushes as far as southern Tasmania during winter, 98-007 moved only 200–300 miles southeast of the GAB and remained in an area west of the Bass Strait for 3 months. This area experiences seasonal upwelling during late summer and it seems likely that the fish remained in this area to take advantage of higher productivity associated with the upwelling. Occasional but regular dives to 300–600 m indicate that the fish remained in ocean waters or close to the continental shelf break throughout autumn. However, it was predominantly surface oriented, spending over 75% of its time in the upper 50 m of the water column. Ambient temperature and depth data from the tag show that the fish frequently moved across strong thermal gradients (Figure 6), indicative of movement in and out of the warm front. Associations with fronts and eddies are common in most archival data sets and it appears that SBT use warm core eddies or warm currents as thermal refuges while taking advantage of increased productivity often associated with frontal systems (Franks, 1992). SBT 98-007 fed on 46 of the 80 days it spent in the area west of Bass Strait during autumn.

In July, 98-007 moved further offshore into the Southern Ocean where it remained for almost a month. In early August it began swimming steadily westward, and continued to do so for 2 months. By late September it had reached 90° E and covered a straight-line distance of 7700 km in 50 days (Figure 7). This equates to an average swimming speed over the ground of 6.4 km per hour, or 1.8 m per second. As the archival data indicate significant vertical movement and we pre-

Fig. 5. Frequency distributions for (A) depth and (B) ambient water temperature for SBT 98-007 in the GAB during 1998, in the western Bass Strait, while migrating to and from the GAB, in the Indian Ocean, and in the GAB during the summer of 1999 before being caught. (C) Depth frequency distributions for full moon and new moon periods while SBT 98-007 was in the Indian Ocean feeding grounds.

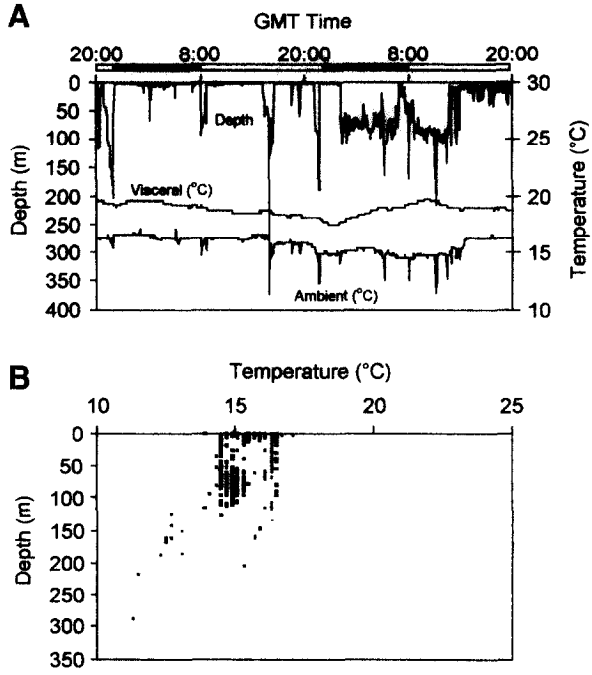


Fig. 6. (A) Archival tag records of depth and ambient and visceral temperature showing a 2-day period in the western Bass Strait area, during which the fish moved back and forth across a 2°C temperature front. (B) Temperature and depth data for the period shown in A indicating the two different water masses in which the fish was swimming, along with the mixed water between.

sume the fish was also making fine-scale horizontal movements during this time, the true swimming speed through the water was likely to have been much higher. On the outward migration the fish also swam directly against the west wind drift, which at that time of year is at its strongest in the "roaring 40s." While migrating, feeding occurred on 36 of the 50 days, and although it spent 30% of the time in the upper 10 m, a significantly higher proportion of the time was spent at depths greater than 100 m than had been the case in the GAB or Bass Strait. There was no obvious reduction in the oscillatory diving behavior during the migration, nor a bimodal distribution of depth such as that seen in actively migrating yellowfin (Holland *et al.*, 1990). As the fish migrated across the Southern Ocean and into the Indian Ocean, it moved progressively into colder water, and by the time it reached its western-most position at 90°E, surface water temperatures were 11–13°C—up to 10°C colder than during the summer season in the GAB (Figure 5B).

In the Indian Ocean, 98-007 began daily diel vertical migrations, characterized

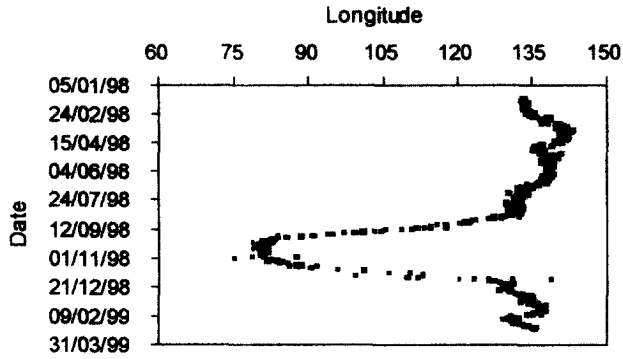


Fig. 7. Longitude estimates derived from an archival tag on SBT 98-007, showing the two periods during which the fish was in the eastern GAB and western Bass Strait region (longitudes 130–144°E), and the two very rapid migrations between these areas and the central Indian Ocean. Estimates were made for 90% of the days at liberty.

by long periods in the upper 40 m during the night and gradual descents starting at sunrise down to 200–400 m, followed by gradual ascents finishing at sunset (Figure 3C). There was also a clear lunar cycle in the depth preferences at night, with the fish being deepest during the full moon and a few days following, and shallowest around the new moon (Figure 5C).

The vertical migration suggests a close association with the scattering layer, very similar to that described for bigeye tuna (Dagorn *et al.*, 2000; Holland *et al.*, 1990). The area in which 98-007 foraged was to the east of St. Paul and Amsterdam islands, on the northern edge of the subtropical convergence zone. In this area a very deep mixed layer (temperatures on the surface were the same as those at 300 m) allowed the fish to forage to considerable depths without having to move into cold, subantarctic water. Productivity in the area, as indicated by NOAA Seaviewing Wide Field-of-view Sensor (SeaWiFs) data, was relatively high, and significantly higher than that in the GAB at the same time.

The predominant food in the diet of SBT caught in the Indian Ocean is omastrophid squid (CSIRO, unpublished data), which are known to undertake large diurnal vertical migrations, also in association with the scattering layer (Nakamura, 1993). Nakamura (1993) found that mature female omastrophids migrate to depths in excess of 600 m each day, with descent dives starting around 1 h before sunrise and ascents around sunset. It seems very likely that the vertical migrations of 98-007 were in response to the squid movement. Visceral temperature data from the tag indicate the fish began digesting a meal shortly after beginning its descent, and small secondary peaks early in the morning were coincident with the ascent dive (Figure 3C). Although we cannot tell from these data whether the fish

continued to feed while at depth during the day, the presence of two modes suggests most feeding occurred at these times, when the squid were actively moving through the depth range in which the fish was foraging.

After less than 2 months in the central Indian Ocean, 98-007 began a return migration towards the GAB. It returned on much the same route it had taken on the way out (Figure 2B), and the return journey was again very fast, taking on the order of 60 days (Figure 7). On 4 January 1999 the fish revisited the shelf break location it had been tagged at almost 12 months before. Once back in the GAB, 98-007 switched back to the behavioral patterns and habitat preferences exhibited the previous summer (Figures 5A and 5B).

In the first 12 months at liberty, 98-007 covered in excess of 18,000 km in straight-line migrations; changed habitats, diving behavior, and dietary preferences; and managed to avoid capture in the extensive Japanese, Korean, and Taiwanese high seas long-line fisheries that operate in the southeast Indian Ocean during the winter–spring period. From the archival tag data we were able to estimate residence times in the different feeding grounds and determine what proportion of the time it had been foraging or migrating in fishing grounds.

Early in the morning of 18 February, the fish was caught by the purse seiner FV *Kathy BJ* while swimming in a large school off the continental shelf in the eastern GAB. The tag data show the dramatic change in diving behavior following the fish's transfer into a cage in which it was towed back to Port Lincoln on the coast of South Australia. In Port Lincoln, the fish was fattened for 6 months before being harvested for the Japanese sashimi market. Over these 6 months we see in the archival tag record the daily feeding cycles of the aquaculture operators (see Gunn *et al.*, 2001).

2. Atlantic Bluefin

Atlantic bluefin are another tuna species for which we have inadequate understanding of movement patterns, where and when they breed, or how populations are structured despite over 2000 years of exploitation (Block *et al.*, 1998a). Like southern bluefin, stocks of Atlantic bluefin tuna are now considered overexploited (National Research Council, 1994). They are managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT), and stock assessments currently consider the Atlantic bluefin tuna as two separate populations with limited mixing and distinct breeding grounds. One stock is proposed to reside in the west Atlantic with a spawning ground in the Gulf of Mexico; another stock is proposed to exist in the east Atlantic with a spawning ground in the Mediterranean Sea (National Research Council, 1994). Importantly, conventional tag data have demonstrated that all size classes of Atlantic bluefin are capable of making trans-Atlantic crossings in short durations (National Research Council, 1994); however, there is little information in the conventional tagging data with which to define stock boundaries. To learn more about the biology, migrations, and stock structure

of bluefin tuna, an archival tagging program was initiated in the west Atlantic in 1996 (Block *et al.,* 1998a,b, 2001a,b).

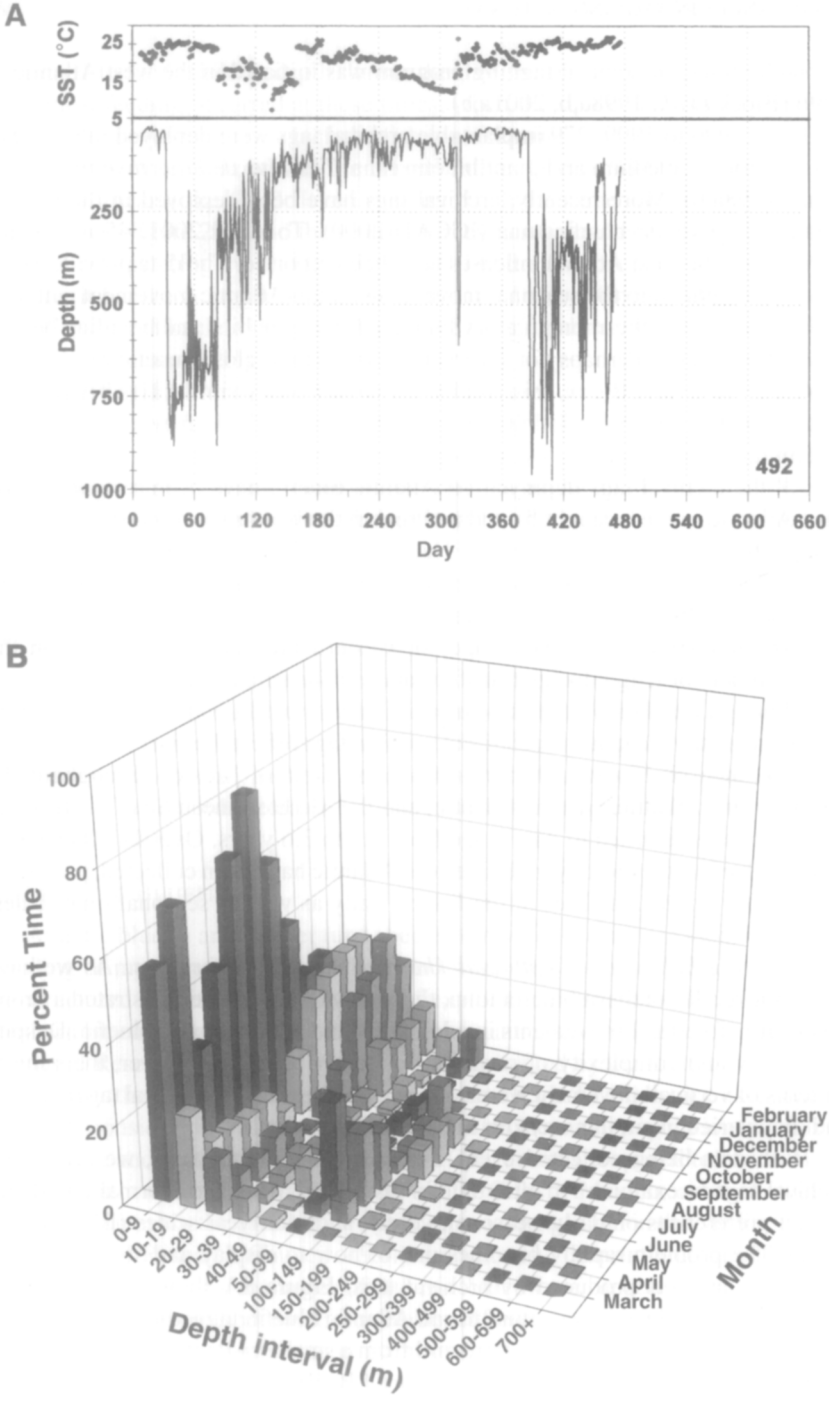
From 1996 to 1999, 279 implantable archival tags were deployed in the western Atlantic on medium and giant bluefin tuna, *Thunnus thynnus thynnus* (Block *et al.,* 1998a,b). More recently, archival tags have been deployed in the eastern Atlantic in juvenile bluefin tuna (ICCAT, 2000). To April 2001, 45 recaptures (16%) from the west Atlantic releases have been reported. The data provide exciting new insights into the seasonal movements, trans-Atlantic movement patterns, depth preferences, thermoregulatory biology, feeding habits, and breeding behaviors of the species. Perhaps not surprisingly given their close genetic relationship (Collette, Reeb, and Block, this volume), there are many similarities between the data collected on Atlantic bluefin and those described above for southern bluefin tuna.

All the archival tags deployed on Atlantic bluefin have been released in the west Atlantic, on fish caught by rod and reel in the winter sport fishery that operates on the U.S. east coast near Cape Hatteras and Cape Lookout, North Carolina (35°N, 75°W). The implantable archival tagged fish ranged in size from 170 to 254 cm CFL (curved fork length), and at this size fish are considered to be either western adolescents (7 years of age) or western breeders (8+), based on the ICCAT model of length to age transformations (Turner and Restrepo, 1994).

Although the data on the movement of each fish while at liberty are fishery independent, the recapture locations of archival tags reflect the current distribution of the known bluefin tuna fishery—from the Gulf of Mexico throughout the northwestern Atlantic, eastern Atlantic, and the Mediterranean Sea. The times at liberty for tags returned to date range from 0.2 to 3.6 years. Over 14,700 days of data on bluefin tuna biology in the western Atlantic have been collected, providing information on the activities of the fish on daily as well as seasonal time scales.

a. Diving Behavior—Depth and Thermal Habitat Preferences. As we have seen in juvenile southern bluefin tuna, the archival tag data demonstrated a broad repertoire of vertical movements in adolescent and adult Atlantic bluefin. Despite the variety and complexity of some of the diving records, however, the general patterns of vertical movement were common throughout our archival tag data sets, and they varied in similar ways on a seasonal basis.

With data being collected every 2 min for months to years, we have used archival tags to examine Atlantic bluefin diving behavior and thermal and depth habitat preferences on daily, seasonal, yearly, and multiyear scales (Block *et al.,* 2001). The problem rapidly becomes one of how to display and summarize the extensive data sets produced by archival tags. Figure 8A shows the maximum depth and sea surface temperature for an Atlantic bluefin tagged in 1999 (218 cm curved fork length, CFL). A depth record from a smaller Atlantic bluefin (193 cm) archival tagged in 1997 is shown in Figure 8B. Both fish display characteristic


A
SST (°C)
25
15
5
Depth (m)
250
500
750
1000
492
0
60
120
180
240
300
360
420
480
540
600
660
Day
B
Percent Time
100
80
60
40
20
0
0-9
10-19
20-29
30-39
40-49
50-99
100-149
150-199
200-249
250-299
300-399
400-499
500-599
600-699
700+
Depth interval (m)
February
January
December
November
October
September
August
July
June
May
April
March
Month

behaviors observed in many of the archival recaptures. While in the western Atlantic, diving behavior varies seasonally in response to changes in location and can be divided into an inshore North American continental shelf residency period (winter and summer) and an offshore pattern exhibited in the spring and early summer while fish are either along the Gulf Stream frontal zone or in warmer waters near Bermuda or north of the Bahamas. Bluefin archival tagged on the Carolina shelf region typically display an on-shelf shallow period in the winter, followed in the spring by an offshore deep-diving period reflecting a change in feeding behavior (Figures 8, 9A, and 9D). During the on-shelf period, dives are often shallow and brief, and water temperatures are warm (18–23°C). During the offshore period the bluefin make deeper dives—occasionally to depths as great as 700–1000 m (Figure 8A). Once back on the shelf in the summer and early fall, the Atlantic bluefin are primarily occupying the upper 200–300 m of the water column limited in depth by the continental shelf.

Figure 9 shows the typical behaviors of bluefin tuna during the year in more detail. The archival tagged Atlantic bluefin often remained in the vicinity of the Carolina coast for periods of 30–90 days after release. In several cases, data from the tags indicate that the period of residency ends on the same day or within a few days of each other in the winter or early spring, as the bluefin migrate offshore. While in the shallow Carolina region, the continental shelf limits vertical excursions. Once the bluefin leave Carolina there are several patterns often observed. Some fish move north immediately and encounter cooler waters as they enter the Labrador current north of the Gulf Stream. Surface waters are often cooler (5–10°C) than the waters at depth (inversions) at this time of year, and bluefin respond by swimming in the warmer deeper waters (Figure 9B). The tagged fish swim for long periods—in some cases weeks—in inversions and show a prefer-

Fig. 8. (A) Sea surface temperature (dots) and maximum daily depth (solid line) for a bluefin tuna (229 cm CFL). The bluefin remained in the west Atlantic for the duration of the tag mission. The maximum daily depth shows the deepest depth reached by the bluefin on a daily basis and provides a view of the maximum diving patterns. Upon release off the Carolina coast the bluefin was limited in vertical excursions by the continental shelf. A warm eddy from the Gulf Stream was situated in the region the fish was tagged in and provided warm 18–20°C waters. Once off the shelf and in the Gulf Stream in March, the bluefin made occasional deep dives throughout the late winter. By early spring the fish had moved considerably north and was moving away from the frontal boundary of the Gulf Stream and into cold northern waters. Summer was spent feeding on the shelf. The second season the fish moved offshore in the late fall and moved south into the warmer waters to the east of the Carolinas. The fish did not revisit the Carolina coastal province. (B) Monthly depth histograms compiled from archival data for bluefin tuna WC-019. This fish was a 193-cm (CFL) individual tagged on 7 March 1997. This fish displayed western residency in its track, which was characterized by shelf behavior in the winter in Carolina, the late summer in New England, and once again in the second winter off Carolina.

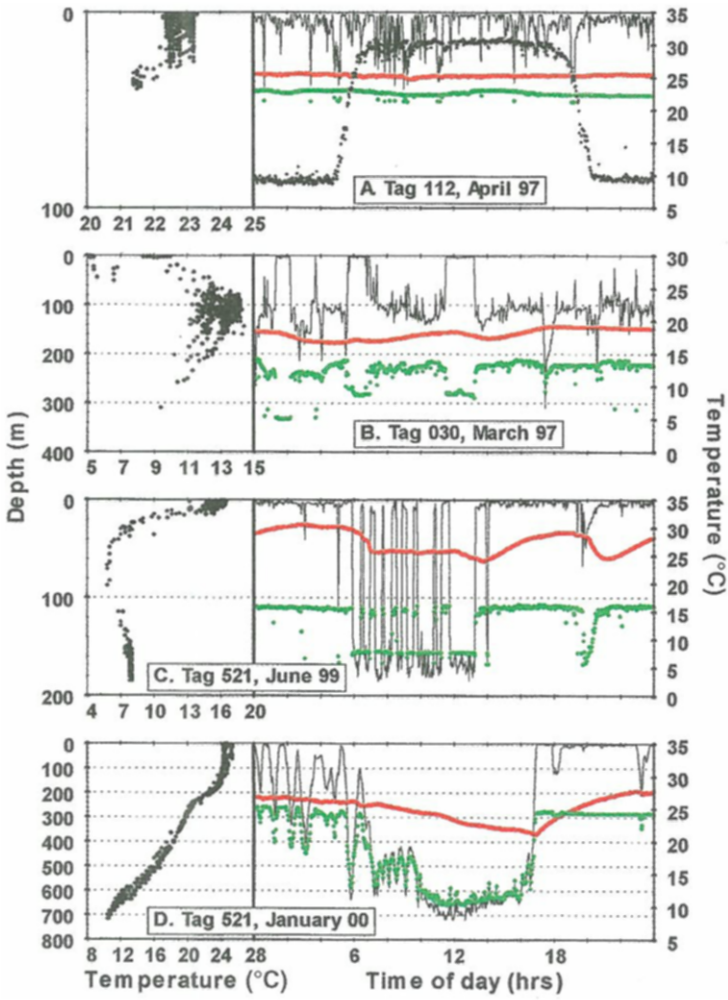


Fig. 9. Four days from archival tagged bluefin tuna at different times of year displaying the typical seasonal cycle. For each day a profile of depth and ambient temperature (left panel, closed circles) has been obtained from the data on the archival tag and is displayed. In the right-hand panel the 2-min records from archival tags are displayed with depth as black; body temperature, red; water temperature, green; and light in the first right-hand panel as black circles. (A) A bluefin off of Cape Hatteras, North Carolina. (B) A bluefin encountering an inversion with cooler surface waters often swims where the water is warmest, which is usually at depth. In this case the fish shows a preference for 100 m where the water temperature is 13–14°C. Surface waters are 5–6°C. (C) In New England, bluefin often dive to the shelf bottom but surface at regular intervals. (D) Offshore of the Carolinas in early winter, bluefin often display a diurnal vertical migratory pattern characteristic of feeding on the scattering layer organisms. All times are U.S. Eastern Standard Time.

ence for the warmer water, often at 100- to 200-m depths (Figure 9B). Temperature–depth profiles of the water column obtained by rapid dives called "Tuna bathythermographs" (TBTs) reveal the structure of the water column (Figures 9 and 11B). Other fish move due east or southeast along the frontal zones of the Gulf Stream or into the Gulf Stream waters south of the Carolinas. Fish moving along the edges often work the warm core rings. In summer and early fall, the archival tag data indicate that the bluefin of the year classes tagged are most often on the continental shelf off New England and Canada (Figure 9C). During this period, bluefin commonly dive at dawn and dusk, and spend the morning hours feeding and afternoon hours basking near the surface. Feeding is often associated with the periodic reductions in peritoneal temperatures and concomitant warming that can exceed 32°C. Body temperature often approaches 30°C during the basking periods. Periodically in the spring and the early winter months when offshore, most often while in the Gulf Stream, the bluefin display behaviors that include long periods of diurnal vertical migratory diving (Figure 9D) similar to that reported for swordfish (Carey and Robison, 1981) and those seen in bigeye (Holland *et al.*, 1990, 1992) and southern bluefin tuna (this chapter). We hypothesize that in all these species the diurnal periodicity in deep-diving behavior is associated with feeding on squid, crustaceans, or octopus within the deep scattering layer. In support of this hypothesis, we have often found squid, deep-water octopus, and even a nautilus in the stomachs of fish (B. Block, unpublished data).

A demonstration of the endothermic capacity of Atlantic bluefin is displayed during diel vertical migrations when Atlantic bluefin often keep their peritoneal temperatures elevated throughout dives, which last for many hours. The bluefin display significant seasonal variation in the thermal excess maintained between ambient water and visceral cavity temperature, and there is considerable evidence to support the contention that Atlantic bluefin tuna are the most endothermic teleost in the ocean (Carey *et al.*, 1971). Our data demonstrate Atlantic bluefin frequent waters between 2.8 and 29.0°C (Figures 8, 9, 12; Block, unpublished data), and throughout this range peritoneal temperatures remain significantly above ambient. In warm Gulf Stream waters (20–26°C), peritoneal temperatures were 3–6°C above ambient, and relatively constant with a range in mean peritoneal temperatures of 25.2–26.6°C. In these warm waters, deep dives to 300–1000 m resulted in very small drops in peritoneal temperatures. In contrast, when in cooler shelf or offshore oceanic waters, Atlantic bluefin maintained a differential of 10–15°C between peritoneal and ambient temperatures. In some individual bluefin, but not all, when challenged by extremely cold surface waters (5–10°C) for prolonged durations, the core temperature has dropped significantly. We hypothesize that the bluefin may be dumping heat from the oxidative muscle and viscera to the cardiac system to protect the heart over long durations from prolonged cold. The lowest peritoneal temperature recorded is 13°C. In addition, in some but not all bluefin, when deep dives were made in cool surface waters (SST 5–10°C) for

prolonged periods, the fish often returned to the surface repeatedly. A similar pattern has been reported in bigeye tuna, and is indicative of a thermal limitation and behavioral thermoregulatory responses (Holland *et al.*, 1992). Thus, while bluefin show a remarkable ability to maintain a thermal excess above ambient, there are occasions in cold waters when a physiological process is clearly limiting the bluefin's dive time.

b. Seasonal Movements. Archival tag data indicate that bluefin tuna tagged in the west Atlantic display at least three distinct types of behaviors: (1) western residency with no visitation to spawning areas, (2) western residency with Gulf of Mexico breeding, and (3) trans-Atlantic migrations to the east Atlantic or Mediterranean Sea (Block *et al.*, 2001a,b). Archival-tagged western bluefin tuna have been located in both known breeding areas, the Gulf of Mexico and the Mediterranean Sea, during the peak of breeding season. The movements of a 1997 tagged Atlantic bluefin (NMT 153) are shown over 3 years in Figure 10. This record is typical of western recovered archival-tagged Atlantic bluefin tuna and shows 3 consecutive years of western residency. This fish was among the youngest fish tagged and the behavior most likely represents an adolescent feeding route.

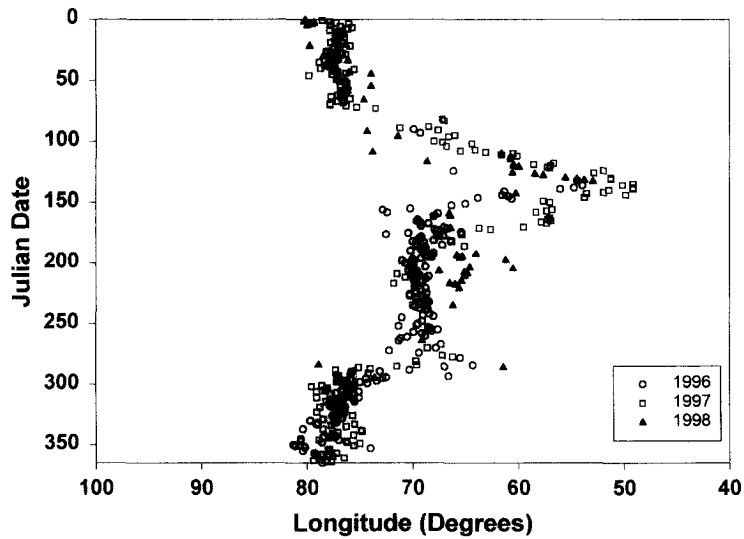


Fig. 10. Three years (1996–1999) in the life of a bluefin tuna (NMT 153) showing three seasons of western residency with no visitation to the Gulf of Mexico. The general pattern is Carolina waters in the winter, offshore in the spring, New England in the summer, and back to Carolina in the fall. Many of the 1997 archival returns show this pattern of movement. Larger fish tagged in 1999 displayed eastern migrations. Bathymetry and sea surface water temperature are used to augment the light data set to determine latitude (not shown).

All of the archival tracks begin in the winter (Julian date 1–90) at the longitude of the release point, off the coast of the United States in the vicinity of North Carolina (75°W), and most often proceed offshore in the spring along the path of the Gulf Stream. Many of the tags display a similar western loop of travel with no visitation to the Gulf of Mexico spawning ground. These fish move toward the mid-Atlantic after tagging, sometimes crossing the 45°W meridian that forms the stock boundary. Bluefin tuna displaying a western residency pattern move back toward the New England and Canadian shelf in early summer (67–70°W) and proceed down the North American continental shelf toward the Carolinas in late October and November. In "western loop" tracks the bluefin were often located at the same longitude of release (75°W) a year later. Importantly, these fish show no visitation during this year to the Gulf of Mexico spawning ground (>82°W). External temperature data throughout the tracks do not show residency in any waters that are considered warm enough for breeding (SSTs greater than 24°C for extended periods of time in the spring and summer). In contrast, these tracks often have water temperatures and bathythermograph profiles in the springtime that are strikingly cold, characteristic of moving north after the Carolina residency period. The remainder show movement along the frontal edges of the Gulf Stream. There are several cases in which bluefin tuna that display western loops without Gulf of Mexico visitation are in waters in June and July that are 23–25°C and warm enough for breeding (Block *et al.*, 2001a).

Bluefin tuna that move from the Carolinas to a known breeding ground (Gulf of Mexico or the Mediterranean) show movement patterns that raise many new questions about the biology of Atlantic bluefin tuna. Bluefin are capable of rapidly moving to the Gulf of Mexico (for example) from oceanic feeding regions thousands of nautical miles away from the breeding grounds in a very short period of time. The records are marked by a striking temperature pattern that reveals residency in warm waters during the May, June, or July period (Block *et al.*, 2001a). Temperatures during this period range from 25 to 29°C, as expected for breeding in this species. Diving behavior for the bluefin at the breeding grounds is considerably distinct from the repertoire of behavior observed in feeding bluefin tuna. The most striking aspect of the breeding ground visitation is the short duration (often less than a month). This suggests that in giant bluefin, spawning durations are perhaps much shorter than previously thought.

To date a total of 15 archival tags have been reported as having been recaptured (fourteen with physical evidence such as the conventional green tag) in the eastern Atlantic or Mediterranean Sea yet only 7 archival tags have been physically returned for analysis. Six fish have been reported near the straits of Sicily, or south of Malta, in May and June. Three from the mid-Atlantic, one a few degrees south of Iceland, three near the Straits of Gibraltar, and three north of the Canary Islands. The recovered archival tags in the eastern Atlantic and Mediterranean Sea document trans-Atlantic crossing in short durations (50 days; Block *et al.*, 2001a). Importantly these tags indicate that mature bluefin tuna in the west are capable of

moving quickly into the eastern Atlantic and Mediterranean Sea (Block *et al.*, 2001a). Several fish show residency in the Mediterranean during the peak spawning time, suggestive that they may have fed in the west for 1 to 3 years prior to returning to the Mediterranean to breed. Many of these fish show long periods of western residency followed by eastern migration, perhaps to spawn.

3. Bigeye

Three archival tagging projects have independently tagged bigeye in different parts of the Pacific Ocean over the last 2 years—in Hawaii (R. Brill, M. Musyl, and C. Boggs, personal communication), the eastern tropical Pacific (K. Schaefer, personal communication), and the southwest Pacific (J. Gunn and J. Hampton, personal communication). The data from returns are now being analyzed and will provide invaluable information on the extent and nature of regional differences in behavior and movement.

Bigeye pose a difficult problem for those interested in using archival tag data to estimate geoposition. As various researchers have reported from acoustic tracking studies (Holland *et al.*, 1990, 1992; Dagorn *et al.*, 2000), bigeye undertake significant diel vertical migrations that begin with a descent at first light each day (before the sun rises) and end in an ascent at around last light (often after sunset). Thus, estimating sunrise and sunset—two critical parameters for estimating geolocation—from archival tag light data is often impossible. Boggs *et al.* (1999) successfully used the regular diving ascents and descents of archival tagged bigeye to calculate position.

The archival tag data we have collected to date support many of the observations made by acoustic tracking studies. The data come from two 12-kg fish released in the Coral Sea and recaptured after 3 and 9 months at liberty. These show regular diel vertical migrations from mean depths at night of 50 m down to mean depths of between 450 and 500 m during the day. The maximum depths recorded by both tags were greater than the 1000-m maximum readings provided by the tag. During the day fish were regularly swimming in water temperatures of 7–9°C (SST was 25–27°C), and the lowest temperature recorded was 3.5°C, at a depth estimated from the slope of the temperature–depth relationship to be over 1500 m.

C. Summary

In summary, archival tags have been used successfully in three species of tuna to collect over 20,000 days of data from more than 150 individual fish. This compares with around 120 days of tracking data from 60 fish using acoustic tags.

From the two most comprehensive data sets, on southern bluefin and Atlantic bluefin, we have been able to define residency for tagged fish in various habitats as they undertake seasonal and annual migrations. The cyclic nature of these migrations in both bluefin species—whereby animals were recaptured very close to their point of release, but after making migrations of many thousands of miles—

is a striking reminder of some of the limitations of conventional tagging experiments. In a conventional tagging experiment, the net movement of each fish would have been minimal, and unless significant returns had been recorded at locations along the migration route, the inferences made of migratory patterns incorrect. In the case of Atlantic bluefin, archival tags have provided the first details of trans-Atlantic movements. In SBT the tags have shown that many fish move into areas where fisheries no longer operate—an important observation in the context of current debate about geographic contraction of the stock.

The power of archival tag data is in the ability to link behavior and environmental data over long time series and ocean-basin geographic scales. This link cannot be made as directly as in an acoustic tracking study. However, the integration of tag-derived data (fish position, diving behavior, feeding patterns, and preferences and shifts in thermal habitat) with climatological and remotely sensed oceanographic data (e.g., SST, ocean color, ocean height) provides an unparalleled opportunity to study and perhaps explain patterns of migration, particularly where these are related to feeding rather than spawning. Answering some of the key questions regarding the causal factors behind large-scale migrations and habitat shifts should provide us with a much better basis for interpreting large-scale changes in abundance of tunas such as those described in association with El Nino cycles in the Pacific (Lehodey *et al.*, 1998).

Although the appeal of archival tag technology is obvious, there remain some serious limitations to its use in some tuna species. The first is that we remain dependent on fishers to return the tags for data to be collected. For Atlantic bluefin, in more than 20% of the recaptures of tagged fish, tags have not been physically returned. In southern bluefin, the recapture rates for high seas long-line fleets are significantly lower than expected given their catch rates on tagged cohorts. As with conventional tag reporting rates, there are many reasons why fishers choose not to cooperate. Regardless of the reason, low recapture and/or low reporting and return rates seriously compromise archival tagging experiments, and it is likely that the likelihood of success will relate to how much cooperation one is likely to get from fleets catching the tagged fish. Interestingly, however, return rates for archival tags are significantly higher than those for conventional tags in SBT and Atlantic bluefin tuna, indicating either much lower shedding rates, or higher reporting.

The second major limitation of archival tags derives from the interaction between the behavior of fish and the technology. Over the 7 years archival tags have been used on tunas, there have been problems with the reliability of every generation or model of tag used, and it is clear that tunas provide a harsh test on the engineering skills of manufacturers and the durability of components. Failures due to deep diving, wear and tear on tag stalks, battery reliability, extreme temperature shifts over short periods as fish dive from tropical surface waters to great depths where 3–4°C temperatures occur. Limitations of the light sensors have resulted in lost data and compromised some of the data collected. It is also clear that geolocation estimation from light data is going to be a problem for species (or size

classes) that make diel migrations. We have been using cutting edge technology, and perhaps it is too much to expect failure-free operations. However, an improvement in the reliability of tags at this stage is much more important than major advances in tag functionality.

IV. POP-UP SATELLITE TAGS

The recovery rates of conventional and archival tags for many species of tunas and billfish are low, and likely to be fishery dependent. Thus, the concept of a tag that could be attached to a fish for a predetermined period and then automatically release and float up to the surface, where it would report its position, has been a very attractive "potential tagging technology" (Hunter *et al.*, 1986) for many years. Throughout the 1990s satellite tracking technology proved highly successful for monitoring large-scale movements of marine mammals, sea turtles, and albatross (Papi *et al.*, 1995; Renaud and Carpenter, 1994). For animals large enough to carry satellite-linked data recorders (cetaceans, seals, sea turtles), significant information on geoposition, swimming speed, diving behavior, and migrations has been obtained for periods of a year or more (McConnell *et al.*, 1992; Martin *et al.*, 1993; LeBoeuf *et al.*, 1996). Satellite telemetry has also been successfully applied to animals that spend significant amounts of time close to the surface, and are large enough to tow a floating satellite tag [e.g., basking sharks (Priede, 1984), whale sharks (Stevens *et al.*, 1998), and blue sharks (F. Carey, unpublished data)]. However, for tunas and other oceanic vertebrates that remain continuously submerged, these approaches are challenging to implement.

On a trial basis Gunn *et al.* (1995) used "pop-up radio tags" to define the short-term movements and school fidelity of juvenile SBT. Using radio transmitters housed in a buoyant tag body, and a timed galvanic release, they released a group of tags in different schools. A plane fitted with a radio receiver was then used to examine the pop-up location of the tags. Only a small number of tags were detected, leaving open the question of whether fish had moved out of the search area, or the bad weather experienced during the search period seriously attenuated the radio signals from the floating tags. Since 1997, single-point pop-up satellite tags and archival pop-up satellite tags have been used very successfully to study the movement of large Atlantic bluefin tuna (Block *et al.*, 1998b; Lutcavage *et al.*, 1999a), Pacific bluefin tuna (Marcinek *et al.*, 2001), and yellowfin and albacore tuna (B. Block, unpublished data). Our objective here is to describe the evolution of the technology, and review the available data.

A. Technology and Methods

Two manufacturers—Wildlife Computers, Inc., of Seattle and Microwave Telemetry, Inc., of Maryland—produced their first generations of single-point pop-

up tags in the late 1990s. The tags were very similar in design and functionality. They consisted of a lithium battery, microprocessor, low-power satellite transmitter, and thermistor. The electronics were packaged in a carbon fiber or polyurethane tube, to the trailing end of which a streamlined float constructed of syntactic foam, a micro-balloon resin composite, was attached (Block *et al.*, 1998b). The tags were designed to be attached externally to a fish; release at a preprogrammed time through activation of a current to a corrosive link; float to the surface; and then transmit continuously for a period of days to weeks to ARGOS satellites. The ARGOS satellites serve to both uplink data and calculate an end-point location. The tag's final position is calculated using the Doppler shift of the transmitted radio frequency in successive uplinks received during one pass. If the tag remains attached to the fish for all of the time between attachment and pop-off, it provides a fisheries-independent measure of the straight-line distance traveled from the point of tagging (Block *et al.*, 1998b; Lutcavage *et al.*, 1999a).

The original single-point tags produced by Microwave Telemetry provided an end-point location and limited temperature data. The first tags utilized recorded hourly temperature measurements and reported back 61 single hourly points during deployments of 1–3 days (Block *et al.*, 1998b). The first software revision applied to the first-generation tag permitted the tags to record hourly a single measurement and compile a daily average ambient temperature based on the 24 measurements. The tag logged 1500 individual ambient temperature measurements that were summarized into 61 daily average temperatures. This limited data storage capacity provided useful data on the overall ambient temperature preferences of the fish carrying the tag but was often seen as a limitation to the early tag design. However, the objectives of the initial deployments were to perfect the tag design, improve the flotation collar based on transmission results, and examine survivorship of fish carrying the tags. The preliminary studies proved immediately successful—pop-up rates in short (3–14 days) as well as longer (60–90 days) durations were high in their first applications on Atlantic bluefin tuna.

Short-term experiments were designed to test not only the new technology but also the survivorship of bluefin tuna released after capture with rod and reel techniques and attachment of the tag (Block *et al.*, 1998b). Using the heaviest tackle (60- and 90-kg line) and circle hooks, fishermen were able to keep times for capture down to a minimum, even for the large fish. In all cases, the bluefin tuna were pulled on board the vessel onto a vinyl wet foam pad, blindfolded, and irrigated with a seawater hose. Tags were carefully positioned at the base of the second dorsal fin and almost always the hook could be removed. All of the above presumably cut down stress of capture and handling. One hundred percent of the nine short-term tags (<14 days) surfaced and provided data. Long-term tags (deployed for 60–90 days) provided end-point data positions and archived a limited temperature data set (25 of 28), providing information on whether the tag remained on the fish and if the fish survived. Additional studies, conducted in the summer and fall of 1997, demonstrated that pop-up tags could be attached to Atlantic bluefin as well as other marine

fish for long durations (blue marlin were tagged for 60–270 days; B. Block and H. Dewar, unpublished data). Lutcavage *et al.* (1999a) attached tags to Atlantic bluefin for as long as 270 days. Once the pop-up tags were attached for longer durations, new concerns arose as it became extremely difficult with the use of the limited archive of temperatures to discern if the tags remained on the fish or had prematurely released. This was particularly problematic in species of fish that frequented warm waters with deep mixed layers (such as the blue marlin). The need for a pop-up tag with increased archival capabilities as well as a pressure sensor was apparent. Another shortcoming in the early generation of pop-up satellite tags that was exposed by data coming in from archival tags was that they were possibly not able to withstand the pressures exerted at the depths large bluefin can swim to—commonly in excess of 1000 m (Block *et al.*, 2001a).

Pop-up satellite tag technology evolved quickly through several generations of tags in the late 1990s. Second-generation pop-up tags constructed by Wildlife Computers recorded temperature every 30 min and provided a continuous record from deployment to the pop-off date. Although the basic external design was similar to the first-generation tags, several major changes improved performance. This generation of tag was significantly lighter in water and had a weight distribution that prevented the nose cone from rubbing into the fish's body, a problem with first-generation technology. The antenna was constructed of a flexible material that has memory and was smaller than that of the first-generation tags. This reduced potential interaction with the body of the fish. The pop-off stainless steel tube used for release was recessed into the nose cone of the tag, protecting the stainless steel from interactions with the body of the fish. The float had a more efficient surface to volume ratio maximizing buoyancy for a given mass, and a high-density syntactic foam capable of withstanding pressures over 1500 m was used. Five of these tags were placed on hook-and-line caught fish or harpooned onto free-swimming giant bluefin tuna released in purse seines in 1998 off New England, and all provided end-point positions and continuous thermal data. The increased thermal archive was particularly useful for discerning whether the tag had remained on a fish throughout its programmed attachment—an uncertainty for earlier generation tags.

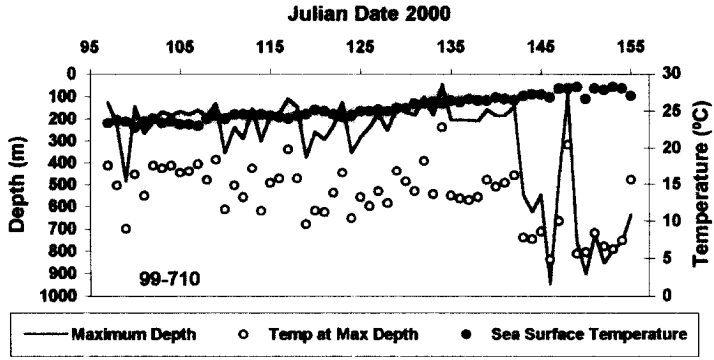
The most recent generation of Wildlife Computers pop-up satellite archival tags—incorporating a fully functional archival controller board, as well as pressure and light sensors—represents a major step forward in the evolution of the technology. Increased efficiency of the satellite transmissions, resulting from alterations to the antenna and the use of a spectrum analyzer to tune the frequency output of the PTT, is providing significant improvements in the volume of usable data being transmitted per tag. This generation of tags archives data on temperature, depth, and light intensity, and if recovered, the data set that can be downloaded is identical in quality to those from archival tags (pressure, ambient temperature, and light-based geolocation estimates based on light intensity data).

Perhaps most excitingly, this tag has software that estimates local noon (required for calculation of longitude; Figure 11C) and transmits these data together with a selection of light data that can be used in the calculation of longitude and latitude. The tag also provides depth–temperature profiles, sea surface temperatures, and maximum depth readings (Figures 11A and 11B). Data collected on depth and temperature preferences recorded in user set intervals (1 to 2 min) are stored as histograms and transmitted back (Figure 12). Software functions allow the user to prioritize which data to send back.

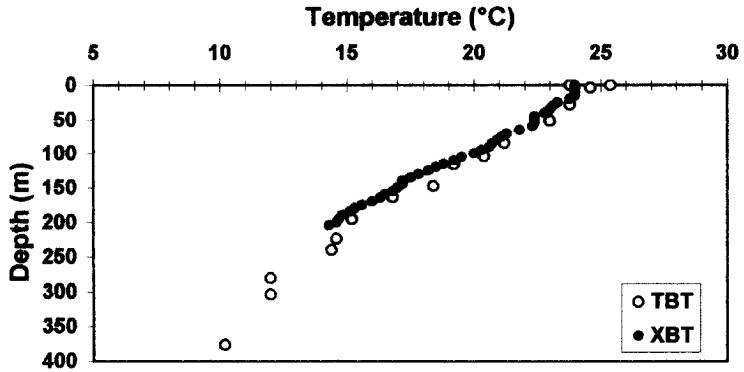
Recent generations of the Microwave Telemetry tags also provide on-board geolocation estimates and increased data storage capacity. Lutcavage *et al.* (2000b,c) report on the release of 21 "fully archival" Microwave Telemetry tags on giant bluefin. The limited data shown in the second paper indicate that these tags provide estimates of latitude and longitude, and allow the track of an individual to be reconstructed based on daily position estimates. Using "proprietary software written by Microwave Telemetry," Lutcavage *et al.* (2000c) report an accuracy of 2° and 1° for latitude and longitude, respectively, and cite work in preparation (Paul Howey, Microwave Telemetry, Inc.) which allows for more accurate geoposition estimates to be estimated following additional data processing.

The scientific community has benefited immensely from the collaborative approach taken by the two pop-up tag manufacturers with scientists using the technology. As a result, we have significantly advanced the capabilities of these tags in a very short time. Work on ground-truthing or validating the data collected by the tags has been slow, and to some extent has taken a back seat to the applications work we discuss below. It is very exciting to get hold of a new technology, and very tedious finding out how reliable it is. Perhaps the major challenge of the next few years is to examine rigorously the potential of pop-up tags to accurately calculate geolocation on board. We have seen in archival tags that estimating geolocation from light data is potentially very difficult, even where one has all of the data collected every 2 to 4 min over periods of months to years available for analysis. In addition, low transfer rates to ARGOS receivers (they can uplink only 32 bytes of data during each transmission) and the need to keep tags down to a minimum size (the battery is the largest component in the tag) mean that it is currently impossible to transmit all the data collected by pop-up tags for post-processing and analysis of geolocation. There are additional complications—the percentage of data recovered and the error rates in transmissions are heavily influenced by weather during transmission, water temperature, and latitude. The battery life at the surface for the current generation of Wildlife Computers tags has averaged 12.3 days in 18°C waters, and our experience suggests that 32-byte message transmissions have at best a 20–30% error rate over an entire data set. Future tags will need to incorporate software that can calculate positions on board and, to maximize the uploading of data, also be able to time transmission of data to coincide with passes of satellites.

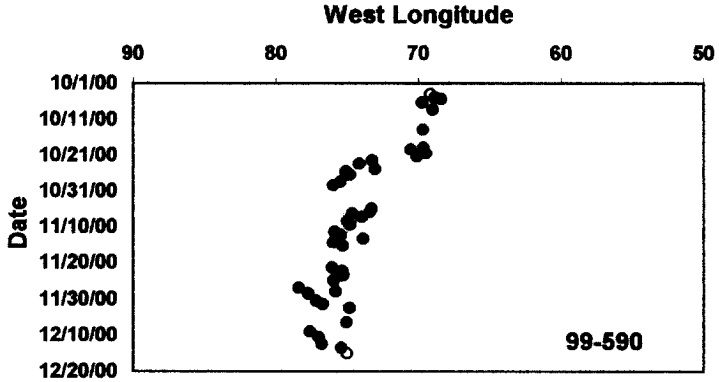
A


Julian Date 2000
95
105
115
125
135
145
155
Depth (m)
0
100
200
300
400
500
600
700
800
900
1000
Temperature (°C)
30
25
20
15
10
5
0
99-710
Maximum Depth
Temp at Max Depth
Sea Surface Temperature

B


Temperature (°C)
5
10
15
20
25
30
Depth (m)
0
50
100
150
200
250
300
350
400
TBT
XBT

C


West Longitude
90
80
70
60
50
Date
10/1/00
10/11/00
10/21/00
10/31/00
11/10/00
11/20/00
11/30/00
12/10/00
12/20/00
99-590

Users also require an objective test of the accuracy of position estimates made by the tags. To provide these, at least in the best-case scenario of tags attached to fixed buoys, experiments similar to those conducted for archival tags by Welch and Eveson (1999) and Musyl *et al.* (2001) are currently under way. Experiments examining the accuracy of pop-up satellite tag estimates are also being conducted by attaching both pop-up and conventional satellite transmitters to marine mammals (R. Hill and B. Block, unpublished data).

B. Application of Pop-Up Satellite Tags on Tunas

Over the last 4 years, pop-off tags have been successfully deployed on four species of tuna (Table I). Although there is some question surrounding the ability of small tunas to carry pop-up tags for significant time periods, the current generation of tags have been successful on tunas ranging from 18 kg (albacore) to 400 kg (giant bluefin tuna).

The technology has been used most extensively on Atlantic bluefin tuna (Block *et al.*, 1998b, 2001; Lutcavage *et al.*, 1999a, 2000). These applications started with testing of the technology and examination of attachment strategies in 1997 by Block *et al.* (1998b), and more recently the tags have been used for targeted studies on specific biological and stock structure questions associated with the management of the bluefin fishery in the Atlantic and Mediterranean Sea. We are aware of approximately 300 pop-up satellite tag deployments on Atlantic bluefin, at various locations throughout their range, by a number of different tagging teams. These deployments have met with varying degrees of success, and have resulted in pop-ups after durations ranging from 3 to 365 days (Block *et al.*, 1998b, 2001; Lutcavage *et al.*, 1999a, 2000b,c,d).

Block *et al.* (1998b, 2001, and unpublished data) have collected a comprehensive data set on movements of medium and giant Atlantic bluefin over the last 4 years, and have been able to compare these Doppler-based end-point positions and archived pressure and temperature data sets with archival tag data collected on fish released in the same areas (Boustany *et al.*, 2001; Block *et al.*, 2001b).

Fig. 11. The types of data that are transmitted via ARGOS from the archived data set on a Wildlife Computers pop-up satellite-transmitting archival tag. (A) Maximum depth (solid line), surface temperature (black circles), and temperature at maximum depth (open circles) from an Atlantic bluefin tuna in the Gulf of Mexico. (B) Comparison of a tuna bathythermograph (TBT) and an Expendable bathythermograph (XBT) profile from a Gulf of Mexico fish. (C) An example of longitude data transmitted from an Atlantic bluefin tuna released in Nantucket, Massachusetts, with a pop-up position off of Cape Hatteras, North Carolina. Release and recovery are shown with an open circle. In addition to these data, depth and temperature measurements obtained at a user set interval (usually 2 min; see Figure 12) are transmitted back, and a full archival record can be obtained if the tag is recovered..

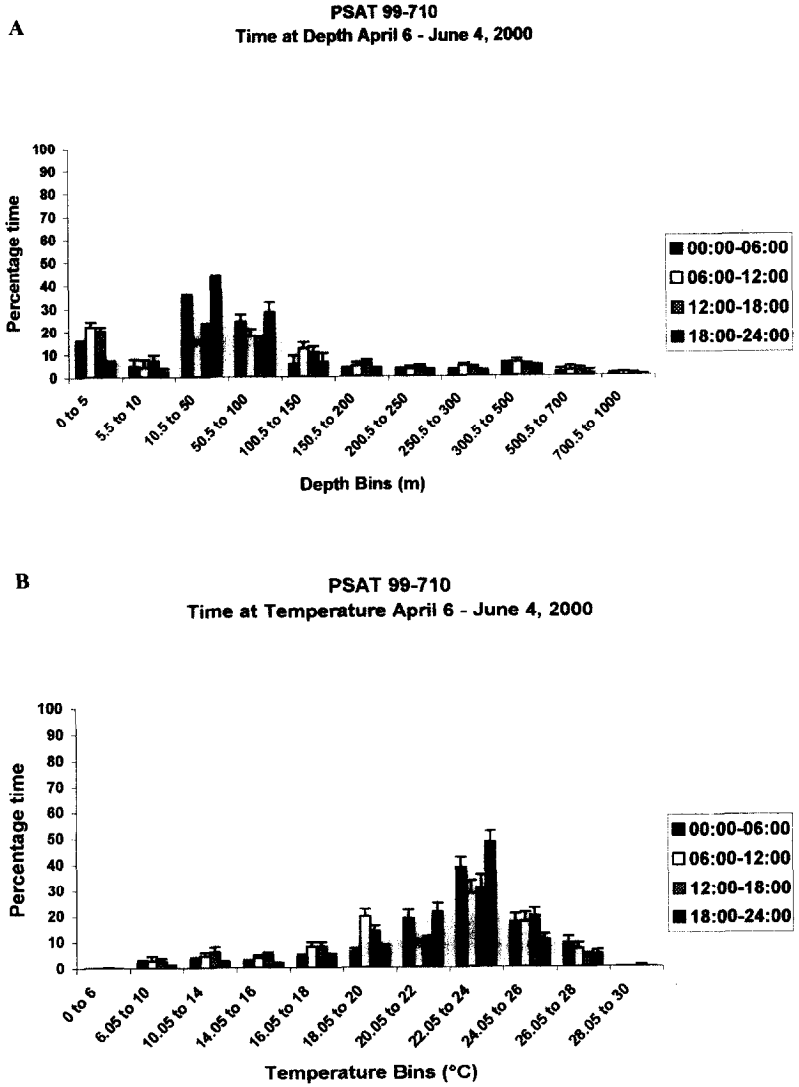


Fig. 12. Pop-up satellite depth and temperature data compiled from a bluefin tuna in the Gulf of Mexico. The pressure and ambient temperature data were collected for 2-min intervals for the duration of the deployment and summarized into the bins as shown. Bluefin tuna in the Gulf of Mexico have a wide depth range and a preference for warmer temperatures.

Table I
Deployment of Pop-Up Satellite Tags on Tuna Species, 1997–2000

Fish species	Year	Tag manufacturer	Tag generation	Number tagged	Duration (days)	Size (kg)	% successful data recovery
Atlantic bluefin tuna	1997–1998	Microwave Telemetry	1	42	3–365	81–121	92
Atlantic bluefin tuna	1998–1999	Wildlife Computers	2	38	30–180	70–300	90
Atlantic bluefin tuna	1999–2000	Wildlife Computers	3	110	4–365	40–300	90[a]
Yellowfin tuna	1997	Microwave Telemetry	1	2	60	30–40	50
Yellowfin tuna	2000	Wildlife Computers	2	10	2–97	30–89	70
Pacific bluefin tuna	1999	Wildlife Computers	2	3	14–60	20–30	100
Pacific bluefin tuna	2000	Wildlife Computers	3	6	14–60	15–25	100[a]
Albacore tuna	2000	Wildlife Computers	1	2	7–14	18	50

From Block (1998a; unpublished data) and Marcinek *et al.* (2001).
[a]Ongoing research (Block 1998a, 2001a) and % reflects success of tags that have come up to date.

They have successfully pop-up tagged fish off North Carolina in the northwest Atlantic (125), the Gulf of Mexico (20), New England (25), and the Mediterranean Sea (25). Many tags are still on fish and due to pop up in 2001; however, the distribution of the single end points from fish tagged in the western Atlantic in 1997–2000 mirrors the archival data. Tags programmed for durations of 3 to 365 days, released initially in the Carolinas (n = 68) as well as New England (n = 10), show a seasonal distribution around the western north Atlantic. Four bluefin have crossed into the eastern Atlantic close to the 45° meridian. To date no pop-up tagged western Atlantic bluefin tuna has been reported from the Mediterranean Sea. The difference between the pop-up satellite and archival data sets (where 30% of the recovered archival tags are in the eastern Atlantic and Mediterranean Sea) is most likely due to the length of time that the pop-up satellite tags are placed on bluefin (3–365 days versus as long as 3–6 years). Archival tagged bluefin apparently have diffused across their range whereas the pop-up tags to date reveal primarily western Atlantic movement patterns with some crossover in the spring period at the 45° meridian.

The pop-up end-point positions from release of some of the Atlantic bluefin tuna tagged in the vicinity of North Carolina and New England are shown in Figure 13. From these data (tags were deployed for 60–365 days) the seasonal movements of the bluefin emerge and corroborate the archival data set. Carolina-released bluefin show an inshore period of residency along the Carolina coast in the winter months and an offshore one along the productive front of the Gulf Stream in the spring, and report from several locations in the summer (New England, as well as offshore). Several of these latter fish have popped up in the warmer waters surrounding Bermuda as well as the mid-Atlantic in the spring and early summer (Block *et al.*, 1998b; Block *et al.*, 2001a). Bluefin tagged on the Gulf of Mexico spawning grounds in spring have remained there for up to 60 days, and several have moved outside the Gulf into the Florida Straits, the Bahamas, and off the coast of the Carolinas (not shown in figure). The Gulf-tagged bluefin tuna show a wide range of depth preferences and a characteristically warmer water preference at this time of year (Figure 12). Giant bluefin tagged in New England have migrated along the North American continental shelf in the fall and early winter, similar to the positions observed on archival tags for this season, and have in some cases popped up in the Carolinas. Several New England fish have popped up in the mid-Atlantic, and one showed fidelity back to the New England region a year later. As with archival tag data, the positional information can be overlaid on SST and ocean color remote imagery to provide information on the movements in relationship to oceanographic features such as fronts or regions of upwelling (Figure 14). Perhaps the most remarkable aspect of the 1997–2000 deployments in the western Atlantic is the high recovery rate of data—90% of the tags reported position and archived data sets.

Based on successful pop-ups of 49 tags deployed between 1997 and 1999 on

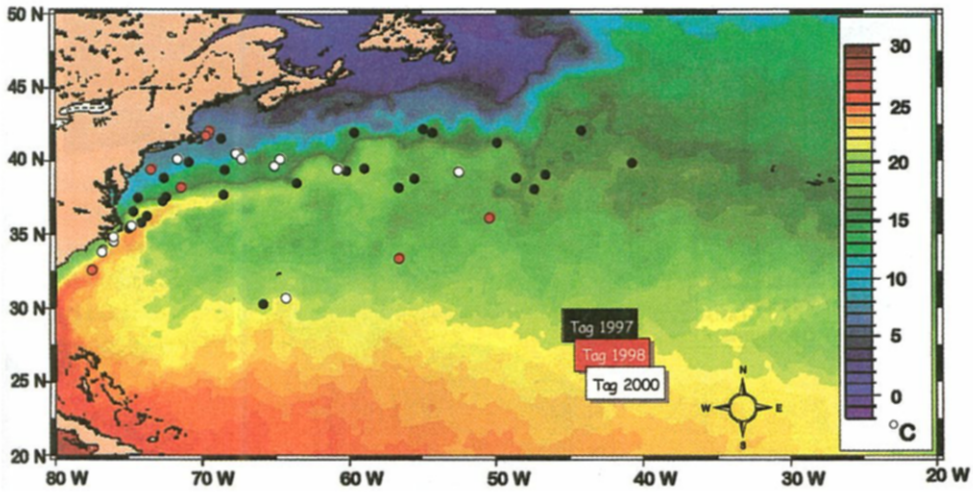


Fig. 13. Distribution of some of the pop-off end points (<60 days) from bluefin tuna released in 1997 (black circles) and 2000 (white circles) from the Carolinas, and in 1998 from New England (red circles). All tags shown are deployed for 60–180 days.

giant bluefin off New England in the northwest Atlantic Ocean, Lutcavage *et al.* (1999a, 2000b,c,d) have argued for a reconsideration of the current assumptions about the species' migration patterns, mixing rates, spawning areas, and stock structure in the western Atlantic. While the majority of tags released in these studies popped up in the west Atlantic in locations similar to those reported above by Block and colleagues, a significant percentage (30%) of the recovered releases (n = 9) reported back from east of the 45°W parallel of longitude used as the separator between "eastern" and "western" stocks. Lutcavage and her co-workers indicate that these tags have reported back from the central Atlantic at times when "western" Atlantic bluefin are known to spawn in the Gulf of Mexico. From this she concludes that spawning may also be occurring in the mid-Atlantic. This is obviously a very interesting hypothesis; however, further clarification is required as in some cases the date the tag surfaced (e.g., March) and the size of the fish tagged may not be inclusive of western breeders. Most recently (Lutcavage *et al.*, 2000c) data from archival pop-up tags have also provided detailed information on the tracks taken by tagged fish as they migrate out into the central Atlantic. Although the data shown in this paper indicate that some individuals move as far south as the Bahamas before joining the Gulf Steam on a northeasterly migration, thus far no fish from this study has migrated into the Gulf of Mexico.

In corroboration of Lutcavage's observations, both archival and pop-up satellite data sets of Block *et al.* (1998a, 2001a,b) indicate bluefin are often outside the

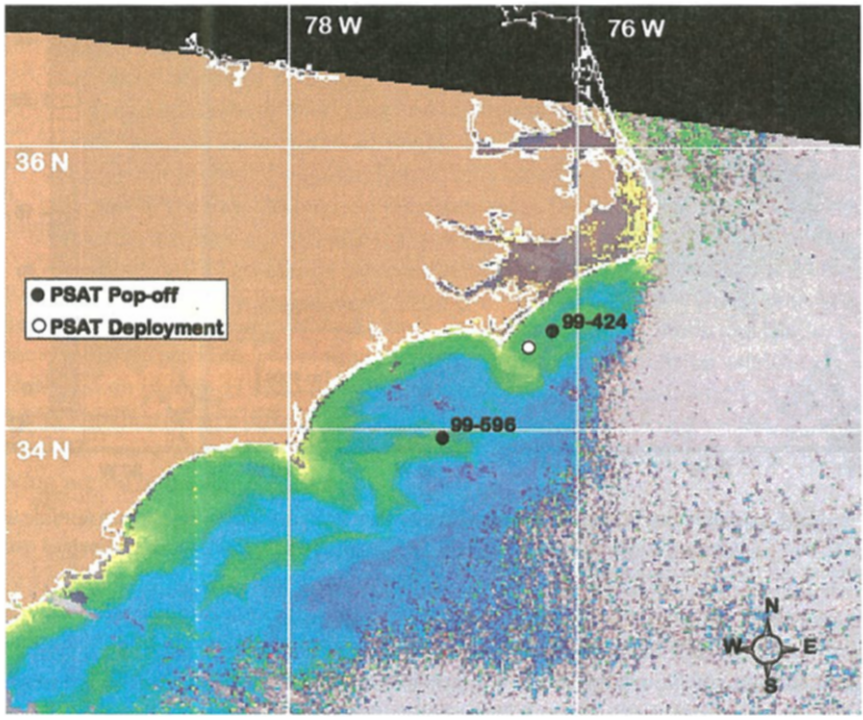


Fig. 14. Pop-up end points (black circles) on SeaWiFs data showing the productivity around the Capes in the winter season. The productive waters attract menhaden, and bluefin appear to congregate in this region to feed.

Gulf of Mexico at a time when breeding occurs. However, archival tag data suggest that the length of time individual fish spend in the Gulf of Mexico breeding ground is relatively short (as small as 2 weeks) and that fish that breed in the Gulf of Mexico can be back in New England, the Bahamas, or the mid-Atlantic in a very short period after visitation to the breeding ground. Clearly this is a fascinating and important area for future research. The plausible explanations for the data collected to date by pop-up and archival tags appear to be one of the following: (1) Eastern Atlantic spawners are on the west Atlantic side and move back to the east to spawn (which is consistent with both data sets showing western-tagged fish moving back to the east) (Block *et al.*, 2001a). (2) Spawning occurs outside the Gulf of Mexico; however, clarifying when and where is premature with single-point pop-up tags with limited archival capabilities. (3) Atlantic bluefin do not make annual spawning migrations. (4) The spawning period is extremely short lived (as suggested by implantable archival data) and fish can be half an ocean

away in a short duration after spawning. With more releases of archival pop-up tags planned over the next 2 years by both the Block and Lutcavage teams, and a continuation of archival tag returns also expected over this period, there is likely to be more data available to examine the latter two alternatives. Conclusive evidence for the second option, however, would require the capture of larval Atlantic bluefin in this area.

In southern bluefin tuna, large, adult fish are often caught in locations thousands of miles away from the spawning grounds during the species' extended summer season. These fish are not believed to be spawning, and it is unknown whether they make very quick migrations to the spawning ground, or alternatively do not spawn every year.

C. Summary

Although in many ways we are still in the early stages of the development of pop-up tag technology, it has quickly demonstrated that it can be a useful and powerful tool in our quest for information on tunas and other large pelagic fishes. Its most appealing and important feature is the capability of delivering data on movement and behavior completely independent of fisheries and fishers. If we can validate the accuracy of smart, on-board software currently being developed by the two major manufacturers to calculate positions on board fish and/or to choose data that when downloaded can allow users to calculate positions back in the laboratory, then pop-up tags have the potential to answer many of the most critical questions posed by Hunter *et al.* (1986) in their watershed review.

V. THE PROBLEM OF ATTACHMENT

The development of new electronic tagging technologies, many of which require the tag to remain on the fish for periods of months to many years, has presented researchers with the challenge of developing new methods of attaching tags in such a way that they do not affect the behavior, do not adversely affect survivorship, and do not fall off.

Over the years, acoustic tags have been attached successfully to tunas in many different ways—for example, harpooned into free-swimming fish (Carey and Lawson, 1973); strapped to the dorsal musculature (Holland *et al.*, 1990); with anchors implanted into the dorsal musculature (Block *et al.*, 1997; Brill *et al.*, 1999; Dagorn *et al.*, 2000); inside the stomach, either free or attached to special "hooks" to provide longer retention (Yuen, 1970; Davis *et al.*, in press); or intraperitoneally (Klimley and Holloway, 1999). However, because tracking studies generally last for only a few hours to days, the long-term retention of the tags and their effects on survivorship have rarely been examined. Klimley and Holloway

(1999) found acoustic tags placed into the peritoneal cavity of yellowfin tuna remained in place for 9 months, and presumably did not affect the survivorship.

Early experiments with archival tags compared the long-term retention of external and intraperitoneal placements (J. Gunn and T. Davis, CSIRO, unpublished data). In these experiments, 100 of each of the two types of tags were deployed on juvenile SBT in southern Australia. The return rate for the intraperitoneal tags was 8% (approximately the same return rate as conventional tagging studies conducted at the same time), with tags returned after periods of liberty of 3–24 months. No external tags were reported recaptured, and the conclusion drawn was that the external placement had caused mortality in the tagged fish.

Gunn *et al.* (1994) adopted the intraperitoneal placement throughout their SBT archival tagging program, which has had recapture rates of >15% from 514 releases. The recapture rates for archival tags are higher than those for conventional tagging releases conducted at the same time on fish of the same cohorts (CSIRO, unpublished data), suggesting that reporting may be higher, and/or shedding of internal tags may be lower. Similarly Block and colleagues have also used intraperitoneal placement for archival tagging Atlantic bluefin and have approximately a 16% recovery rate from 279 releases. Intraperitoneal placement has the advantages that tag shedding appears to be zero and, where the species has a visceral rete, it is possible to determine when a fish has eaten from the internal temperature sensor archival tag data (Gunn *et al.*, 2001).

Brill *et al.* (1997) also conducted experiments with intramuscular placement of archival tags. These were conducted with scaled-down dummy tags in an aquarium and proved long-term retention is possible, along with quick healing of the wound if the tag is directly inserted into the dorsal musculature, rather than making a deep incision.

Tags that are to be carried for a long period require insertion and acceptance of a foreign object into the fish (the applicator dart), and placement that avoids direct injury to the animal. The preferred placement for PAT tags on tunas is at the base of the second dorsal fin. Experiments on captive fish with early generations of the dummy PAT tags demonstrated that tags placed close to where the body narrows posterior to the second dorsal fin, had minimal contact with the body and did not disturb normal swimming patterns. Also, at the base of the second dorsal fin there are a series of bony processes which provided an ideal site to secure the anchor. The pop-up tags were initially designed to be placed in this position to avoid interaction with the body of the animal. Short stiff leaders constructed with extra-hard 1.8-mm-diameter monofilament have provided optimal results on Atlantic and Pacific bluefin tuna, blue marlin, and lamnid sharks. The leaders are crimped with stainless steel sleeves and are coated with shrink wrap to protect the fish from injury from the monofilament and sleeves as well as to increase the stiffness of the leader. The general concept is to have the tag lifted off

the surface of the fish by the short, stiff leader with the additional aid of the buoyant float. In the case of the Wildlife Computers-constructed PAT tags, floats used for Atlantic bluefin tuna are larger than the original floats designed for the single-point tags (Block *et al.*, 1998b). Large bluefin are capable of carrying the extra drag and the increased buoyancy pulls the instrument package off the body of the fish. This prevents as much as possible tag and fish interaction, which is most likely the leading cause of PAT tag failure to transmit. From controlled studies in the laboratory, the most severe interaction occurs at the point of attachment and at the maximum width of the float. Together these two areas can cause large subdermal injuries that can cause mortality.

In all attachments, the critical factor is to achieve a deep insertion (10–12 cm in a large fish; 7.5 cm in a small fish) of the applicator dart across the pterygiophores. Once inserted correctly, few darts of any type will pull out. Over-the-side applications are more difficult due to the challenge of exact placement of the tag into the desired position. Two types of anchor materials are often used: titanium darts and medical grade plastic darts. In studies on the Atlantic and Pacific bluefin tuna, conducted on both captive and wild caught bluefin, the flat-head titanium dart retained with high reliability (no premature release from over 60 deployments). Nylon darts in our experiments showed poor retention both in the lab and in the field for long durations; however, some studies have had relatively high success with these darts although it would be difficult to know if tags were on for long durations without a continuous temperature archive (Lutcavage *et al.*, 1999a).

VI. THE FUTURE OF ACOUSTIC, ARCHIVAL, AND POP-UP TAGGING

A. Technology

The exciting results recently achieved with the latest generations of pop-up archival satellite tags begs the question as to whether this will become the tagging technology of choice for tunas in the 21st century, making the other technologies redundant. Our feeling is that pop-up satellite archival tags are going to revolutionize what we know about tunas. However, all three electronic tagging techniques have applications that are useful and it is really up to the experimental questions and the species as to whether or not we can use a particular technology.

Acoustic technology remains the most appropriate tool for studying fine-scale movements and behavior. When combined with the array of oceanographic measurements possible on modern research vessels, acoustic data provide the user with an unparalleled opportunity to examine the links between fine-scale oceano-

graphic features and the vertical and horizontal movement of a single fish. Additionally, for physiological data with high data acquisition rates, the memory of the archival and PAT tags are not capable of storing the large data sets, so acoustic technologies remain the only solution (e.g., tailbeat and EMG). Although the cost of following individual fish has limited the number of acoustic data sets we have for tuna, their importance cannot be underestimated. We do not need to make large numbers of these fine-scale observations for them to be useful in interpreting what tuna are doing in their open ocean environment. As they have for bigeye and southern bluefin, acoustic data provide a valuable basis for interpretation of longer term, but less detailed, data sets collected by archival or pop-up archival satellite tags. Three foci on which more acoustic observations would be very useful are:

- Tuna in open ocean habitats, where directional movement and behavior are unlikely to be influenced by topographic features or FADs
- Tuna within schools to provide a better understanding of the dynamics of individuals within schools
- Feeding activity to identify how this differs from searching or traveling behavior

As the most recent version of the pop-up satellite archival tags can be downloaded if the fish is recaptured prior to pop-off, and thereby provide data similar to those collected by archival tags, the choice of whether to use archival or pop-up tags will depend heavily on the fish you are planning to tag and the objectives of the study:

- *What is the probability of recapturing the fish?* If the probability is low, regardless of other issues, pop-up tags provide the best option for obtaining data. Archival tags currently sell for around U.S. $1400–$1800, and pop-up tags for U.S. $3500–$4500. If one expects a 10% return rate for archival tags, each tag data set costs on the order of $14,000–$18,000. If one assumes a 100% success in pop-ups, the cost per data set is $3500–$4500.
- *What temporal scale is the hypothesis testing?* Currently, only archival tags are capable of collecting data for periods of much more than 1 year. Until upload rates to ARGOS (or similar new generation) receivers are improved, the trade-off between data logging life and the amount of data that can be transmitted suggests that for long-term experiments archival tags would be the best option. The long-term attachment of a pop-up tag is unproven and, particularly in tropical areas, marine fouling may make this difficult.

Additionally, if one wishes to collect data on feeding behavior, an internal temperature sensor is required and an archival tag is the preferred choice.

- *What resolution is required in the spatial data?* In terms of their ability to deliver accurate information using light-based geolocation, archival tags

currently outperform pop-up satellite archival tags. While both use light to estimate geolocation, the archival tag, with the ability to examine all the data stored in memory, allows the user more flexibility and power in estimating longitude and latitude. The current pop-up tags each have limitations primarily based on the challenges of delivering data sets back through ARGOS satellites. If a tag comes up in bad weather or hits a beach shortly after surfacing, little to no data will be returned. The PAT tag is capable of delivering geolocation for the duration of the mission; however, memory limitations as well as current software will limit this to at most a 1.2-year record.

- *What size tuna are you tagging?* Archival tags have been deployed on tunas as small as 50-cm FL (Japanese National Research Institute of Far Seas Fisheries, unpublished data), and although pop-up tags have been successfully used in a short deployment on an 18-kg albacore (B. Block, unpublished data), the current designs are best suited for much larger fish, particularly if long-term deployments are required. Lotek Wireless, Inc., of Canada is currently testing an archival tag small enough to deploy on 30-cm FL tunas, which will allow researchers to study behavior and movement of young-of-the-year tuna. If the objective of the study is to study juvenile fish, or to examine ontogenetic changes in behavior and movement, archival tags currently provide the best option. As manufacturers reduce the size of pop-up satellite tags substantially over the next few years, they will no doubt increase the utility of this form of electronic tagging on smaller individuals.

There are a number of important improvements that would make archival and pop-up tags more useful.

First, they need to be made more robust. The failure rates experienced by users of both technologies over the last few years are perhaps to be expected given the rapid speed of development and the many unknowns regarding tuna behavior (how deep they dive, what temperature extremes are they likely to experience, etc.). However, as the technology matures, it is essential that these failures are not repeated. It is in the interest of the manufacturer and researcher alike for this to happen as funding agencies tend to balk at researchers who repeatedly have to make apologies for failed equipment.

Second, manufacturers have to be willing to collaborate in studies validating the hardware and software they produce. As geolocation is a critical feature of both technologies, it is essential that researchers have access to data and software that allows them to independently validate the estimates of position being produced by tags. To accept positions produced by tags or by software used to analyze the data without adequate validation of the methods is poor science.

Third, while current Wildlife Computers tags provide evidence of premature release of the tag or fish mortality, all pop-up tags of the future must provide

researchers with an ability to tell whether a fish has died while carrying the tag, or if the tag has become detached and floated to the surface. The former would be invaluable in examining postrelease mortality, and even natural mortality over long time scales if pop-up tag life can be extended.

B. The Future Application of Electronic Tags and Integration of Data into Spatial Dynamics Models

Over the last decade the application of acoustic, archival, and pop-up satellite tag technology has contributed significantly to our understanding of the movement, behavior, biology, and physiology of a number of tunas species. For southern bluefin and Atlantic bluefin in particular, electronic tags have provided some quantum leaps in our understanding of the timing, directionality, and seasonality of movement; the residence times in different parts of their range; and the links between these and environmental factors. We have been able to determine how often these fish eat, and perhaps in the future we will also be able to determine the amount of food eaten each day (Gunn *et al.*, 2001). These parameters remain largely unknown for yellowfin, bigeye, albacore, and Pacific bluefin, and as such represent critical uncertainties in the assessments of these species (Hunter *et al.*, 1986). We still require resolution of the stock structure of bluefin in the Atlantic, and bigeye and yellowfin in the Pacific and Indian oceans. To correctly standardize the catch per unit of effort indexes of abundance that are the central plank of most stock assessments, we urgently require a better understanding of the horizontal and vertical distributions of all tuna species, and how these are affected by oceanographic variation.

Encouragingly, the successful applications of archival tags, pop-up archival tags, and acoustic listening stations over the last decade have demonstrated that we now have the tools to reduce uncertainties. Archival and pop-up tagging of Pacific bluefin and bigeye has begun, and is already showing promising results (T. Itoh *et al.*, unpublished data; Marcinek *et al.*, 2001). Similarly, pop-up tagging has begun on southern bluefin, Pacific bluefin, yellowfin, and albacore. There is every reason to expect that these studies will provide similar advances to those we have seen for the bluefin species.

Electronic tagging programs, from tracking individual fish to attaching pop-up tags to hundreds of large adult bluefin tuna, are relatively costly. Yet the advances made in the last few years suggest that returns on investment in these studies are substantial. It is important to recognize that electronic tags alone will not provide all of the answers to our questions on tuna movement and habitat preferences. There is also a demonstrable need to conduct well-designed, large-scale conventional tagging programs that will provide the large sample sizes of coarse-scale data on movement along with estimates of exploitation rates, mixing rates, and growth. Combining genetic data with electronic tagging data provides

increasing opportunities to compare contemporary movements with historical patterns of phylogeography.

In the near future, it seems likely that the integration of movement and behavioral data from conventional and electronic tagging studies with remotely sensed and observational oceanographic data on ocean temperature, color, and height will provide the basis for meaningful models of the movement dynamics of populations or stocks. To date no one has attempted this multidisciplinary integration. However, Sibert and Fournier (2001) have examined the potential for using the concepts of a biased random walk and diffusion–advection equations as a basis for integration of conventional and electronic tagging data, with promising results. Advection–diffusion models have also been successfully used with oceanographic data in the analysis and interpretation of the large-scale movement and distribution of tunas (Lehodey *et al.*, 1997, 1998; Maury and Gascuel, 1999).

The imperative for addressing the uncertainties in tuna movement dynamics, stock structure, and the influence of the environment on recruitment and production has never been greater, particularly in heavily or overexploited stocks. Given due attention, allocation of adequate resources for well-defined research projects, and a multidisciplinary approach, the advances in tagging technology and modeling techniques over the last decade mean we are better placed than ever to address these critical issues.

ACKNOWLEDGMENTS

The preparation of the manuscript benefited from the contributions of the Tag-A-Giant scientific team. We thank, Andreas Walli, Susanna Blackwell, Heidi Dewar, Tom Williams, Andre Boustany, Eric Prince, and Charles Farwell. Many others made the research possible. The Atlantic bluefin tuna research described herein was primarily supported by the NMFS, NSF, the Packard, Pew, MacArthur and Monterey Bay Aquarium Foundations. The southern bluefin tuna research has involved contributions from a large team of CSIRO researchers, notably Jason Hartog, Simon Wotherspoon, Andrew Betlehem, Tim Davis, Naomi Clear, and Tom Polacheck. The archival tag research was supported by the Australian Fisheries Management Authority and the Japan Marine Fishery Resource Research Centre, and industry associations in Australia and Japan.

REFERENCES

Anonymous (1996). IUCN red list of threatened animals.

Anonymous (1998). Report of the fourth meeting of the scientific committee, Tokyo, Japan.

Block, B. A., Keen, J. E., Castillo, B., Dewar, H., Freund, E. V., Marcinek, D. J., Brill, R. W., and Farwell, C. (1997). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Mar. Biol.* **130,** 119–132.

Block, B. A., Dewar, H., Williams, T., Prince, E. D., Farwell, C., and Fudge, D. (1998a). Archival tagging of Atlantic bluefin tuna (*Thunnus thynnus thynnus*). *Mar. Tech. Soc. J.* **32,** 37–46.

Block, B. A., Dewar, H., Farwell, C., and Prince, E. D. (1998b). A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proc. Natl. Acad. Sci. U.S.A.* **95,** 9384–9389.

Block, B. A., Dewar, H., Blackwell, S. B., Williams, T., Prince, E. D., Farwell, C., Boustany, A., Teo, S., Seitz, A., Walli, A., and Fudge, D. (2001a). Migratory movements, depth preferences and thermal biology of Atlantic bluefin tuna. *Science* **293,** 1310–1314.

Block, B. A., Dewar, H., Blackwell, S., Williams, T., Prince, E. D., Farwell, C., Boustany, A. M., Dau, D. J., and Seitz, A. (2001b). Archival and pop-up tagging of Atlantic bluefin tuna. *Reviews in* "Methods and Technologies in Fish Biology and Fisheries" (Sibert, J., and Nielsen, J., Eds.), Vol. 1. Kluwer Academic, Dordrecht, The Netherlands. In press.

Boggs, C. H., Musyl, M. K., Curran, D. S., and Brill, R. W. (1999). Geolocation by crepuscular diving behaviour and lunar influences on depth distribution in a bigeye tuna (*Thunnus obesus*) carrying an archival tag. *In* "Proceedings of 50th Annual Tuna Conference, May, 1999, Lake Arrowhead," pp. 24–27. NMFS, Honolulu.

Boustany, A., Marcinek, D., Dewar, H., Keene, J., Kade, T., and Block, B. A. (2001). Behaviour and environmental preferences of bluefin tuna (*Thunnus thynnus*) off the coast of North Carolina inferred from acoustic, archival and pop-up satellite tags. *Reviews in* "Methods and Technologies in Fish Biology and Fisheries" (Sibert, J., and Nielsen, J., Eds.), Vol. 1. Kluwer Academic, Dordrecht, The Netherlands. In press.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfish, and dolphinfish. *Comp. Biochem. Physiol.* **113,** 5–15.

Brill, R. W., Cousins, K., and Klieber, P. (1997). Test of the feasibility and effects of long-term intramuscular implantation of archival tags in pelagic fishes using scale model tags and captive juvenile yellowfin tuna (*Thunnus albacares*). NMFS Administrative Rep. H-97-11.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: Implications for the physiological ecology of pelagic fishes. *Mar. Biol.* **133,** 395–408.

Bushnell, P. G., and Jones, D. R. (1994). Cardiovascular and respiratory physiology of tuna: Adaptations for support of exceptionally high metabolic rates. *Environ. Biol. Fish.* **40,** 303–318.

Carey, F. G., and Lawson, K. D. (1973). Temperature regulation in free-swimming bluefin tuna. *Comp. Biochem. Physiol.* **44,** 275–292.

Carey, F. G., and Olson, R. J. (1982). Sonic tracking experiments with tunas. *Collect. Vol. Sci. Pap. ICCAT* **17,** 458–466.

Carey, F. G., and Robison, B. H. (1981). Daily patterns in the activities of swordfish, *Xiphias gladius,* observed by acoustic telemetry. *Fish. Bull.* **79,** 277–292.

Carey, F. G., and Scharold, J. V. (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* **106,** 329–342.

Carey, F. G., Teal, J. M., Kanwisher, J. W., Lawson, K. D., and Beckett, J. S. (1971). Warm-bodied fish. *Am. Zool.* **11,** 137–145.

Carey, F. G., Kanwisher, J. W., and Stevens, E. D. (1984). Bluefin tuna warm their viscera during digestion. *J. Exp. Biol.* **109,** 1–20.

Caton, A. E. (1991). Review of aspects of southern bluefin tuna biology, population and fisheries. *In* "World Meeting on Stock Assessment of Bluefin Tunas: Strengths and Weaknesses" (Deriso, R. B., and Bayliff, W. H., Eds.), IATTC Special Report no. 7, pp. 181–350. IATTC, La Jolla, CA.

Cayré, P. M. (1991). Behaviour of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish aggregating devices (FADs) in the Comoros Islands as determined by ultrasonic tagging. *Aquat. Living Resources* **4,** 1–12.

Cayré, P. M., and Marsac, F. (1993). Modelling the yellowfin tuna (*Thunnus albacares*) vertical distribution using sonic tagging results and local environmental parameters. *Aquat. Living Resources* **6,** 1–14.

Chaprales, W., Lutcavage, M. E., Brill, R. W., Chase, B., and Skomal, G. B. (1998). Harpoon method for attaching ultrasonic and popup satellite tags to giant bluefin tuna and large pelagic fishes. *Mar. Tech. Soc. J.* **32,** 104–105.

Dagorn, L., Bach, P., and Josse, E. (2000). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Mar. Biol.* **136,** 361–371.

Davis, T. L. O., and Stanley, C. A. (in press). Vertical and horizontal movements of southern bluefin tuna, *Thunnus maccoyii*, in the Great Australian Bight observed with ultrasonic telemetry. *Fish. Bull.*

Delong, R. L., Stewart, B. S., and R. D. Hill (1992). Documenting migrations of northern elephant seals using day length. *Mar. Mamm. Sci.* **8,** 155–159.

Dewar, H., Deffenbaugh, M., and Thurmond, G. (1999). Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. *J. Exp. Biol.* **202,** 2693–2699.

Dickson, K. A. (1995). Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environ. Biol. Fish.* **42,** 65–97.

Dizon, A. E., Brill, R. W., and Yuen, H. S. H. (1978). Correlations between environment, physiology, and activity and the effects on thermoregulation in skipjack tuna. *In* "The Physiological Ecology of Tunas," pp. 233–259. Academic Press, New York.

FAO (1998). "Atlas of Tuna and Billfish Catches." FAO. Rome.

Franks, P. J. S. (1992). Phytoplankton blooms at fronts: Patterns, scales and physical forcing mechanisms. *Rev. Aquat. Sci.* **6**(2), 121–137.

Gunn, J. S., Polacheck, T., Davis, T. L. O., Sherlock, M., and Betlehem, A. (1994). The development and use of archival tags for studying the migration, behaviour and physiology of southern bluefin tuna, with an assessment of the potential for transfer of the technology to groundfish research. Proc. I.C.E.S. Mini-Symposium on Fish Migration. Mimeo. 23p.

Gunn, J. S., Polacheck, T. W., and Klaer, N. (1995). Describing the school integrity of SBT in the Great Australian Bight using radio telemetry 1994/95 progress report. CSIRO Marine Research Report, Recruitment Monitoring Workshop. RMWS/95/7. CSIRO, Australia.

Gunn, J., Hartog, J., and Rough, K. (2001). The relationship between ration and visceral warming in southern bluefin tuna (*Thunnus maccoyii*): Can we predict how much a tuna has eaten from archival tag data? *Reviews in* "Methods and Technologies in Fish Biology and Fisheries" (Sibert, J., and Nielsen, J., Eds.), Vol. 1. Kluwer Academic, Dordrecht, The Netherlands.

Hampton, J. W., and Gunn, J. S. (1998). Exploitation and movements of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) tagged in the north-western Coral Sea. *Mar. Freshwater Res.* **49,** 475–489.

Hilborn, R., and Sibert, J. (1988). Is international management of tuna necessary? *Mar. Policy* **12,** 31–39.

Hill, R. (1994). "Theory of Geolocation by Light Levels," pp. 227–236. Univ. of California Press, Berkeley, CA.

Hill, R. D., and Braun, M. J. (2001). Geolocation by light-level. The next step: Latitude. *Reviews in* "Methods and Technologies in Fish Biology and Fisheries" (Sibert, J., and Nielsen, J., Eds.), Vol. 1. Kluwer Academic, Dordrecht, The Netherlands.

Hilton-Taylor, C. (2000). 2000 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland and Cambridge, UK. xviii + 61pp.

Holland, K. N., and Sibert, J. R. (1994). Physiological thermoregulation in bigeye tuna, *Thunnus obesus*. *Environ. Biol. Fish.* **4,** 319–327.

Holland, K. N., Brill, R. W., and Chang, R. K. C. (1990). Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish. Bull.* **88,** 493–507.

Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R., and Fournier, D. A. (1992). Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **35,** 410–411.

Hunter, J. R., Argue, A. W., Bayliff, W. H., Dizon, A. E., Fonteneau, A., Goodman, A., and Seckel, G. R. (1986). The dynamics of tuna movements: An evaluation of the past and future research. FAO Fish. Tech. Pap. no. 277. FAO, Rome.

Hynd, J. S. (1969). New evidence on southern bluefin stocks and migrations. *Aust. Fish.* **28,** 2–7.

Josse, E., Bach, P., and Dagorn, L. (1998). Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* **371, 372**(37), 61–69.

Kitagawa, T., Nakata, H., Kimura, S., Itho, T., Tsuji, S., and Nitta, A. (2000). Effect of ambient temperature on the vertical distribution and movement of Pacific bluefin tuna revealed with archival tags. *Marine Ecology Progress Series.* **206,** 251–260.

Klimley, A. P., and Holloway, C. F. (1999). School fidelity and homing synchronicity of yellowfin tuna, *Thunnus albacares. Mar. Biol.* **133,** 307–317.

Klimley, A. P., Prince, E. D., Brill, R. W., and Holland, K. (1994). Archival tags 1994: Present and future. NOAA Technical Memorandum NMFS-SEFSC-3570, 42p.

Lacroix, G. L., and Knox, D. (2000). Finding the smoking gun: Where do Atlantic salmon from the inner bay of Fundy go at sea [abstract]? *In* "Symposium on Tagging and Tracking Marine Fish with Electronic Devices Abstracts," February 7–11, 2000, Honolulu. Available on-line: http://www.soest.hawaii.edu/PFRP/pdf/symp abstracts.pdf.

Laurs, R. M., Yuen, H. S. H., and Johnson, J. H. (1977). Small-scale movements of albacore, *Thunnus alalunga,* in relation to ocean features indicated by ultrasonic tracking and oceanographic sampling. *Fish. Bull.* **75,** 347–355.

LeBoeuf, B. J., Morris, P. A., Blackwell, S. B., Crocker, D. E., and Costa, D. P. (1996). Diving behavior of juvenile northern elephant seals. *Can. J. Zool.* **74,** 1632–1644.

Lehody, P., Bertignac, M., Hampton, J., Lewis, A., and Picaut, J. (1997). El Nino southern oscillation and tuna in the western Pacific. *Nature (London)* **389,** 715–718.

Lehodey, P., Andre, J. M., Bertignac, M., Hampton, J., Stoens, A., Menkes, C., Memery, L., and Grima, N. (1998). Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model. *Fish. Oceanogr.* **7,** 317–325.

Leigh, G. M., and Hearn, W. S. (2000). Changes in growth of juvenile southern bluefin tuna (*Thunnus maccoyii*): An analysis of length-frequency data from the Australian fishery. *Mar. Freshwater Res.* **51,** 143–154.

Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., and Howey, P. W. (1999a). Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: Do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Can. J. Fish. Aquat. Sci.* **56,** 173–177.

Lutcavage, M. E., Brill, R. W., Porter, Stomal, G., Chase, B., Howey, P. W., and Murray, E., Jr. (2000d). (Rev.) Preliminary results from the joint US-Canadian pop-up satellite tagging of giant bluefin tuna in the Gulf of Maine and Canadian Atlantic region, 1998–1999. ICCAT Coll. Vol. Sci. **50,** 347–354.

Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., Goldstein, J. L., and Tutein, J. (2000a). Tracking adult north Atlantic bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry. *Mar. Biol.* **137,** 347–358.

Lutcavage, M. E., Brill, R. W., Porter, J., Howey, P. W., Skomal, G., and Chase, B. (2000b). They do get around: An update on North Atlantic bluefin tuna tagging results in the NW Atlantic. *Reviews in* "Methods and Technologies in Fish Biology and Fisheries" (Sibert, J., and Nielsen, J., Eds.), Vol. 1. Kluwer Academic, Dordrecht, The Netherlands. In press.

Lutcavage, M. E., Brill, R. W., Porter, J., Howey, P., Murray, E., Mendillo, A., Chaparales, W., Genovese, M., and Rollins, T. (2000c). Summary of pop-up tagging of giant bluefin tuna in the joint US-Canadian program, Gulf of Maine and Canadian Atlantic. ICCAT SCRS/00/95, 9p, in press.

Marcinek, D. J., Blackwell, S. B., Dewar, H., Freund, E. V., Farwell, C., Dau, D. J., Seitz, A., and Block, B. A. (2001). Depth and muscle temperature of pacific bluefin tuna examined with acoustic and pop-up satellite tags. *Mar. Biol.*, **138,** 869–885.

Martin, A. R., Smith, T. G., and Cox, O. P. (1993). Studying the behaviour and movements of high Arctic belugas with satellite telemetry. *Symp. Zool. Soc. London* **66,** 195–210.

Maury, O., and Gascuel, D. (1999). SHADYS, a GIS based numerical model of fisheries. Example application: The study of a marine protected area. *Aquat. Living Resources* **12,** 77–88.

McConnell, B., Chambers, C., and Fedak, M. A. (1992). Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Sci.* **4**(4), 393–398.

Metcalfe, J. D., and Arnold, G. P. (1997). Tracking fish with electronic tags. *Nature* **38,** 665–666.

Murphy, G. I., and Majkowski, J. (1981). State of the southern bluefin tuna population: Fully exploited. *Aust. Fish.*, 20–29.

Musyl, M. K., Brill, R. W., Curran, D. S., Gunn, J. S., Hartog, J. R., Hill, R. D., Welch, D. W., Eveson, J. P., Boggs, C. H., and Brainard, R. E. (2001). Ability of archival tags, submerged at varying depths on a stationary mooring line in the Pacific Ocean, to provide estimates of geographical position based on light intensity. Reviews in "Methods and Technologies in Fish Biology and Fisheries" (J. Siber and J. Nielsen, Eds.), vol. 1. Kluwer Academic, Dordrecht, The Netherlands. In press.

Nakamura, Y. (1993). Vertical and horizontal movements of mature females of *ommastrephes bartramii* observed by ultrasonic telemetry. *Rec. Adv. Fish. Biol.*, 331–336.

National Research Council (1994). "An Assessment of Atlantic Bluefin Tuna." National Academy Press, Washington, DC.

Papi, F., Liew, H. C., Luschi, P., and E. H. Chan. (1995). Long-range migratory travel of a green sea turtle tracked by satellite: Evidence for navigational ability in the open sea. *Mar. Biol.* **122,** 171–175.

Polacheck, T. W., Hearn, W. S., Millar, C., and Stanley, C. A. (1998) Updated estimates of mortality rates for juvenile SBT from multi-year tagging cohorts. CCSBT/SC/98/20, Hobart, Australia.

Priede, I. G. (1984). A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing. *Fish. Res.* **2,** 201–216.

Renaud, M. L., and Carpenter, J. A. (1994). Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bull. Mar. Sci.* **55,** 1–15.

Sharp, G. D., and Dizon, A. E. (1978). "The Physiological Ecology of Tunas." Academic Press. London. 85p.

Sibert, J., and Fournier, D. A. (2001). Possible models for combining tracking data with conventional tagging data. *Reviews in* "Methods and Technologies in Fish Biology and Fisheries" (Sibert, J., and Nielsen, J., Eds.), Vol. 1. Kluwer Academic, Dordrecht, The Netherlands.

Smith, P., and Goodman, D. (1986). Determining fish movements from an "archival" tag: Precision of geographical positions made from a time series of swimming temperature and depth. *NOAA Technical Memorandum,* NMFS–SWFC–60, 13p.

Stevens, E. D., and McLeese, J. M. (1984). Why bluefin tuna have warm tummies: Temperature effects on trypsin and chymotrypsin. *Am. J. Physiol.* **246,** R487–R494.

Stevens, E. D., Kanwisher, J. W., and Carey, F. G. (2000). Muscle temperature in free-swimming giant Atlantic bluefin tuna (*Thunnus thynnus* L.). *J. Thermal Biol.* **25,** 419–423.

Stevens, J. D., Norman, B. M., Gunn, J. S., and Davis, T. L. O. (1998). Movement and behavioural pattern of whale sharks at Ningaloo Reef: The implications for tourism. National Ecotourism Grant Final Report. CSIRO, Australia.

Tsuji, S., Itoh, T., Nitta, A., and Kume, S. (1999) The trans-Pacific migration of a young bluefin tuna.

Thunnus thynnus, recorded by an archival tag. Working Paper ISC2/99/15, Interim Scientific Committee for Tuna and Tuna-Like Species in the North Pacific Ocean, January 15–23, 1999, Honolulu.

Turner, S. C., and Restrepo, V. R. (1994). A review of the growth of Atlantic bluefin tuna, *Thunnus thynnus,* estimated from marked and recaptured fish. *ICCAT Coll. Vol. Sci. Pap.* **42**(1), 170–172.

VEMCO (2000). Communicating History Acoustic Transponders. On-line at: http://www.vemco.com./chatdata.htm.

Weihs, D. (1973). Mechanically efficient swimming techniques for fish with negative buoyancy. *J. Mar. Res.* **31,** 194–209.

Welch, D. W., and Eveson, J. P. (1999). An assessment of light-based geoposition estimates from archival tags. *Can. J. Fish. Aquat. Sci.* **56,** 1317–1327.

Wilson, R. P., Ducamp, J. J., Rees, W. G., Culik, B. M., and Niekamp, K. (1992). Estimation of location: global coverage using light intensity. In: I. G. Priede and S. M. Swift (eds.) *Wildlife Telemetry: Remote Monitoring and Tracking of Animals.* Ellis Horwood. London. pp. 131–135.

Yonimori, T. (1982). Study of tuna behavior, particularly their swimming depths, by the use of sonic tags. *News1. Enyo (Far Seas) Fish. Res. Lab. Shimizu* **44,** 1–5.

Yuen, H. S. H. (1970). Behavior of skipjack tuna, *Katsuwonus pelamis,* as determined by tracking with ultrasonic devices. *J. Fish. Res. Bd. Can.* **27,** 2071–2079.

6

REPRODUCTIVE BIOLOGY OF TUNAS

KURT M. SCHAEFER

I. Introduction
II. Gonadal Development
  A. Ovaries and Oogenesis
  B. Testes and Spermatogenesis
III. Maturation
IV. Spatiotemporal Spawning Patterns
V. Spawning Behavior
VI. Spawning Frequency
VII. Fecundity
VIII. Sex Ratios
IX. Reproductive Energetics
X. Concluding Remarks

I. INTRODUCTION

Comprehensive reviews on the anatomy and physiology of reproduction in teleosts can be found in previous volumes of this series, including the classic by Hoar (1969), and the two-part volume on fish reproduction (Hoar *et al.*, 1983). This chapter is intended to provide an overview and perspective of our present understanding of some aspects of the reproductive biology of tunas which are fundamental to fisheries science. The taxonomic nomenclature used throughout this chapter follows that of Collette *et al.* (this volume). *Allothunnus fallai,* although considered the most primitive member of the tribe Thunnini, will be excluded from this chapter and from references to the reproductive characteristics of the tunas.

Tunas are predominantly dioecious, and there appears to be no sexual dimorphism in external morphological characters. Tunas are oviparous, have asynchronous oocyte development, and are considered to be multiple or batch spawners, shedding their gametes directly into the sea, where egg fertilization occurs (Wallace and Selman, 1981; de Vlaming, 1983). Spawning patterns within the tribe

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

are diverse and complex. There are three types of spawning patterns exhibited by the tunas: (1) confluent throughout tropical and subtropical regions (*Katsuwonus pelamis, Thunnus albacares,* and *Thunnus obesus*), (2) regionally confined and protracted (*Auxis* spp., *Euthynnus* spp., *Thunnus atlanticus,* and *Thunnus tonggol*), and (3) migratory and spatiotemporally confined (*Thunnus alalunga, Thunnus maccoyii, Thunnus orientalis,* and *Thunnus thynnus*). Common to all these species within the tribe is the relationship between spawning activity and sea-surface temperatures in excess of about 24°C. Because of their mode of reproduction, repetitive broadcast spawners, tunas must have very high lifetime fecundities to be successful. This is achieved through various degrees of protracted spawning, along with a combination of high spawning frequencies and relative batch fecundities. For nearly all species investigated, males attain greater sizes than females, which is the opposite of what is observed for most marine fish.

The reproductive characteristics of a stock along with those of growth and mortality are among the most important factors in determining the regenerative ability of a population (Quinn and Deriso, 1999). Understanding the reproductive biology of tunas and quantifying size-specific parameters provides the means, when incorporated into length- and/or age-structured models, for predicting the effects of fishing on the reproductive potential of a stock. Although there has been some progress in the past 20 years on elucidating some important life history processes in tunas, for the majority of the species our knowledge regarding reproductive patterns and parameters is meager. Accurate interpretation and classification, in recent years, of reproductive condition and estimates of spawning potential for tunas have largely been the result of utilizing histological techniques and appropriate classification criteria (Grier, 1981; Wallace and Selman, 1981; Hunter *et al.,* 1985; Hunter and Macewicz, 1985a; Schaefer, 1998). Most of the investigations conducted on reproductive biology of tunas in the past 50 years have, unfortunately, utilized inaccurate methodologies for assessing reproductive parameters and the spawning potential of stocks.

II. GONADAL DEVELOPMENT

Tunas, like all other scombrids, are primarily heterosexual. However, a few instances of hermaphroditism have been reported for *Katsuwonus pelamis,* in which both testicular and ovarian tissues were observed in the gonads of the same fish (Raju, 1960; Uchida, 1961).

The paired, elongate, gonads are suspended by mesenteries inside the abdominal cavity, and extend almost the entire length along the dorsal wall of the coelom. The gonads develop from relatively small, inconspicuous structures into large masses. The gonads are fused caudally where the cavities join to form a short duct that terminates at the external opening in the anal region (Bara, 1960; Hoar,

1969; Harder, 1975). The paired gonads are nearly symmetrical, although there are some differences in sizes, with the right ovary and testis being larger than the left within some species (e.g., *Thunnus alalunga;* Ratty *et al.,* 1990).

Most studies of gonadal development in tunas, intended to describe maturation and spawning distributions, have been based on ovaries and have utilized various formulations of the gonosomatic index for classification of condition (Yuen, 1955; Schaefer and Orange, 1956; Orange, 1961; Kikawa, 1962, 1966). If a gonosomatic index is calibrated, for instance, through use of histology, it can potentially be used for determination of spatiotemporal spawning distributions, but it is not accurate for classification of maturity or reproductive activity (de Vlaming *et al.,* 1982). Other methodologies which are appropriate for interpretation and classification of the gonadal development and reproductive activity of individual fish (West, 1990) include the use of oocyte diameters from the most advanced batch of oocytes present in an ovary (Buñag, 1956; Yoshida, 1966; Schaefer, 1987; Ramon and Bailey, 1996) and histology of ovarian and testicular tissues (Cayré and Farrugio, 1986; Goldberg and Au, 1986; Hunter *et al.,* 1986; McPherson, 1991; Nikaido *et al.,* 1991; Batalyants, 1992; Timohina and Romanov, 1996; Farley and Davis, 1998; Schaefer, 1998). Histological examinations of microscopic slides of ovarian and testicular tissues provide the greatest precision for classification of reproductive state of tunas (Schaefer, 1998).

A. Ovaries and Oogenesis

Undeveloped tuna ovaries are round in cross-section, and if excised will roll smoothly between the fingers due to the presence of a lumen. Developed ovaries are fusiform (spindle-shaped), yellowish in color because of the presence of yolk, and circular in cross-section.

Tuna ovaries are considered asynchronous because oocytes in various developmental stages are present in the ovary simultaneously (Wallace and Selman, 1981; de Vlaming, 1983). This is definitive of fish which spawn numerous times during a single protracted spawning season. The histological classification of tuna ovaries for assessments of reproductive biology should be based on the system of Hunter and Macewicz (1985a), as modified by Schaefer (1996, 1998). Detailed reviews on this topic for teleosts in general, which are relevant to tunas, are given by Harder (1975), Wallace and Selman (1981), Nagahama (1983), de Vlaming (1983), and Tyler and Sumpter (1996). A brief description of oogenesis and histology of tuna ovaries is provided here.

Oogenesis begins with the proliferation of oogonia by mitotic divisions within the oogonial nest, which become primary oocytes (Figure 1A). The oocytes considered within this developmental category are unyolked. The initial primary oocyte has a relatively narrow, densely staining basophilic cytoplasm and a large clear nucleus. The cytoplasm increases in size with oocyte growth, and shows

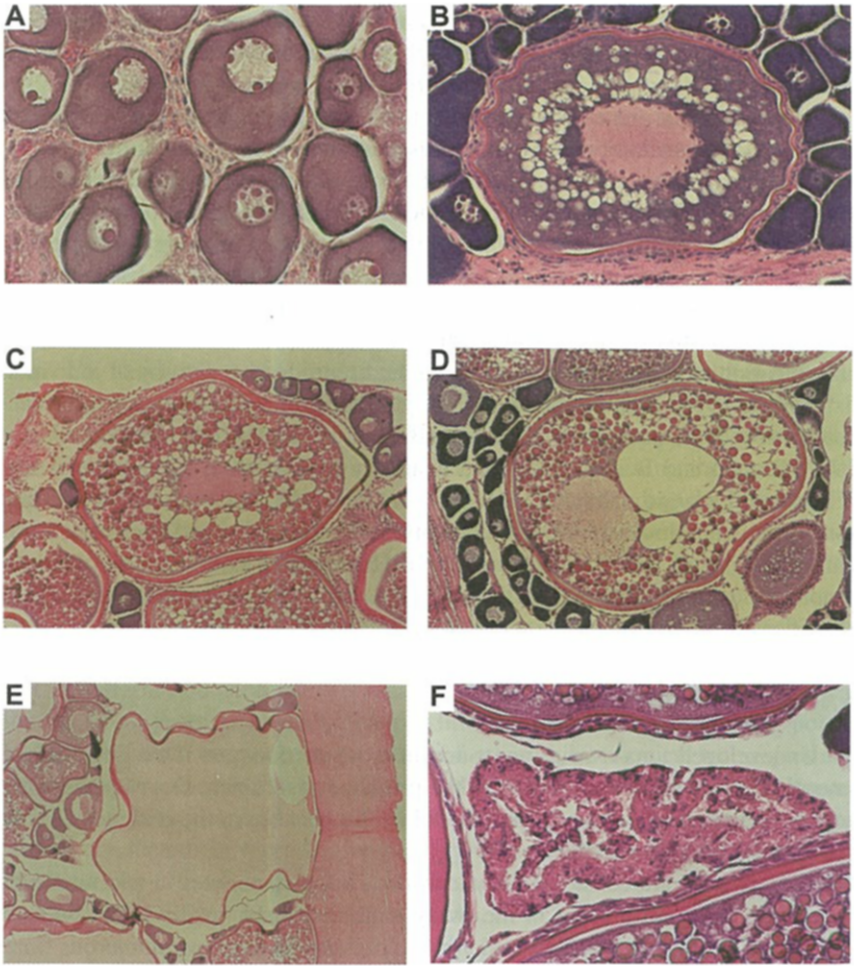


Fig. 1. Developmental stages and oogenic cells observed in *Thunnus albacares* ovaries. (A) Unyolked oocyte (×160). (B) Early yolked oocyte (×100). (C) Advanced yolked oocyte (×40). (D) Migratory-nucleus-stage oocyte (×40). (E) Hydrated oocyte (×25). (F) Postovulatory follicle less than 12 h after ovulation (×160).

differentiation in staining, with inherent lighter oval areas, possible precursors of yolk vesicles. In the nucleus, multiple nucleoli are distributed around the periphery. This is considered the early perinucleus stage, characterized by the enlargement of the oocyte, along with an increased number of peripheral nucleoli and the appearance of lampbrush chromosomes in the nucleus. At this point the oocyte is surrounded by an inner layer of granulosa cells and a thin flat layer of thecal cells.

The oocytes next enter a prolonged secondary growth phase in which the enlargement of the oocyte is caused by formation and accumulation of yolk (vitellogenesis), which depends on pituitary gonadotropin (Ng and Idler, 1983). The yolk vesicles are the first structures to appear in the oocyte cytoplasm, distributed at first in a peripheral position in the ooplasm and then subsequently spreading toward the perinuclear zone. Yolk granules begin to appear and replace the majority of the yolk vesicles (Figures 1B and 1C). There are three distinct types of structures within the cytoplasm during vitellogenesis: yolk vesicles, yolk granules, and lipoid vesicles.

In early yolked oocytes (Figure 1B) numerous euvitelline nucleoli appear homogeneously around the nuclear membrane, with no true nucleolus present. There is an increase in the lipoid vesicles and yolk granules, and the zona radiata can be distinguished in the follicular epithelium as development proceeds (Figure 1C). In the more advanced stages of vitellogenesis, where the oocytes are advanced yolked, sharply staining yolk granules occur throughout the ooplasm, along with larger lipoid vesicles.

Vitellogenesis ceases once these oocytes are fully developed, and eventually undergo maturation and ovulation after an appropriate hormonal stimulation (Masui and Clarke, 1979; Wallace and Selman, 1981). The first observed histological change associated with the final maturation of the oocyte is the migration of the nucleus (germinal vesicle) toward the animal pole where the micropyle is located. During this process coalescence of the lipoid vesicles takes place within the cytoplasm (Figure 1D). After the germinal vesicle reaches the animal pole, the membrane of the germinal vesicle disintegrates and its contents become confluent within the cytoplasm. Early hydration of the oocyte begins at this time with the initiation of the fusion of the yolk granules to form yolk plates. The final maturation of the oocyte occurs during the later stage of hydration when the yolk plates completely fuse and form a homogeneous yolk mass (Figure 1E), during which time the oocyte significantly increases in size due to hydration or the uptake of fluid by the oocyte (Wallace and Selman, 1981). This fusion of yolk granules and hydration gives the oocyte a translucent (hyaline) appearance in fresh or preserved whole oocytes (Schaefer, 1998).

Upon completion of maturation the hydrated oocytes are expelled through a rupture in their surrounding follicles into the ovarian lumen. The postovulatory follicle remains as a distinct involuted structure within the ovigerous lamellae, and consists of an inner epithelioid layer of granulosa cells and an outer connective tissue layer of thecal cells. The postovulatory follicle is transitory (Bara, 1960; Yamamoto and Yoshioka, 1964; Hunter and Goldberg, 1980; Goldberg *et al.*, 1984), and in *Katsuwonus pelamis* and *Thunnus albacares*, by 24 h after ovulation, postovulatory follicles cannot be accurately identified (Hunter *et al.*, 1986; Schaefer, 1996). At the time of spawning the new postovulatory follicles have an involuted shape, with numerous folds and a relatively open follicular cavity. The

granulosa epithelioid cell layer lining the lumen shows regularly aligned cuboidal to columnar cells with prominent basal nuclei. The theca is now about the same thickness, and in only loose contact with the granulosa. The degenerating postovulatory follicle is smaller, has fewer involutions, and has a follicular cavity (Figure 1F). A thick thecal layer now surrounds the relatively thin granulosa cell layer, and the two layers are in much closer contact. Degenerating cells of the thecal and granulosa layers have sharply staining pycnotic nuclei, and an irregular alignment of the cell walls and nuclei (Hunter *et al.*, 1986; Schaefer, 1987, 1996, 1998).

B. Testes and Spermatogenesis

Undeveloped tuna testes are relatively flat in cross-section, and if excised do not roll smoothly between the fingers because they are solid, apart from a longitudinal sperm duct (vas deferens) medially, which can be seen with the unaided eye if the testis is illuminated. Developed testes are somewhat flattened and white in color because of the presence of milt. Tuna testes are considered as an unrestricted spermatogonial testis type, because the distribution of spermatogonia may occur along the entire length of the tubule (Grier, 1981). The histological classification of tuna testes development should be based on the degree of spermatogenesis as described by Grier (1981) and the classification system of Schaefer (1996, 1998) for assessments of reproductive biology. Detailed reviews on this topic (for teleosts in general) which are relevant to tunas are given by Grier (1981, 1993) and Nagahama (1983). A brief description of spermatogenesis and histology of tuna testes is provided here.

Each lobe of tuna testes is composed of interstitial and germinal (lobular) compartments. The germinal compartments are situated within lobules that radiate perpendicularly from the vas deferens or efferent duct and terminate at the periphery of the lobe, the tunica albuginea. The lobules are separated by interstitium composed of fibrous connective tissue. The lobular compartments containing the germ cells are lined peripherally by specialized somatic cells referred to as lobule boundary cells (Nagahama, 1983). These lobule boundary cells are considered to be homologous with Sertoli cells, and often occur in close proximity to spermatids and developing sperm, and appear to be involved in phagocytosis of degenerating germ cells and transport of metabolites (Grier, 1981; Nagahama, 1983).

During maturation, all germ cells within a cyst are at about the same stage of development. The four cellular stages that can be differentiated in sperm maturation are spermatogonia, spermatocytes, spermatids, and spermatozoa (Figures 2A, 2B, 2C, and 2D). Primary spermatogonia, distributed along the lobule lengths, undergo a series of mitoses which produce cysts containing several spermatogonial cells, called secondary spermatogonia. The primary spermatogonia are spherical and acidophilic, possess a single prominent nucleolus in each, and are the largest germ cells in the testis (Figure 2A). A second series of mitotic divisions

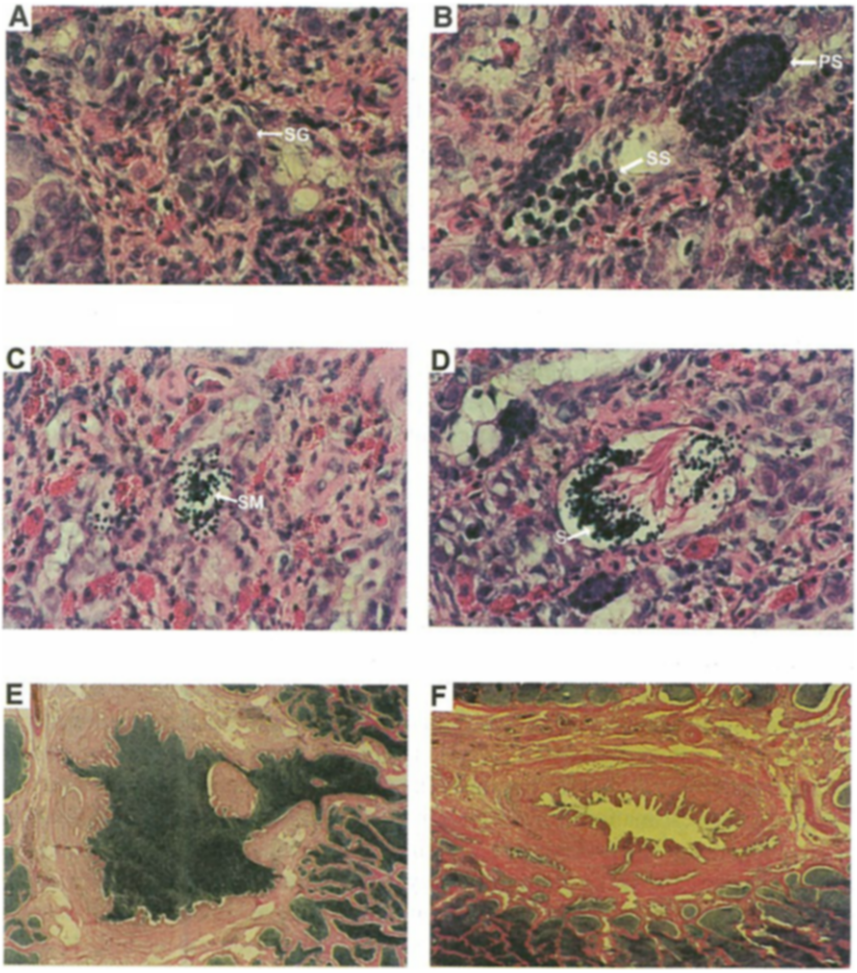


Fig. 2. Developmental stages and spermatogenic cells observed in *Thunnus albacares* testes. (A) Primary spermatogonia (SG; ×240). (B) Primary spermatocyte (PS) cells and secondary spermatocyte (SS) cells (×240). (C) Spermatids (SM; ×240). (D) Spermatozoa (S; ×240). (E) Prespawning stage in mature testis with vas deferens filled with spermatozoa (×10). (F) Postspawning stage (<12 h) in mature testis with the vas deferens almost completely devoid of spermatozoa (×10).

results in the formation of cysts full of primary spermatocytes. These stain basophilically, have more condensed nuclei, and are smaller (Figure 2B). The next developmental stage in the maturation process is secondary spermatocytes (Figure 2B) which are formed after the first meiotic division, and are retained within the cysts until they eventually burst through the cyst's capsule into the lobular

lumen, where they develop after a second meiosis into spermatids. Each spermatid develops into a spermatozoon, a process termed spermiogenesis. A spermatid has a condensed and intensely staining basophilic nucleus (Figure 2C). Mature spermatozoa possess a distinct rounded basophilic head and a long acidophilic flagellum (Figure 2D). An electron micrograph of an individual sperm from *Thunnus alalunga* is shown in Ratty *et al.* (1990).

The lobular lumens are continuous with the vas deferens, which are straight tubes with thick, muscular walls, which merge caudally and exit through a pore in the anal region. The lumen of the vas deferens is lined along its length with cuboidal to columnar epithelium, and varies in general appearance from smooth to convoluted (Harder, 1975; Schaefer, 1996). Histological evidence of recent spawning activity in male *Thunnus albacares* is apparently detectable for only about 12 hours after the spawning event, based on appearance of the epithelial lining and the amount of sperm present in the vas deferens (Figures 2E and 2F; Schaefer, 1996).

III. MATURATION

An individual tuna must reach a minimum size or age before it is physiologically capable of initiating full gametogenesis in response to the appropriate environmental cues. The size and/or age at which a certain fraction (e.g., 50%) of a population of tunas reaches maturity, and is thus capable of reproducing, is an important life history parameter. Unfortunately, this concept has not received sufficient attention nor proper evaluation. There has been a considerable amount of nonquantitative estimation of sizes and/or ages at maturity for tunas based mostly on invalid gonosomatic indexes (de Vlaming *et al.*, 1982). Many such studies have reported the apparent size at first maturity. That value is equivalent to the minimum size individual, sampled from a population, observed to be sexually mature. Reporting only the size at first maturity is useless, and even misleading. It is the functional statistical relationships between proportion mature and size and/or age which need to be derived to estimate proportions mature from a population.

The first requirement in the process of the estimation of proportions mature is to define precise criteria for the classification of maturity. Histological examinations and criteria are necessary to attempt to correctly classify female and male tuna as to sexual maturity. Particularly for females, histological information is required because of the inadequacy of gonad indexes or oocyte diameters for separating developing ovaries, in a stage of early vitellogenesis, from postspawning ovaries, in atretic stages of resorption. The histological classification scheme used by Schaefer (1998) for female and male *Thunnus albacares* provides the basis to distinguish between mature and immature individuals. Females classified as mature can be classified as reproductively active or inactive. Females are classified as

active when the ovary contains advanced yolked oocytes, and there is no atresia or only minor alpha atresia present. Females classified as mature-inactive have ovaries with oocytes in developmental stages of either unyolked or early yolked, and also contain alpha atresia of yolked oocytes and/or beta atresia. Also included in this class are ovaries with advanced yolked oocytes, of which more than 50% are atretic. The immature class consists of females whose ovaries contain unyolked or early yolked oocytes, but no signs of atresia. Males are classified as mature if there is histological evidence of sperm in the sperm duct and immature if there is no sperm in the sperm duct.

The second consideration is the implementation of an appropriate experimental design based on previous knowledge of the spawning locations and times for the species under consideration. Probably the most limiting factor in most studies of the reproductive biology of tunas, particularly estimation of maturity, is the difficulty in obtaining suitable tissues from specimens over a desired size range to encompass immature to 100% maturity during the period of reproductive activity. This can be further complicated by potential gear avoidance and biases caused by gear selectivity as a result of vertical stratification of individuals in different reproductive states (Suzuki, 1994; Davis *et al.*, 1998).

The final consideration should be the use of an appropriate statistical procedure for evaluation and interpretation of the data included in the experimental design. A weighted nonlinear predictive regression model fit directly to these sigmoidal data is probably the most appropriate (Schaefer, 1987, 1998). The model can then be used to predict proportions mature at specific lengths and/or ages for the stock being investigated.

The available estimates of lengths at 50% maturity of female tunas are given in Table I. These estimates, for just 3 of the 15 species of tunas, appear to be the only reliable estimates available at this time. For some of the other species there are estimates of the lengths, and in some instances presumed ages, at first maturity.

Table I
Estimates of Lengths at 50% Maturity for Female Tunas

Species	Length (cm)	Area	Reference
Euthynnus lineatus	47	Eastern Pacific	Schaefer (1987)
Katsuwonus pelamis	42	Atlantic	Cayré and Farrugio (1986)
Katsuwonus pelamis	42	Western Indian	Stéquert and Ramcharrun (1996)
Katsuwonus pelamis	43	Western Indian	Timohina and Romanov (1996)
Thunnus albacares	108	Western Pacific	McPherson (1991)
Thunnus albacares	92	Eastern Pacific	Schaefer (1998)

However, most all of those estimates are based on invalid methodologies and classification criteria.

For *Auxis* spp. and *Euthynnus* spp., which have been investigated in various oceans of the world, there is a limited amount of information regarding maturation. Yesaki and Arce (1994), summarizing investigations based on gonad indexes and anatomical scales, report the length at 50% maturity for *Auxis thazard* from the Gulf of Thailand to be 34 cm, and lengths at 50% maturity for *A. thazard* and *Auxis rochei* off India to be 30.5 and 24 cm, respectively. Yesaki (1994a) reports the apparent length at 50% maturity for *Euthynnus affinis* off India, based on an investigation using an anatomical scale, to be 43 cm. Although there are reported lengths at first maturity for *Euthynnus alletteratus* based on gonosomatic indexes (Yoshida, 1979) there do not appear to be any estimates of lengths at 50% maturity. The relationship between proportion of female *Euthynnus lineatus* mature and length from the eastern Pacific (Schaefer, 1987) is given in Figure 3, and the estimated length at 50% maturity in Table I.

The estimated lengths at 50% maturity given in Table I for female *T. albacares* from studies conducted in two different oceanic regions are quite variable. These differences may be more a function of the experimental designs and classification procedures employed than geographic variation. The relationship between proportion of female *T. albacares* mature and length from the eastern Pacific is given in Figure 3. In the study by Schaefer (1998) the estimated length at 50% maturity

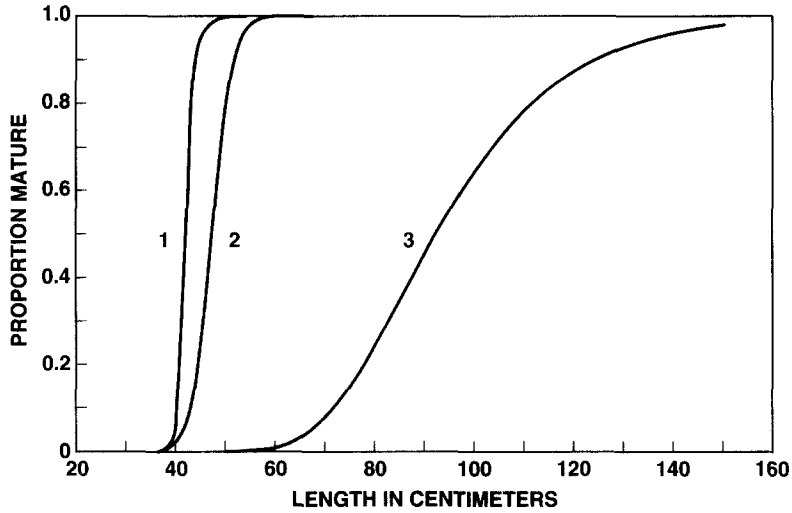


Fig. 3. Relationships between proportion of female tunas mature and length: (1) *Katsuwonus pelamis* (Stéquert and Ramcharrun, 1996), (2) *Euthynnus lineatus* (Schaefer, 1987), and (3) *Thunnus albacares* (Schaefer, 1998).

for females of 92 cm corresponds to an age of about 2 years (Wild, 1986). As an example of the size at first maturity, and the potential misuse of such information, the minimum length at sexual maturity of females was 59 cm. Males were found to mature at lesser lengths than females, with an estimated length at 50% maturity for males of 69 cm. For both sexes, there were statistically significant differences in annual and geographical estimates of lengths at 50% maturity. In the eastern Pacific *T. albacares* and *Katsuwonus pelamis* were found to mature at lesser sizes off Central America than in the northern areas off southern Baja California, the southern part of the Gulf of California, and the Revillagigedo Islands (Schaefer and Orange, 1956; Orange, 1961).

The relationship between proportion of mature female *K. pelamis* and length, from the Indian Ocean, is given in Figure 3. The shape of the maturation curve is noticeably different than that for *T. albacares,* but similar to that for *E. lineatus.* It appears that in *K. pelamis* and *E. lineatus,* once the critical size and/or age is attained, there is a strong selection pressure for individuals to initiate maturation. The estimated lengths at 50% maturity given in Table I for female *K. pelamis* from studies conducted in two different oceanic regions are almost identical. In the study by Timohina and Romanov (1996), the estimated 43-cm length at 50% maturity for females reportedly corresponds to an age of about 1.5 years. In this same study males were reported to mature at lesser lengths than females, with the estimated length at 50% maturity for males being 40 cm. However, in the other two studies (Cayré and Farrugio, 1986; Stéquert and Ramcharrun, 1996) males were reported to be slightly larger than females at 50% maturity. These differences are probably a result of the criteria used for classification of maturity. I expect that male *K. pelamis,* as observed for male *T. albacares* (Schaefer, 1998), become functionally mature with sperm present in the sperm duct before the females are capable of reproducing.

There is a very limited amount of information available on size and/or age at maturity in *Thunnus thynnus.* A maturity schedule based on valid histological criteria has not been derived. A study was conducted by Baglin (1982) in the western Atlantic to derive information on reproductive biology, including size and age at maturity, but mature fish were not obtained. Rodriguez-Roda (1967) conducted research on the reproductive biology of eastern Atlantic and Mediterranean *T. thynnus,* but had a very small sample size upon which conclusions were based regarding size at maturity. Regardless of these inadequate experimental designs and invalid conclusions for *T. thynnus,* subsequent researchers have accepted the age of 100% (knife edge) maturity for the west Atlantic to be 10 years of age (200 cm), and 5 years of age (130 cm) in the eastern Atlantic (Clay, 1991; Magnuson *et al.*, 1994).

Even less research has been carried out on reproductive biology of *Thunnus orientalis* in the Pacific Ocean, and size and/or age at maturity is poorly understood. However, since 1970 at Kinki University, Oshima Experimental Station,

Japan, studies on the aquaculture of *T. orientalis* have been conducted. Five-year-old fish spawned in a tank for the first time in 1979. A group of about 200 7-year-old fish spawned in captivity in 1994 at this facility in cages, and have continued to spawn seasonally. In 1998 at the Japan Sea Farming Association Amami Station, *T. orientalis* estimated to be 10 years old began spawning (Lee, 1998). Although these observations for captive *T. orientalis* indicate that spawning has occurred for fish after 5 years in captivity, it is necessary to sample wild fish from the spawning grounds to derive reliable maturity schedules for the stock.

For *Thunnus maccoyii,* Warashina and Hisada (1970) reported size at first maturity to be about 130 cm. Campbell (1994), using their data, estimated that the mean size at first maturity was in the range of 150 to 160 cm. Davis (1995), using oocyte diameter and gonad index data for southern bluefin tuna caught south of the spawning grounds, estimated the mean size at first maturity to be 152 to 162 cm. This parameter has been inadequately defined in the past, and is likely to be upward of around 164 cm (T. Davis, CSIRO, personal communication). The estimated age for *T. maccoyii* at this length is about 13 to 14 years (Gunn *et al.*, 1996).

Two other tuna species, *Thunnus alalunga* and *Thunnus obesus,* both of high commercial value, have also been investigated for obtaining an understanding of their reproductive biology in various oceans of the world. However, maturity schedules are not available for either, and there is only some fragmentary information on their sizes at first maturity. *Thunnus alalunga* are reported to reach sexual maturity in the size range of 85 to 90 cm (Ueyanagi, 1957; Otsu and Hansen, 1962) when they are about 6 to 8 years old (Labelle *et al.*, 1993). *Thunnus obesus* have been reported to reach sexual maturity at a size of 100 to 130 cm when they are about 3 years old (Calkins, 1980). These estimates of size at first maturity, however, should not be considered valid or useful.

For testing hypotheses regarding geographical or temporal variation in sizes and/or ages at maturity through evaluations of shifts in maturity schedules, or statistics at 50% maturity, it is imperative that the techniques employed to derive the parameters are comparable. These should be based on precise methodologies, such as histology and statistical estimation procedures, including nonlinear models fit directly to adequate data sets. It is also important for researchers to precisely specify the histological criteria used for classification as to maturity so as to permit valid comparisons among oceanic regions.

IV. SPATIOTEMPORAL SPAWNING PATTERNS

Current knowledge of spatial and temporal spawning distributions for tunas is presented in this section. Although larval surveys targeting tunas in appropriate locations and times can provide fine-scale information on spawning (Davis *et al.*, 1990; Leis *et al.*, 1991; Boehlert and Mundy, 1994), patchiness of tuna larvae

makes this technique inefficient for large-scale spawning distribution surveys (Ahlstrom, 1971, 1972; Nishikawa *et al.*, 1985; McGowan and Richards, 1989). Sampling ovarian tissues from adult tunas from commercial or recreational landings is a more efficient process for mapping of spatiotemporal spawning distributions. Histological assessment of all individual female ovarian tissues is not required for defining general spawning patterns. Gonosomatic indexes or, better yet, maximum oocyte diameters can be calibrated with histological information and then used for classification of spawning activity and defining geographical and temporal spawning distributions (Schaefer, 1987, 1998; West, 1990). In addition, the presence of residual hydrated and ovulated oocytes in ovarian lumens is evidence of recent spawning. There are numerous examples in the literature, based on inadequate sampling of gonads and larvae, which draw conclusions about the seasonal characteristics of tuna spawning in tropical waters (Stéquert and Marsac, 1986; Fonteneau and Marcille, 1988; Shomura *et al.*, 1994).

Although there are exceptions, it appears that most species of tunas exhibit year-round spawning patterns in the tropical regions of their distributions, and spawning is seasonally restricted only in subtropical regions. Four species of the genus *Thunnus* (*alalunga, maccoyii, orientalis,* and *thynnus*) are the only truly migratory species of the tribe Thunnini. These species differ in their reproductive patterns from the other tunas, exhibiting directed seasonal migrations to relatively discrete areas. Two other species of the genus *Thunnus* (*atlanticus* and *tonggol*) have relatively restricted geographical, but not temporal, spawning distributions as a result of their distributional ranges in the western Atlantic and the western Pacific, respectively (Collette and Nauen, 1983). A common factor among the 15 species, excluding *Allothunnus fallai,* is that spawning takes place at sea-surface temperatures of about 24°C and higher. The worldwide spatial extent of the potential spawning habitat for each species, within its geographical distribution, can be approximated by the area encompassed by the 24°C surface isotherms (Figure 4). The northward and southward seasonal movements of the 24°C isotherms are responsible for the pronounced seasonal spawning of tunas in the subtropical regions.

Auxis has been observed to spawn throughout its range in tropical and subtropical waters (Uchida, 1981). In the eastern Pacific Ocean, *Auxis* spawning occurs from coastal to oceanic waters throughout the year where sea-surface temperatures remain at around 24°C or higher, and spawning occurs seasonally in more northern and southern latitudes, correlated with temperature (Klawe, 1963; Klawe *et al.*, 1970; Ahlstrom, 1971, 1972; Lauth and Olson, 1996). Larvae have been found over a temperature range of 21.6 to 30.5°C (Richards and Simmons, 1971). In other regions of the world it appears that *Auxis* spawning distributions are somewhat restricted to coastal regions (Uchida, 1981; Nishikawa *et al.*, 1985). In the Indian Ocean, *Auxis* spawning was reported to occur for at least the 8 months during which data were collected (Bogorov and Rass, 1961).

The three endemic species of *Euthynnus* (Collette and Nauen, 1983) spawn

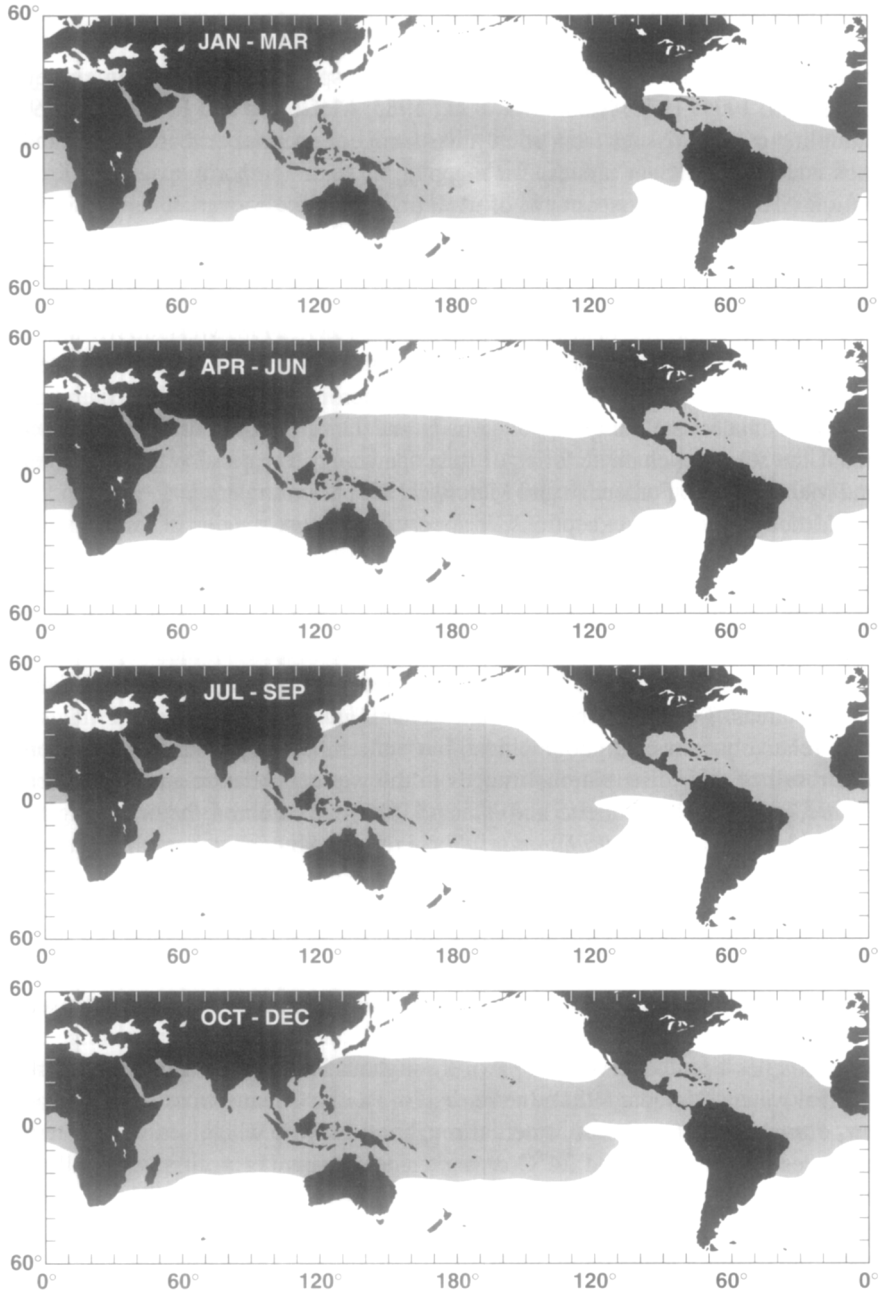


Fig. 4. Seasonal composite distributions of *in situ* sea-surface temperatures equal to or greater than 24°C. The boundaries of the shaded areas are the positions of the 24°C isotherms from Levitus and Boyer (1994).

extensively, both geographically and temporally, throughout their respective ranges (Buñag, 1956; Marchal, 1963; Richards *et al.*, 1969a,b, 1970; Klawe, 1963; Yoshida, 1979; Nishikawa *et al.*, 1985; Schaefer, 1987; Lauth and Olson, 1996). Although spawning distributions of all three species have been reported to be restricted primarily to peripheral areas and around islands within their respective ocean basins (Yoshida, 1979; Nishikawa *et al.*, 1985), spawning in the eastern tropical Pacific has been shown to be widely distributed from coastal to oceanic waters (Schaefer, 1987).

Katsuwonus pelamis spawning occurs throughout the year in tropical waters and seasonally in subtropical waters in all major oceans (Matsumoto *et al.*, 1984; Nishikawa *et al.*, 1985). For the Pacific and Atlantic oceans the latitudinal range in the spawning distribution has been shown to coincide with the area delineated on the north and south by the 24°C isotherm (Ueyanagi, 1969; Cayré and Farrugio, 1986). However, *K. pelamis* larvae have been collected at temperatures as low as 22°C (Matsumoto *et al.*, 1984; Boehlert and Mundy, 1994). In the western part of the equatorial Indian Ocean, *K. pelamis* spawning also occurs throughout the year, with some apparent periods of greater sexual activity (Stéquert and Ramcharrun, 1996; Timohina and Romanov, 1996). It was previously assumed that *K. pelamis* did not reproduce in the eastern Pacific, but migrated to the central Pacific to spawn (Rothschild, 1965). This hypothesis has recently been tested, and the results indicate that significant spawning of *K. pelamis* occurs in areas of the eastern Pacific where sea-surface temperatures are equal to or greater than 25°C (Schaefer, 2001).

Thunnus albacares, like *K. pelamis,* spawns over vast areas of the Atlantic, Indian, and Pacific oceans and throughout the year in the warm northern equatorial waters, but in the more northern and/or southern regions it is restricted to the summer months when the sea-surface temperatures exceed 24°C (Nishikawa *et al.*, 1985; Stéquert and Marsac, 1986; Fonteneau and Marcille, 1988; Suzuki, 1994; Wild, 1994). Minimum temperatures where *T. albacares* larvae have been captured with nets are around 24°C (Richards and Simmons, 1971; Boehlert and Mundy, 1994). *Thunnus albacares* spawning is reported as year-round in warm waters of the central Pacific (Matsumoto, 1958), but only seasonally near Hawaii (Matsumoto, 1966). In the eastern Pacific, where spawning of *T. albacares* occurs continuously between 0° and 20°N, the proportions of reproductively active females is positively correlated with fluctuations in elevated sea-surface temperatures (Schaefer, 1998). In that study the minimum temperature at which yellowfin spawning occurred, based on gonadal histology, was 22°C, although 85.3% of the spawning took place at temperatures between 26 and 30°C. The expansion of suitable spawning habitat for *T. albacares* in the eastern Pacific with the northward and southward movements of the 24°C surface isotherms into the subtropical regions north of 20°N and south of 0° during the northern and southern hemisphere summer months, and the apparent movement of yellowfin into these regions and

subsequent spawning, is possibly the mechanism which generates the two observed cohorts about 6 months apart in the yellowfin length–frequency data for the population (Schaefer, 1998). Furthermore, interannual events such as El Nino-La Nina apparently increase and decrease favorable spawning habitat in the eastern Pacific, and may be the mechanism for the apparent subsequent increases in recruitment of juvenile *T. albacares* to the population following El Nino events (Bayliff, 1989).

Thunnus obesus spawning is reported to occur year-round and throughout the equatorial regions of the Atlantic, Indian, and Pacific oceans (Nishikawa *et al.*, 1985; Stéquert and Marsac, 1986; Fonteneau and Marcille, 1988; Miyabe, 1994; Pallarés *et al.*, 1998; Stobberup *et al.*, 1998). However, spawning distributions have been inferred primarily from uncalibrated gonad indexes and larval distributions, which are suspect because of uncertainties in the identification of larvae of the genus *Thunnus* (Richards *et al.*, 1990). Although spawning apparently occurs widely across the equatorial Pacific Ocean, the greatest reproductive potential for *T. obesus* appears to be in the eastern Pacific, based on apparent maturation, size frequencies, and catch per unit of effort (Kikawa, 1966). Kume (1967) reported a correlation between the occurrence of sexually inactive *T. obesus* and sea-surface temperatures below 23 to 24°C. Hisada (1979), reporting on the results of a study carried out in the Pacific, found that for maturation and reproductive activity to occur in *T. obesus* requires a mixed layer depth of at least 50 m and a temperature of at least 24°C.

Thunnus alalunga exhibit distinct northern and southern spawning distributions and peak seasons as the result of two apparent stocks in both the Pacific and Atlantic oceans (Nishikawa *et al.*, 1985; Fonteneau and Marcille, 1988; Bartoo and Foreman, 1994; Murray, 1994). Peak spawning apparently occurs during the respective northern and southern summer months in oceanic subtropical waters of the Pacific, centered around 15°N and 15°S latitudes, with a separation of these zonal regions by a band between 10°N and 10°S where there is limited spawning observed (Ueyanagi, 1969; Nishikawa *et al.*, 1985). However, spawning does occur year-round in the northern spawning area of the western Pacific (Nishikawa *et al.*, 1985) and is apparently protracted over several months in the southern spawning area as well (Otsu and Hansen, 1962; Ramon and Bailey, 1996). Although the vast majority of spawning in the Pacific appears to occur in the western and central regions, larvae have been collected in the eastern Pacific as well (Nishikawa *et al.*, 1985). In the Indian Ocean, spawning by *T. alalunga* occurs widely south of about 10°S during at least the period of October to March (Nishikawa *et al.*, 1985; Stéquert and Marsac, 1986). The spawning habitat of *T. alalunga* is characterized by a mixed layer depth to about 50 m and a temperature over 24°C, with no strong thermocline above about 250 m (Ueyanagi, 1969).

Thunnus orientalis spawning in the Pacific is confined to a very restricted time–area strata in the western North Pacific, relative to their Pacific-wide distri-

butional range (Collette and Nauen, 1983). The spawning occurs from off the northern Philippines to central Japan, about 18°N to 35°N, and from the 200-m isobath of the East China Sea to around 150°E, from April to August. This spawning area is occupied by the Kuroshio Current. Spawning begins in the south off the Philippines in April-May and moves northward to off southern Honshu in July. Peak spawning is reported to occur in May-June (Nishikawa *et al.*, 1985; Bayliff, 1994). Spawning of *T. orientalis* also occurs in the Japan Sea during August, which may consist of a separate stock (Okiyama, 1974, 1979).

In the Atlantic Ocean, where *T. thynnus* is also widely distributed, spawning occurs in two relatively restricted locations and times, the Gulf of Mexico in April-June and the Mediterranean Sea in June-August (Clay, 1991). In the Gulf of Mexico it appears that the greatest concentration of spawning occurs in the central region north of 25°N in May. *Thunnus thynnus* spawning in the western Atlantic has also been reported from the Straits of Florida and off the Carolinas (Baglin, 1982; Clay, 1991). The western Mediterranean and Adriatic seas are considered spawning areas, but, the greatest spawning apparently occurs between southern Italy and the Belearic Islands off Spain. Spawning may also occur, however, in the eastern Mediterranean (Clay, 1991).

Thunnus maccoyii spawning is restricted to a relatively small area off northwestern Australia in the eastern tropical Indian Ocean (Nishikawa *et al.*, 1985; Caton, 1991). Spawning is reported to occur in all months except July, although the main spawning season appears to be from September to April, with a peak in January and February (Caton, 1991; Farley and Davis, 1998). Adult *T. maccoyii* are distributed globally in waters south of 30°S, and evidence from tag-recapture data (Shingu, 1978) suggests that *T. maccoyii* make extensive migrations in the Southern Ocean. *Thunnus maccoyii*, *T. orientalis*, and *T. thynnus* are the best adapted of all tunas to cold water (Carey, 1973), which permits them to exploit productive temperate waters. However, like the other tunas, spawning is restricted to surface water temperatures in excess of about 24°C (Yukinawa, 1987).

Thunnus tonggol has a relatively restricted geographical distribution, being endemic to the Indo-West Pacific (Collette and Nauen, 1983). Spawning of *T. tonggol* is reported to be confined to coastal waters, based on the occurrence of their larvae which were collected at surface water temperatures of 28°C (Nishikawa and Ueyanagi, 1991). It appears there are two distinct spawning seasons for *T. tonggol* off the west coast of Thailand: a major spawning period during the northeast monsoon from January to April and a minor spawning period during the southwest monsoon in August-September. Spawning is also apparently seasonal for *T. tonggol* off Papua New Guinea and off New South Wales, occurring during the austral summer (Yesaki, 1994b).

Thunnus atlanticus is restricted to the western Atlantic (Collette and Nauen, 1983). *Thunnus atlanticus* spawning is reported to occur off Miami, Florida, from April to November (Idyll and de Sylva, 1963). Spawning has also been docu-

mented in the Gulf of Mexico from May to October (Juarez and Montolio, 1975), in the Caribbean in March, July, and August (Richards *et al.*, 1974), and around the Bahama Banks in August (Juarez, 1978).

V. SPAWNING BEHAVIOR

Nocturnal spawning appears to be common among scombrids, as well as other groups of fishes (Ferraro, 1980; Helfman, 1986). Spawning of *Thunnus albacares* at night was reported by Harada *et al.* (1980) on the basis of running-ripe and fully hydrated oocytes. Based on oocyte developmental stages and new postovulatory follicles, the assumption was made that *T. albacares* spawn after 2200 h in the Coral Sea (McPherson, 1991) and *T. obesus* from about 1900 to 2400 h off Java and southwest of Hawaii (Nikaido *et al.*, 1991). The times of day at which *T. albacares* spawn in the eastern Pacific were estimated by Schaefer (1996, 1998) by examining the times of day at which the various reproductive states occur. Spawning of *T. albacares* around Clipperton Atoll was determined, on the basis of the presence of migratory-nucleus and hydrated-stage oocytes and new postovulatory follicles in ovaries of females sampled at different times of the day and night, to occur between 2230 and 0330 h (Schaefer, 1996). From a large-scale study of spawning behavior of *T. albacares* in the eastern Pacific it was reported that spawning occurs almost entirely at night, between approximately 2200 and 0600 h (Schaefer, 1998).

It appears that subsurface longline-caught female *T. albacares* have significantly lower gonad indexes than do purse-seine-caught female *T. albacares* of the same sizes caught in the same area–time strata in the eastern and western Pacific (Suzuki *et al.*, 1978; Koido and Suzuki, 1989; Bayliff, 1994). It seems likely that these differences reflect behavioral differences in reproductively active and inactive *T. albacares*. These differences suggest that mature, but reproductively inactive, *T. albacares* seldom inhabit the near-surface warmer waters of the mixed layer, where they would be vulnerable to capture by purse-seine gear. The spawning time during 1992 for a group of 3- and 6-year-old captive *T. albacares* held in sea pens at the Yaeyama Station, Ishigaki, Japan, of the Japan Sea Farming Association (JASFA), was between 2000 and 0800 h, but mostly between 2000 to 2400 h (Masuma *et al.*, 1993). During 1993 at the Yaeyama Station, the courtship behavior of 3-, 4-, and 7-year-old *T. albacares* in the same sea pen would normally consist of similar-size males and females chasing one another. Commonly more than one male was observed to be chasing after the same female, and the males but not the females were identified as displaying body stripes during this period (S. Masuma, JASFA, personal communication).

A population of 44 *T. albacares* held in a large (17-m-diameter, 6-m-depth, 1,361,900-liter) concrete in-ground tank at the Inter-American Tropical Tuna

Commission's (IATTC) Achotines Laboratory in Panama first spawned in October 1996 (Bayliff, 1998). The initial spawning involved only two or three pairs of the largest fish (>90 cm in length). Each spawning event occurred around sunset, and was preceded by courtship behavior during the late afternoon. The courtship behavior included pairing of individuals, chasing, rapid color flashes exhibited by individual fish, and rapid horizontal or vertical swimming. During the following 3 months of 1996 spawning was continuous, with many of the fish exhibiting courtship behavior prior to each spawning event, which generally occurred between 1700 and 2000 h at water temperatures from 26.7 to 28.0°C. Behavioral sequences associated with courtship become more pronounced and at higher frequency approaching time of fertilization (V. Scholey, IATTC, personal communication). During most of 1997 spawning continued at nearly daily intervals in water temperatures from 24.4 to 29.5°C. Spawning ceased during the upwelling period (mid-March to mid-April) when water temperatures ranged from 20.0 to 24.0°C.

Davis *et al.* (1998) has shown that size partitioning by depth occurs in *Thunnus maccoyii* in their spawning area. The smaller fish are more abundant in the catches by deep longline gear and the larger fish are more abundant in catches of shallow gear. This size partitioning by depth is apparently related to spawning activity, with spawning fish being at the surface and nonspawning fish being deeper. As fish get larger they spend proportionally more time spawning while on the spawning ground.

The spawning time during 1998 and 1999 of *Thunnus orientalis* broodstock held at the Amami Station, JASFA, Japan, was between 1900 and 2300 h. The observed courtship behavior is apparently similar to that for captive *T. albacares*, with more than one male commonly chasing after the same female and body stripes and/or darker coloration displayed by the males during this period (S. Masuma, JASFA, personal communication).

Katsuwonus pelamis captured at sea and placed in land-based tanks at the Kewalo Research Facility of the National Marine Fisheries Service, Honolulu, Hawaii, have spontaneously spawned about 8 h after capture at about 2400 h at water temperatures of 23 to 24°C. However, spawning does not continue, probably due to the stress of captivity, and atresia of yolked oocytes within ovaries is observed within 24 h. The spawning around 2400 h by captive *K. pelamis* appears to be close to the time of natural spawning, on the basis of histological examinations of skipjack ovaries (Hunter *et al.*, 1986).

Euthynnus lineatus held in a 6.4-m-diameter, 37,000-liter tank at the IATTC's Achotines Laboratory in Panama spawned nearly continuously during 1994, with the majority of the spawning occurring between approximately 2000 and 2400 h (Bayliff, 1995). Spawning occurred in water temperatures of 25 to 28°C, and when the temperature of the water in the tank decreased to less than 25°C the fish stopped spawning.

Magnuson and Prescott (1966) observed *Sarda chiliensis* in captivity to

exhibit courting and pairing behavior in a sequence previous to the simultaneous and adjacent release of gametes while swimming in a circular path. There are some reported observations of courtship behavior, consisting of pairing, chasing, and wobbling, and lateral body markings and coloration changes in scombrids such as *Euthynnus lineatus* (Hunter and Mitchell, 1967) and *K. pelamis* (Iverson *et al.*, 1970) in the ocean during daylight hours. This courtship behavior, particularly in the later part of the day, although rarely observed in the field, appears to be normal in scombrids, but does not indicate that spawning is occurring at exactly that time.

Investigations of courtship behavior and spawning in captive tunas through assessing the roles of visual, acoustic, and chemical signals should be undertaken in attempts to truly understand the act of spawning in tunas.

VI. SPAWNING FREQUENCY

Being multiple spawners, tunas, like many subtropical and tropical pelagic fishes, continuously produce batches of hydrated oocytes which are released into the sea in separate spawning events (Hunter *et al.*, 1985). The estimation of spawning frequency, as the mean spawning interval between sequential spawning events, is essential for a comprehensive understanding of the reproductive biology of tunas. Previously it was assumed, based on the number of modes present in oocyte size frequency distributions, that almost all tunas, including *Thunnus albacares* and *Katsuwonus pelamis,* spawn more than once during a spawning season, but not more than a few times (Bayliff, 1980; Matsumoto *et al.*, 1984).

Knowledge of the appearance and longevity of postovulatory follicles in ovaries of tunas after spawning is necessary for estimation of spawning frequency (Hunter *et al.*, 1985, 1986; Schaefer, 1996). The age and longevity of postovulatory follicles have been determined only for *K. pelamis* (Hunter *et al.*, 1986) and *T. albacares* (Schaefer, 1996). More thorough validation of postovulatory degeneration and longevity is desirable, especially in species of tunas for which this has not been investigated. However, the frequency of ovaries of mature females containing postovulatory follicles has been used to estimate spawning frequency (Table II) in *K. pelamis* (Hunter *et al.*, 1986), *T. albacares* (McPherson, 1991; Schaefer, 1996, 1998), *Thunnus obesus* (Nikaido *et al.*, 1991), and *Thunnus maccoyii* (Farley and Davis, 1998). Schaefer (1998) estimated the fraction of mature females in the population spawning per day to be 0.66, which is equivalent to a spawning frequency of 1.52 days. This is a mean spawning interval for the average mature female in the population during the 2-year period of that study, and does not imply that individual fish are spawning at this rate throughout the year. In that study the ovaries of 81% of the 565 females collected with migratory-nucleus or hydrated oocytes (evidence of spawning within a few hours) also had postovulatory follicles present (evidence of spawning within 24 h), which is equiva-

Table II
Estimates of Spawning Frequency (Mean Spawning Interval) for Female Tunas

Species	Days	Area	Reference
Katsuwonus pelamis	1.18	Western Pacific	Hunter *et al.* (1986)
Thunnus albacares	1.53	Western Pacific	McPherson (1991)
Thunnus albacares	1.52	Eastern Pacific	Schaefer (1998)
Thunnus maccoyii	1.62	Eastern Indian	Farley and Davis (1998)
Thunnus obesus	1.09	Western Pacific	Nikaido *et al.* (1991)

lent to a spawning frequency of 1.23 days. This implies that reproductively active *T. albacares* spawn almost daily. Similar spawning frequencies have been reported for mature and reproductively active female *T. maccoyii, T. obesus,* and *K. pelamis,* as indicated from the values in Table II. The incidence of both postovulatory follicles and late-stage oocytes indicates daily spawning in tunas (Figure 5). This high frequency of spawning implies that in a reproductively active female there is a continuous maturation of oocytes, which are recruited from the reservoir of primary oocytes.

In the section on spawning behavior it was reported that there are apparent behavioral differences in reproductively active and inactive *T. albacares,* as indicated from sampling of specimens from purse-seine and subsurface longline gears. A recent study (Itano, 2000) of the reproductive biology of *T. albacares* in the central and western Pacific, using histological criteria, confirmed spawning throughout the year within 10° of the equator at a spawning frequency of 1.99 days, based on 5270 mature females sampled from purse-seine and subsurface longline gears. The spawning frequency for purse-seine samples was higher (1.71 days) than that for longline samples (2.29 days), verifying the earlier observations. This disparity was more pronounced when examined from different set types for both gears. The mean spawning interval for mature *T. albacares* taken by purse seines on actively feeding schools was 1.47 days, compared to 2.68 days for samples taken from deep-set longline gear, which targets large tunas that are spread out over large distances.

For the studies on spawning frequency of *T. obesus* (Nikaido *et al.*, 1991) and *T. maccoyii* (Farley and Davis, 1998) the assumption is made that the postovulatory follicles probably do not persist and are not detectable for more than 24 h. This is a reasonable assumption based on the results of the validation studies for *K. pelamis* (Hunter *et al.*, 1986) and *T. albacares* (Schaefer, 1996) which spawn in similar sea-surface temperatures ($\geq$24° C) to those of *T. obesus* and *T. maccoyii.* The rates of postovulatory follicle degeneration and resorption, along with oocyte development, are more rapid in tunas than in fish inhabiting cooler waters, and are

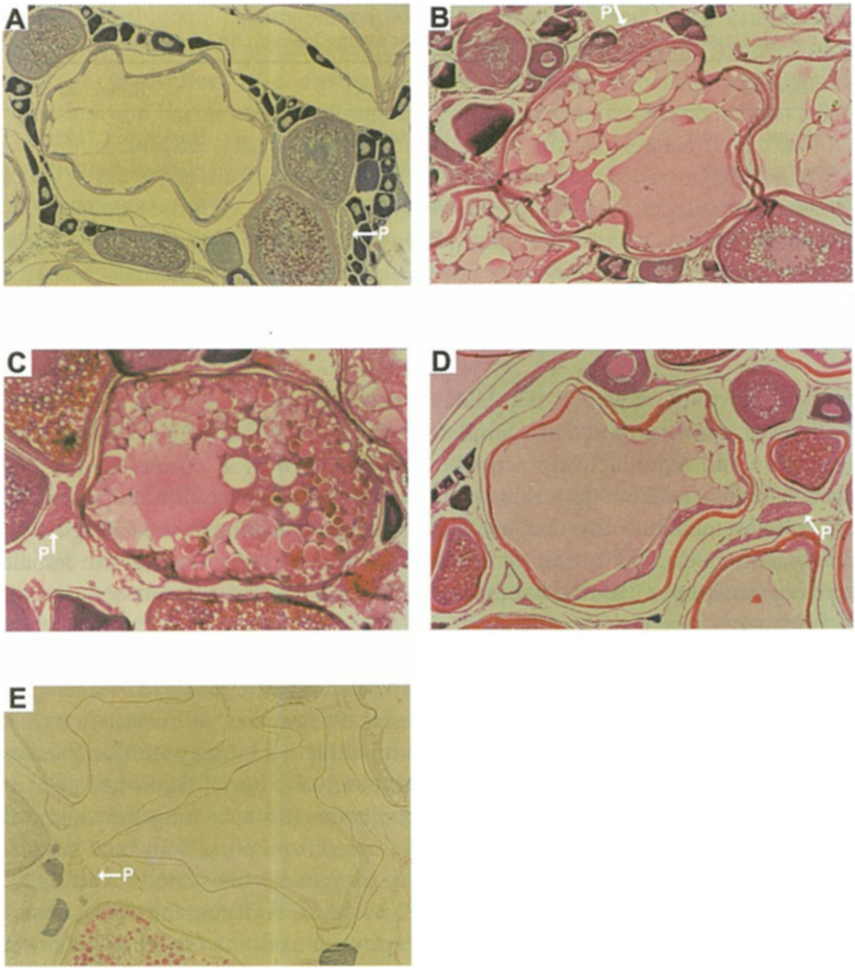


Fig. 5. Migratory-nucleus or hydrated-stage oocytes and postovulatory follicles (p) in advanced stages of degeneration, in five species of tuna. (A) *Katsuwonus pelamis* (×25). (B) *Thunnus albacares* (×40). (C) *Thunnus maccoyii* (×40). Microscopic slide from J. Farley, CSIRO, Hobart, Australia. (D) *Thunnus obesus* (×25). Microscopic slide from H. Nikaido, JASFA, Obama Fukui, Japan. (E) *Thunnus orientalis* (×40). Microscopic slide from S. Tsuji, NRIFSF, Shimizu, Japan.

apparently correlated with temperature (Fitzhugh and Hettler, 1995). For chub mackerel, *Scomber japonicus,* held at 20°C in the laboratory, postovulatory follicles persisted in the ovary, and were detectable for up to 48 h after spawning (Dickerson *et al.,* 1992). The spawning frequency for *S. japonicus* in the Southern California Bight during April-July at sea-surface temperatures presumably less

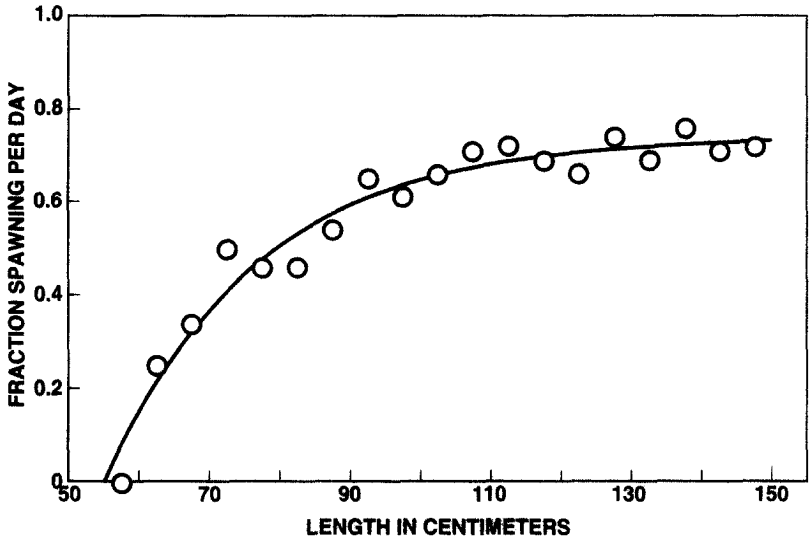


Fig. 6. Relationship between fraction of mature *Thunnus albacares* females spawning per day and length. The circles are for 5-cm-length intervals. (From Schaefer, 1998.)

than or close to 20°C was 10.9 days (Dickerson *et al.*, 1992). The spawning frequency for *S. japonicus* around the Izu Islands, Japan, in sea-surface temperatures of 16.5 to 18.8°C during April to June was 5.7 days during a period of 36 days. Clarke (1987) showed that the Hawaiian anchovy (*Encrasicholina purpurea*) spawns at intervals of about 2 days, as compared with about 7 days for northern anchovy (*Engraulis mordax*), a cooler-water species (Hunter and Goldberg, 1980). The postovulatory follicle can be detected in *E. mordax* for just under 48 h (Hunter and Goldberg, 1980), whereas for *E. purpurea* that period is apparently no more than 24 h.

The relationship between length and the fraction of mature *T. albacares* females spawning is illustrated in Figure 6. The minimum observed length of *T. albacares* at which postovulatory follicles were observed was 60 cm. From that length there is a fairly rapid increase in the fraction spawning per day up to the estimated length at which 50% of the females are mature (92 cm), where the predicted fraction of mature females spawning per day is 0.61. The curve for the relationship slowly approaches the asymptote following that point, and 71% of the females are predicted to be spawning per day at 124 cm, the estimated length at which 90% of the females are mature.

Davis *et al.* (1998) present data on the relationship between relative spawning frequency and length for *T. maccoyii*. Spawning is first observed in the 150- to 159-cm length class, but is minor. From that length class there is a linear increase

in the fraction spawning per day to 0.38 in the 170- to 179-cm length class, 0.72 in the 190- to 199-cm length class, and 0.87 in the 200- to 209-cm length class, the largest length class sampled, which is equivalent to a spawning frequency of 1.2 days. The findings from these two studies indicate the importance of estimating the relationship between spawning frequency and size class in tunas for inclusion in algorithms of the estimation of reproductive potential of stocks.

An alternative method for measuring the spawning rate of tunas is based on the frequency of ovaries containing hydrated oocytes (Hunter and Macewicz, 1985a). The incidence of mature female tunas with hydrated oocytes was used to measure the rate of spawning by Schaefer (1987) for *Euthynnus lineatus*. The frequency of occurrence of female *E. lineatus* throughout the spawning season with ovaries containing hydrated oocytes led Schaefer (1987) to conclude that the average interval between spawnings of *E. lineatus* in the eastern tropical Pacific was 2.1 to 5.7 days, depending on the area. Based on the apparent lengths of the spawning seasons within areas, the estimated number of batches of eggs spawned during the year by *E. lineatus* was 43 to 58. Studies at the IATTC Achotines Laboratory, Panama, during 1994, when spawning of *E. lineatus* was nearly continuous, indicated that a group of eight fish averaging 50 cm in length spawned at intervals of 1 to 5 days (Bayliff, 1995).

In females captured by longline gear in the Atlantic throughout the spawning seasons during 1966 to 1990, the frequency of occurrence of ovaries containing hydrated oocytes led Batalyants (1992) to conclude that the average interval between spawnings was 2.2 to 2.8 days for *T. albacares* and 1.6 to 3.1 days for *T. obesus*. The hydrated oocyte method has the potential for obtaining reliable estimates of the spawning frequency of tunas. However, the preferred method should be the histological identification of postovulatory follicles in freshly fixed ovarian tissues. This is because of the limited time period in which hydrated oocytes are present in tuna ovaries, previous to spawning, and thus the limited time period from which useful samples can be obtained, relative to the merits of the alternative procedure (Hunter and Macewicz, 1985a; Hunter *et al.*, 1986; Schaefer, 1998).

Structural changes over seasonal cycles have been described from histological examinations of teleost testes (Grier, 1981), but there has been almost no research on diel testicular changes in relation to rhythmic spawning activity. Information on testicular histology in tunas is scarce because most researchers have been satisfied with gross morphological or gonosomatic indexes to measure reproductive activity of males. Histological examinations of the testes from *Thunnus alalunga* (Ratty *et al.*, 1990) and *T. obesus* (Nikaido *et al.*, 1991) have provided descriptions of some aspects of spermatogenesis and characteristics of sexual maturity in male tunas. An investigation of histological characteristics of testicular tissues from reproductively active *T. albacares* provided criteria on the structural characteristics of the vas deferens useful for estimation of spawning frequency and reproduc-

tive effort of males (Schaefer, 1996). Structural characteristics of the vas deferens, specifically the amount of sperm present, its shape, and the staining of the epithelium, are useful for detecting whether a male *T. albacares* has recently spawned. Utilizing these criteria for the combined samples from a 2-year study period of *T. albacares* in the eastern Pacific, the fraction of mature active males classified as spawning was 0.97, equivalent to a mean spawning interval of 1.03 days. The main limitation to the technique is that spawning cannot be detected more than 12 h after it occurs. Because *T. albacares* are normally captured during daylight hours in the purse-seine fishery in the eastern Pacific, spawning frequency estimates from males could be determined only for fish caught during the relatively short time between about 0600 and 1200 h. Spawning frequency estimates for tunas are thus better estimated from the presence of postovulatory follicles that are detectable in ovaries from fish captured throughout the entire day, with the assumption that the males spawn at similar times.

VII. FECUNDITY

The fecundity of tunas, like those of other multiple-spawning fishes, is not fixed at the beginning of their spawning period. Their annual fecundity is indeterminate because tunas spawn numerous times during a season or year, and their potential annual fecundity exceeds the number of oocytes within the ovaries at any given time (Hunter *et al.*, 1985). Annual fecundity can be estimated from batch fecundity (the number of oocytes released per spawning) and spawning frequency. However, only at the final stages of oocyte maturation, beginning with the migratory-nucleus phase and followed by hydration, is there a distinct hiatus in the distribution of oocytes from which the batch fecundity estimates can be derived. This method is essential for accurate estimation of batch fecundity in multiple spawners, such as tunas, because only in this developmental stage of oogenesis can unequivocal counts of oocytes in samples from the spawning batch be obtained. Unfortunately, most batch fecundity estimates on tunas and many other multiple-spawning fishes have been based upon counts of oocytes which had not entered their final stages of maturation and from ovarian tissue samples which had been placed in Gilson's fluid. This technique creates a further potential bias in batch fecundity estimates because Gilson's fluid causes significant shrinkage of oocytes and compaction of the oocyte size distribution, which then complicates partitioning of the most advanced group of oocytes from the adjacent group of smaller oocytes.

Migratory-nucleus and hydrated oocytes can be easily distinguished from other oocytes in ovaries of tunas by their larger size ($\geq$0.75 mm) and by their appearance (Hunter *et al.*, 1985; Schaefer, 1998). However, there is only a short period from late afternoon until about 2200 h (previous to spawning) when ovaries

with migratory-nucleus or hydrated oocytes are found in *Thunnus albacares* (Schaefer, 1996, 1998). The batch fecundity should be considered to be the number of migratory-nucleus or hydrated oocytes in the ovary (Hunter *et al.*, 1985). For each female, counts should be made of migratory-nucleus or hydrated oocytes in a minimum of two subsamples of about 0.05 g each weighed to the nearest 0.1 mg (Schaefer, 1998). Ovaries should not be used for batch fecundity estimation when postovulatory follicles $\leq$12 h age are identified through histological examination, or loose hydrated oocytes are observed in the lumen of the ovary. Each of the two subsamples yields an estimate of batch fecundity for each female, calculated from the product of the number of migratory-nucleus or hydrated oocytes per unit weight of the subsample and the total weight of the ovaries. The mean of these two estimates provides the batch fecundity estimate for each fish.

Estimated mean relative batch fecundities for tunas, based on counts of distinct advanced stages of oocytes, are given in Table III. The relative fecundity estimates in Table III for *T. albacares* (67 oocytes/g body weight) and *Thunnus maccoyii* (57 oocytes/g body weight) are similar, but considerably greater than the estimate for *Thunnus obesus* (31 oocytes/g body weight), and considerably less than the estimates for *Katsuwonus pelamis* (82 oocytes/g body weight) and *Euthynnus lineatus* (99–136 oocytes/g body weight). For temperate scombrids, the estimated batch fecundities, based on migratory-nucleus or hydrated oocyte counts, were 168 oocytes/g body weight (Dickerson *et al.*, 1992) and 158 oocytes/g body weight (Yamada *et al.*, 1998) for *Scomber japonicus,* and only 28 to 55 oocytes/g body weight for *Scomber scombrus* (Alheit *et al.*, 1987; Watson *et al.*, 1992). In other studies of tunas in which batch fecundity determinations were made using advanced yolked oocytes which were not yet in the final stages of oogenesis, or tissues were subjected to treatment with Gilson's fluid, the estimates should be considered as biased substantially upward.

Hunter *et al.* (1985) demonstrated that the minimum number of females required for an appropriate estimate of the batch fecundity for northern anchovy, *Engraulis mordax,* was 50. The estimate for *T. albacares* (Schaefer, 1998) is based

Table III
Estimates of the Relative Batch Fecundity (Oocytes per Gram of Body Weight) of Tunas

Species	Fecundity	Area	Reference
Euthynnus lineatus	99–136	Eastern Pacific	Schaefer (1987)
Katsuwonus pelamis	82	Western Atlantic	Goldberg and Au (1986)
Thunnus albacares	67	Eastern Pacific	Schaefer (1998)
Thunnus maccoyii	57	Eastern Indian	Farley and Davis (1998)
Thunnus obesus	31	Western Pacific	Nikaido *et al.* (1991)

on a sample size of 345 females, but all of the other estimates given in Table III are based on inadequate sample sizes. Obtaining females in advanced stages of oogenesis, containing migratory-nucleus or hydrated oocytes, can be difficult. The time period when ovaries are in this developmental stage is only a few hours and availability of samples is normally restricted to the periods of commercial fishing operations, which do not necessarily coincide with the period just previous to spawning. In addition to the importance of appropriate sample sizes in estimation of batch fecundity, there are other sampling considerations. These include, but are not limited to, the length distribution of samples from throughout the size range of reproductively active females and suitable geographic and temporal coverage for the stock under investigation (Hunter *et al.*, 1985, 1992; Schaefer, 1998).

Batch fecundity increases with body length for the species listed in Table III (Figure 7). Although not illustrated in Figure 7, the data for each of these species clearly indicate the high variation in batch fecundity estimates among tunas of similar size. For *T. albacares,* for example, the estimates of relative fecundity ranged from 4.9 oocytes per gram of body weight for a 118-cm fish to 174.0 oocytes per gram of body weight for a 126-cm fish. Although the relationship between batch fecundity and length is expected to be curvilinear, and linear between batch fecundity and weight (Hunter *et al.*, 1985, 1992; Schaefer, 1998), it is analytically possible for the batch fecundity in tunas to be linearly dependent on both weight and length (Schaefer, 1987).

Interannual and geographic variation in batch fecundity estimates has been reported for tunas. Even with the high variability in batch fecundity estimates of fish of the same size, statistical comparisons have indicted significant differences. For example, the predicted batch fecundity estimate for a 125-cm *T. albacares* was 1.454 million oocytes one year, and 2.495 million oocytes the next, within the same area of the eastern Pacific (Schaefer, 1998). The information on annual variation in batch fecundity for marine fish, especially tunas, is very limited because in most instances batch fecundity and other reproductive characteristics are derived from a single year of sampling. For *Engraulis mordax,* whose reproductive biology has been investigated extensively, significant interannual variation in batch fecundity has been observed, the average number of eggs produced per spawning by a standard female varying by a factor of 2 (Hunter *et al.*, 1985). Temporal variation in batch fecundity estimates may be associated with factors such as temperature and prey availability (Wootton, 1982), although there is little empirical evidence for either in the literature pertaining to pelagic marine species sampled in the field. Geographic variation was also observed in batch fecundity estimates for *T. albacares,* with the greatest predicted estimates of batch fecundity in the most northern area in the eastern Pacific (Schaefer, 1998). The batch fecundity of *Euthynnus lineatus* was also shown to increase with latitude in the eastern Pacific (Schaefer, 1987). Geographic variation in fecundity has been reported for several species of fish, with greater fecundities commonly found at

higher latitudes. The batch fecundity of *Engraulis mordax* off Oregon is significantly greater than for those off California (Hunter and Goldberg, 1980; Laroche and Richardson, 1980). Geographic differences in batch fecundity and length at sexual maturity of tunas suggest a lack of complete mixing of fish among areas. These differences appear to reflect genetic variation, although environmental effects also may be partly responsible.

Batch fecundity has also been reported to vary significantly during the spawning season in many fish species (Conover, 1985). A decrease in batch fecundity was reported for *S. scombrus* during the spawning season in the Atlantic as individuals moved northward (Watson *et al.*, 1992). Batch fecundity has been shown to depend upon rations in several laboratory studies of nonscombrids (Wootton, 1979) and probably depends on environmental factors of the habitat of fishes as well (Wootton, 1982). Female haddock, *Melanogrammus aeglefinus,* which is a multiple spawner, produced fewer eggs at successive spawnings when fed at maintenance rations rather than at high rations (Hislop *et al.*, 1978).

As mentioned before, the annual fecundity is the product of the spawning frequency and the batch fecundity. The annual relative batch fecundity (number of oocytes/g body weight/year) was estimated to be 14,141 and 17,280 for the average 2- and 3-year-old *T. albacares,* respectively, in the eastern Pacific (Schaefer, 1998). These estimates illustrate that the annual egg production is far greater for the average 3-year-old than for the average 2-year-old. Predictive models for length at maturity and spawning frequency should be coupled with those for batch fecundity and used with abundance estimates for females to produce estimates of the potential annual egg production of tuna stocks.

VIII. SEX RATIOS

Tunas display no sexual dimorphism in either external morphological characters or color pattern (Bayliff, 1980; Collette and Nauen, 1983). In a recent comparative study of morphological features of thawed *Thunnus albacares* and *Thunnus obesus* it was not possible to distinguish males from females by any of the external characters quantitatively evaluated (Schaefer, 1999). Aside from the previously mentioned rare instances of hermaphroditism reported in *Katsuwonus pelamis* (Raju, 1960; Uchida, 1961), tunas are heterosexual.

Sex ratios reported in most studies on tunas are based on gross examinations of the gonads of individuals from commercial landings. The discrimination of ovaries versus testes, from gross examinations, is problematic in the smaller individuals with undeveloped gonads. In early studies on reproductive biology of *K. pelamis* and *T. albacares* in the eastern Pacific (Schaefer and Orange, 1956; Orange, 1961), and a later study addressing sexual dimorphism in growth (Wild, 1986), the inability to assign sex to smaller specimens is apparent from the clas-

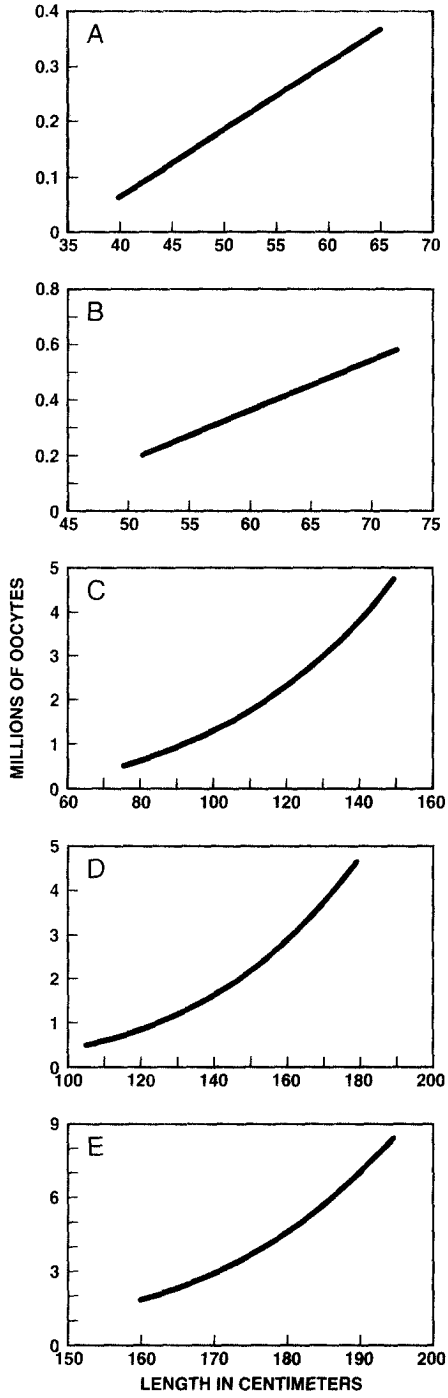


Fig. 7. Relationships between batch fecundity and length. (A) *Euthynnus lineatus* (Schaefer 987). (B) *Katsuwonus pelamis* (Goldberg and Au, 1986). (C) *Thunnus albacares* (Schaefer, 1998) D) *Thunnus obesus* (Nikaido *et al.*, 1991). (E) *Thunnus maccoyii* (Farley and Davis, 1998).

sification of individuals as of indeterminate sex. There are numerous instances in the literature where the sex ratios reported for the smaller fish, especially below lengths at 50% maturity, should be considered suspect when sex identifications were based solely on gross examinations. Criteria developed through microscopic examinations of gonadal tissues for the separation of undeveloped ovaries and testes through gross examinations are practical only down to a limited range in length. It is preferable to obtain positive identifications of sex for smaller fish with undeveloped gonads from microscopic examinations of gonadal tissues. Immunochemical sex discrimination of live *T. albacares* has been conducted (Takemura and Oka, 1998), but the lower size limit for sex discrimination has not been determined. Also, that technique would appear to be most promising for sex discrimination of tunas being held as experimental broodstock.

The overall sex ratios reported for most tuna species, when adequately sampled, do not deviate significantly from the expected 1 : 1 ratio. However, a preponderance of males in the larger length classes has been reported for several tuna species investigated: *Euthynnus affinis* (Yesaki, 1994a), *Euthynnus lineatus* (Schaefer, 1987), *Thunnus alalunga* (Otsu and Sumida, 1968), *T. albacares* (Suzuki, 1994; Wild, 1994; Schaefer, 1998), *Thunnus maccoyii* (Caton, 1991), *T. obesus* (Miyabe and Bayliff, 1998; Pallarés *et al.*, 1998), and *T. thynnus* (Clay, 1991). This is most interesting, since for most fishes it is the females which attain the largest sizes and are predominant in the larger length classes (Pauly, 1994). The differentials in sex ratio within size classes of tunas have been suggested to be due to differences between males and females with respect to growth, mortality, or availability. The almost complete absence of females within the larger size classes of tunas seems to be caused by differential natural mortality rather than differential growth or vulnerability to capture (Schaefer, 1998).

For *T. albacares*, a significant deviation from the expected 1 : 1 sex ratio in the 50- to 54.9-cm class (41.9% males) was observed, based on sex identifications through histological examinations of gonadal tissues (Schaefer, 1998). The preponderance of females in this length interval may be related to differences in growth rates between the sexes, but there is no empirical evidence to support that hypothesis at this time. A higher proportion of females in the smaller length classes has also been reported in other species of tunas, such as *K. pelamis* (Matsumoto *et al.*, 1984), but the determinations of sex in those studies were not based on histology, and the results should thus be considered dubious.

Most sex ratio data for tunas is reported as a by-product of investigations of spawning distributions, maturation, and fecundity and have not been particularly useful for investigating specific hypotheses. Investigations of sex ratio variation within schools, geographically, seasonally, and relative to reproductive activity require proper experimental designs, including adequate sample sizes and, most importantly, accurate determinations of sex. Analyses of sex ratios within schools of *T. albacares* appear to indicate that a significant factor in the observed sex ratio

is the presence of reproductively active females. There may be some segregation of tuna schools by sex and/or a higher proportion of males within schools with reproductively active females present. However, data sets obtained thus far are insufficient for resolution of these questions. Significant deviations from an expected 1 : 1 sex ratio within schools of *Engraulis mordax* have been attributed to behavioral factors such as spawning aggregations (Klingbeil, 1978). Schaefer (1998) indicates the importance of sample sizes in excess of 100 individuals per school in order to test such hypotheses. There is obviously a need to investigate further various aspects of differential sex ratios in tunas.

IX. REPRODUCTIVE ENERGETICS

The environmental temperature of tunas undoubtedly acts upon the reproductive system through the total metabolic rate. Temperature is a controlling factor in physiological processes, and tunas, which have high metabolic rates, have evolved to maximize reproductive success within their habitat (Brill, 1996). Tunas reproduce in regions of near-maximum sea-surface temperatures, permitting high spawning rates, reproductive output, and growth of their offspring.

There is very little information on the energetic costs of reproduction in tunas. Studies on other families of marine and freshwater fishes suggest, however, that the energetic costs associated with reproduction are significant, and can have important consequences affecting growth and mortality rates after sexual maturation (Wootton, 1990). Estimates of energetic costs for reproduction in tunas can be evaluated from a bioenergetics approach (Calow, 1985; Wootton, 1985). A bioenergetics approach to an evaluation of reproductive costs involves the use of an energy budget equation to account for energy gains, losses, and transfer within the organism. The equation for an energy budget follows the general form (Jobling, 1994)

$$R = F + U + M + P,$$

where R is the energy gained as food, F is the loss as feces, M is the energy cost of metabolism, U is additional energy loss, and P is growth or energy storage. The energy retained (P) can be differentiated as that of somatic growth (P_s) or energy channeled into reproductive growth (P_r).

The energetic costs of spawning by female and male *Thunnus albacares* (excluding behavioral activities) have been estimated (Schaefer, 1996, 1998). The energetic cost of spawning by the females is estimated by the product of relative batch fecundity and oocyte weight. The relative batch fecundity for *T. albacares* is 67.3 oocytes per gram of body weight (Schaefer, 1998), and the mean wet weight of a *T. albacares* oocyte in the migratory-nucleus stage, just before the hydration process begins, was estimated to be 0.157 mg (Schaefer, 1996). The

costs of a single spawning, the average daily cost, and that of the annual egg production are estimated to be 1.06, 0.7, and 254% of the body weight for the average female. The energetic cost of spawning by the males is estimated by subtracting the percentage of calculated body weight of the testes just after spawning from the percentage of body weight of the testes just before spawning occurs (Schaefer, 1996). The costs of a single spawning, the average daily costs, and that of the annual sperm production are estimated to be 0.34, 0.33, and 120% of body weight for the average male. Estimates of total daily and annual energy costs for reproductively active *T. albacares* can be obtained from the bioenergetics approach. Olson and Boggs (1986) estimated a mean daily ration of 5.2% body weight from a bioenergetics model incorporating energy expenditures for locomotion, metabolism, energy losses, and growth. The estimated mean energy expenditure for growth was about 0.41% of body weight per day. If the estimated daily cost of spawning for a female of about 0.7% of body weight per day is adjusted to account for waste losses, as in Olson and Boggs (1986), when added to the overall bioenergetics estimate a daily ration estimate of about 6.3% of body weight is obtained for total energy expenditure. The estimated daily ration to account for total energy expenditure in reproductively active males is 5.7% of body weight. The annual investments of energy in reproduction as a proportion of total energy is then estimated to be about 17.5 and 8.8% for the average reproductively active female and male, respectively. In comparison, the annual investment of energy in growth, from Olson and Boggs (1986), as a proportion of total energy is estimated to be about 10 and 11% for females and males, respectively. These estimates of the reproductive energetics of *T. albacares* must be interpreted cautiously. There are numerous assumptions and sources of imprecision in the parameter estimates to the model. These include the estimation of reproductive costs for males and metabolic rates in Olson and Boggs (1986) which do not fully account for the expected differences between juveniles and adults.

Although the energetic investment in eggs is greater than that in sperm, the energetic costs of engaging in reproductive behavior may be markedly higher for the males, and the overall investment in reproduction may be similar for the two sexes (Jobling, 1994). However, Wootton (1990) reports there to be no estimates of energy costs of courtship available, and it seems unlikely that they are a significant component of the energy budget. Wootton (1990) also states that, compared with sperm, each egg which provides the yolk required for development of the larvae to the point of being able to feed exogenously represents a massive cytoplasmic investment.

For *Katsuwonus pelamis,* Hunter *et al.* (1986) estimated the cost of a single spawning to be about 2% of the body weight. Based on an estimated spawning frequency of 1.18 days, the daily cost of spawning a single batch of eggs would be 1.7% of body weight per day. However, reproductive costs are probably overestimated because the relative batch fecundity estimate used 100 eggs per gram as

the estimated weight for a single egg. An estimate of the cost of a single spawning of *Euthynnus lineatus* (Schaefer, 1987) was reported to be 1.77% of the body weight. Based on an estimated spawning frequency of 2.1 to 5.7 days, the daily cost of spawning a single batch of eggs would be 0.31 to 0.84% of body weight per day. This estimate may also be biased because of the inherent problems in an estimation of spawning frequency based on the occurrence of fish with hydrated ovaries, as opposed to the postovulatory follicle method (Hunter and Macewicz, 1985a).

In northern anchovy, *Engraulis mordax,* the annual investment of energy in reproduction is estimated to increase from 8% of the body weight for 1- and 2-year-olds to 11% for 3- and 4-year-olds (Hunter and Leong, 1981). For female pike, *Esox lucius,* the annual investment of energy in reproduction increases from 0% of the body weight in the first year of life to 11 to 16% over the second, third, and fourth years (Diana, 1983a). Diana (1983b) reports that 6 to 18 times as much energy is deposited in the ovaries as in the testes. In males the annual allocation of energy to reproduction increases from 0% of the body weight in the first year of life to 4 to 5% in the second, third, and fourth years.

Somatic and gonadal growth can be considered to be in competition for limited resources, and a decrease is commonly seen in somatic growth rate when fish mature (Jobling, 1994). There are direct trade-offs between growth and reproduction, which are important components of fitness in fish, since energy channeled into the gonads detracts from somatic growth, and hence future fecundity (Ware, 1982; Roff, 1983). For *T. albacares* from the eastern Pacific the estimated lengths at which 50% of the females and males were mature were 92 and 69 cm, respectively (Schaefer, 1998). The potential advantage of males attaining sexual maturity at lesser lengths than females and contributing to the population's gene pool earlier is that it could increase the overall fitness and reproductive success of the population through exchange of genetic material among different age groups. An investigation of growth of *T. albacares* in the eastern Pacific based on otolith increments revealed sexually dimorphic growth, with size at age showing that young females are consistently larger than males of the same age. However, the growth curves cross one another at about 95 cm (2.12 years), and thereafter the males are larger than the females (Wild, 1986). It is possible that these differences in growth pattern are also related to the higher energetic costs of spawning for females. The inflection points in the nonlinear growth models fit to the separate data for females and males were at approximately 1.4 and 1.6 years of age, after which the growth rates begin to slow down. The approximate ages for the lengths at 50% maturity for females and males are estimated to be about 2.0 and 1.5 years of age. These results appear to indicate that the available energy for growth is being allocated toward gonadal development and maturation, and there is a potential decrease in the available energy at this point to maintain the high rate of somatic growth observed during the juvenile stage. The relationships between age,

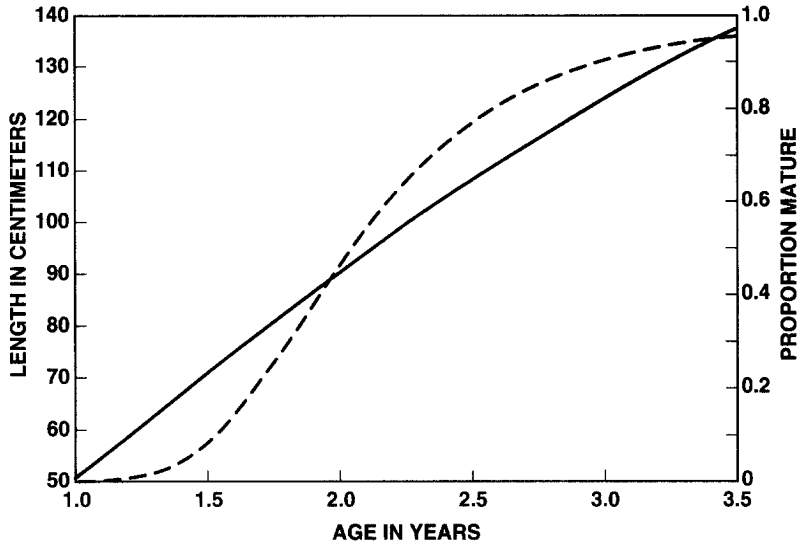


Fig. 8. Relationships for growth and maturation for female *Thunnus albacares* from the eastern Pacific. The growth schedule (solid line) is derived from the predictive function for age at length from Wild (1986), and the maturity schedule (broken line) is derived from predicting age at length, from Wild (1986), for the proportions mature at length from Schaefer (1998).

growth, and maturation in female *T. albacares* are illustrated in Figure 8. The minimum age at maturity in females is about 1.5 years of age, with 80% of the fish mature by about 2.5 years of age, and thus the onset of maturity occurs over a 1-year age span.

Because body size is an important determinant of both maturity and fecundity, variability in growth has potentially important consequences for the estimation of the productivity of the population. A common response to an increase in growth rate of fish is a decrease in the age of maturity. This is sometimes, but not always, accompanied by a change in the size at which the fish reaches sexual maturity (Wootton, 1990). Additional research to evaluate relationships between age, growth, and maturation in *T. albacares* has been conducted (Schaefer, 1998). The investigation consisted of examining geographic variation in growth and maturation of *T. albacares* in the eastern Pacific. The growth rate for the fish from the southern area are apparently greater than that for those from the northern area (where sea-surface temperatures are significantly cooler) until the fish are just under 3 years of age, at which time it decreases. Earlier onset of maturation was observed in the southern area. Differences in maturity appear to be expressed largely as shifts in the maturity schedule along the length axis, rather than as

changes in the shape of the curves once maturation is initiated. For each proportion mature (0.25, 0.50, and 0.75) the southern fish were shorter and younger than the northern fish. One of the energetic implications of these results for *T. albacares* is the fact that the analysis indicates that for the fish of the southern group, which have an earlier age at maturity, there is a decrease in the rate of growth, relative to the northern group, less than 1 year after maturation. This is as expected from energy allocation models of growth and reproduction in fish (Roff, 1983). Reproductive tactics of tunas are, no doubt, determined by the trade-offs between growth and reproduction. There may also be a decrease in survival associated with reproduction. However, in order to assess how growth and reproduction contribute to fitness in tunas it is necessary to know precisely the age- or size-dependent mortality functions (Roff, 1983), which are not available.

Aside from the cost of reproduction leading to an apparent decrease in growth, other costs of reproduction may include increases in mortality, or decreases in future fecundity (Wootton, 1990). The higher natural mortality rate for female *T. albacares* above 135 cm may be due to the much higher estimated energetic costs of spawning for females (0.7% of body weight/day) than for males (0.33% of body weight/day; Schaefer, 1996), and possibly to aggressive reproductive behavior of the males causing injuries to females before and during spawning events. Ware (1984) reports that several theoretical studies for iteroparous fishes demonstrate a link between reproduction and mortality, as both rates often increase with body weight and age during the later stages of the life cycle. Several theoretical studies on the energetic costs of reproductive effort for fish other than tunas have been conducted, but empirical studies are scarce. In laboratory experiments on the Japanese medaka, *Oryzias latipes*, which spawns daily, Hirschfield (1980) found mortality of females to be greatest at high levels of reproductive effort and temperature. The fish with higher reproductive effort lost more body weight, which reportedly led to mortality. Hirschfield also stated that individual fish may allocate insufficient energy to maintenance costs while reproductively active, even at the cost of an increased likelihood of mortality. Anderson and Ursin (1977) and Laevastu and Larkins (1981) have pointed out that spawning stress mortality may be a significant portion of senescent mortality in all fish. Pauly (1994), however, suggests that the "reproductive drain hypothesis" should be refuted for fishes in general; when considering the evidence for tunas, his arguments do not appear justified.

In mature marine species, reproductive growth will apparently continue to the detriment of somatic growth, but when food supplies are limited the reproductive growth will cease and atresia of yolked oocytes occurs. It appears that the greatest effect of food limitation on reproductive effort is a decrease in fecundity, which has been demonstrated in a number of fishes. For *T. albacares* no significant relationship was observed between relative fecundity and body weight, and it thus does not appear that larger females allocate relatively more energy to batch fe-

cundities than do smaller females. The average percent body weight for ovaries containing hydrated oocytes was 2.2% for a 90- to 100-cm female and 2.6% for a 140- to 150-cm female (Schaefer, 1998). Of the 345 females for which batch fecundity estimates were derived in that study, only 22 had alpha atresia present in the ovaries, but 18 of those, or 82%, had less-than-average batch fecundities. The process of atresia in the ovary of tunas is most likely an indicator of the energy reserves in somatic tissues in areas where sea-surface temperatures are consistently above minimum spawning temperatures. In areas where sea-surface temperatures fall below spawning temperatures, however, atresia most likely occurs even when energy reserves remain at reasonable levels to support continued reproductive activity. The low percentage, 7.5%, of reproductively active *T. albacares* females with minor alpha atresia indicates the apparent rapid cessation of reproductive activity once the process of atresia begins (Schaefer, 1998). However, in *Scomber japonicus,* alpha atresia of the advanced yolked oocytes was common throughout the spawning season—even early in the season with 12% of the females having high levels of alpha-stage atresia in their ovaries (Dickerson *et al.,* 1992).

Batch fecundity has been shown to depend upon ration in laboratory studies (Wootton, 1979). Bagenal (1969) found that brown trout, *Salmo trutta,* at higher rations contained significantly more eggs, but at a smaller size. Female haddock, *Melanogrammus aeglefinus,* which is a multiple spawner, produced fewer eggs at successive spawnings when fed at maintenance rations than did fish at high rations (Hislop *et al.,* 1978). Bagenal (1966) stated that populations of plaice which were under the best condition had the highest fecundities. Research conducted on rates of atresia based on starvation of captive *Engraulis mordax,* along with rates of recommencement of spawning after resuming feeding (Hunter and Macewicz, 1985b), provides insight into relationships between feeding, somatic energy reserves, and egg production. Similar laboratory studies for tunas should be encouraged, and also sampling of tissues from wild tunas, to investigate relationships between body composition and egg production. Controlled experimental studies on the allocation of energy among maintenance, growth, and reproduction with varying environmental conditions, including temperature and ration, would be most informative. However, the results of such experiments would need to be evaluated under natural conditions through field studies.

The apparent spawning strategy of tunas, which consists of spreading huge quantities of eggs over enormous areas, either continuously or for prolonged periods in high temperatures, is obviously intended to minimize risk in a highly variable and unpredictable environment (i.e., distributions of prey organisms and predators). In comparison, the related *Scomber* spp. spawns on a more restricted spatiotemporal scale within its habitat when seasonal zooplankton production is highest and temperatures are on the increase (Lambert and Ware, 1984). In the case of tunas, it appears that the limiting factor to maintain reproductive activity

is for the adults to locate and remain in areas of high concentrations of forage. In contrast *Scomber* has opted to focus its strategy on expending its reproductive energy seasonally, to potentially maximize survival of the larvae. In both species the strategies have apparently evolved, within their respective habitats, to exploit high temperatures which allow a high growth rate and optimize the chances for the larvae to pass quickly through their respective predatory fields (Lambert and Ware, 1984).

X. CONCLUDING REMARKS

Temperatures above 24°C appear to stimulate maturation and reproductive activity in tunas. The time of spawning appears to be modified by environmental temperature, with spawning of stocks occurring almost continuously in tropical regions, but at phase in the more northern and southern hemispheres. Whereas temperate marine pelagic fish release several successive batches of eggs over a period of a few months, during predictably high planktonic production, most tunas spawn batches at nearly daily intervals throughout most of the year and over extensive oceanic regions of highly unstable and fluctuating planktonic production. It is the asynchronous oocyte development in ovaries of tunas which enables them to employ the tactic of opportunistic oviposition.

The reproductive patterns of tunas are remarkably diverse, and their evolutionary basis involves the acquisition and allocation of energy resources to maintain high rates of growth and reproduction to survive within the environmental constraints of their respective habitats. We see clearly the divergence in life histories when focusing on the reproductive patterns and characteristics of two groups within the tribe, *Katsuwonus pelamis* and *Thunnus albacares* versus *Thunnus maccoyii, Thunnus orientalis,* and *Thunnus thynnus.* The members of the former group are distributed widely, and spend their lives in tropical and subtropical waters, reaching sexual maturity within 1 to 2 years, and then spawning continuously throughout the remaining few years of their lives. In contrast, members of the latter group are also found in tropical and subtropical seas, but have evolved to exploit highly productive temperate regions as well. They do not reach sexual maturity until several years of age, demonstrate directed spawning migrations, have restricted spatiotemporal spawning distributions, and may live for an additional 20 years after spawning.

A very limited amount of scientifically useful information is available on the reproductive biology for most tunas. Spawning distributions, maturity and fecundity schedules, and size-specific sex ratios have not been adequately investigated, and these important reproductive parameters which should be incorporated into statistical assessment models are essentially nonexistent. The greatest amount of useful information presently exists for *T. albacares, T. maccoyii,* and *K. pelamis,*

although even for these species the information is not complete. With respect to *T. albacares* and *K. pelamis,* parameters should be estimated for the stocks upon which large-scale commercial fisheries operate within the three major ocean basins (Atlantic, Indian, and Pacific). Furthermore, the lack of useful scientific information on the reproductive biology for *T. thynnus* in the Atlantic and Mediterranean is perplexing when considering the historical existence, commercial value, and management for this species.

The rational exploitation and responsible management of stocks of tunas are dependent on the understanding of their biology. Precise knowledge of reproductive biology, growth, and mortality of tunas is essential to conduct proper assessments. Studies focusing on the important reproductive parameters for stocks of commercially valuable species of tunas are needed, but only if proper experimental designs and methodologies are employed. Furthermore, complementary studies on growth and reproductive biology of tunas should be encouraged in attempts to elucidate these interdependent complex physiological processes which are the basis for quantitative ecological evaluations of the reproductive potential of tuna stocks.

ACKNOWLEDGMENTS

Thanks are extended to John R. Hunter and Beverly J. Macewicz for sharing their knowledge and enthusiasm on the reproductive biology of fish. I gratefully acknowledge the reviews of drafts of the manuscript by William H. Bayliff and two anonymous reviewers.

REFERENCES

Ahlstrom, E. H. (1971). Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. *Fish. Bull.* **69,** 3–77.

Ahlstrom, E. H. (1972). Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. *Fish. Bull.* **70,** 1153–1242.

Alheit, J., Cihanqir, B., and Halbeisen, H. (1987). Batch fecundity of mackerel, *Scomber scombrus.* ICES CM 1987/H, 46, 7 pp.

Anderson, K. P., and Ursin, E. (1977). A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorous circulation and primary production. *Medd. Dan. Fisk. Havunders. (Ny Ser.)* **7,** 319–435.

Bagenal, T. B. (1966). The ecological and geographical aspects of the fecundity of the plaice. *J. Mar. Biol. Assoc. U.K.* **46,** 161–186.

Bagenal, T. B. (1969). The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *J. Fish. Biol.* **1,** 167–182.

Baglin, R. E., Jr. (1982). Reproductive biology of western Atlantic bluefin tuna. *Fish. Bull.* **80,** 121–134.

Bara, G. (1960). Histological and cytological changes in the ovaries of the mackerel *Scomber scomber* L. during the annual cycle. *Rev. Fac. Sci. Univ. Istanbul Ser. B. Sci. Nat.* **25,** 49–91.

Bartoo, N., and Foreman, T. J. (1994). A review of the biology and fisheries for North Pacific albacore (*Thunnus alalunga*). *FAO Fish. Tech. Pap.* **336**(2), 173–187.

Batalyants, K. Ya. (1992). On the study of spawning frequency for bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*), based on the Atlantic longline fishery data. *ICCAT Coll. Vol. Sci. Pap.* **39,** 31–38.

Bayliff, W. H., Ed. (1980). Synopsis of biological data on eight species of scombrids. *Inter-Am. Trop. Tuna Comm., Spec. Rep.* **2.**

Bayliff, W. H., Ed. (1989). "Inter-American Tropical Tuna Commission, Annual Report for 1988." IATTC, La Jolla, CA.

Bayliff, W. H., Ed. (1994). "Inter-American Tropical Tuna Commission, Annual Report for 1993." IATTC, La Jolla, CA.

Bayliff, W. H., Ed. (1995). "Inter-American Tropical Tuna Commission, Annual Report for 1994." IATTC, La Jolla, CA.

Bayliff, W. H., Ed. (1998). "Inter-American Tropical Tuna Commission, Annual Report for 1996." IATTC, La Jolla, CA.

Boehlert, G. W., and Mundy, B. C. (1994). Vertical and onshore-offshore distributional patterns of tuna larvae in relation to physical habitat features. *Mar. Ecol. Prog. Ser.* **107,** 1–13.

Bogorov, V. G., and Rass, T. G. (1961). On the productivity and the prospects of fishing in the waters of the Indian Ocean. *Okeanologiya* **1,** 107–109.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. *Comp. Biochem. Physiol.* **113,** 3–15.

Buñag, D. M. (1956). Spawning habits of some Philippine tuna based on diameter measurements of the ovarian ova. *Philipp. J. Fish.* **4,** 145–177.

Calkins, T. (1980). Synopsis of biological data on the bigeye tuna, *Thunnus obesus* (Lowe, 1839), in the Pacific Ocean. *Inter-Am. Trop. Tuna Comm., Spec. Rep.* **2,** 213–259.

Calow, P. (1985). Adaptive aspects of energy allocation. *In* "Fish Energetics New Perspectives" (Tyler, P., and Calow, P., Eds.), pp. 13–31. Croom Helm, London.

Campbell, R. (1994). SBT length at maturity. Report of SBT Trilateral Workshop, Hobart, 4–17 February 1994. CSIRO Marine Research, Hobart, Tasmania.

Carey, F. G. (1973). Fishes with warm bodies. *Sci. Am.* **228,** 36–44.

Caton, A. E. (1991). Review of aspects of southern bluefin tuna: Biology, population and fisheries. *Inter-Am. Trop. Tuna Comm., Spec. Rep.* **7,** 181–350.

Cayré, P., and Farrugio, H. (1986). Biologie de la reproduction du listao (*Katsuwonus pelamis*) de l'Ocean Atlantique. *In* "Proceedings of the ICCAT Conference on the International Skipjack Year Program" (Symons, P. E. K., Miyake, P. M., and Sakagawa, G. T., Eds.), pp. 252–272. ICCAT, Madrid, Spain.

Clarke, T. A. (1987). Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. *Fish. Bull.* **85,** 127–138.

Clay, D. (1991). Atlantic bluefin tuna (*Thunnus thynnus thynnus* (L.)): A review. *Inter-Am. Trop. Tuna Comm., Spec. Rep.* **7,** 89–180.

Collette, B. B., and Nauen, C. E. (1983). "FAO Species Catalogue. Vol. 2. Scombrids of the World. An Annotated and Illustrated Catalogue of Tunas, Mackerels, Bonitos and Related Species Known to Date," FAO Fish. Synop. 125, Vol. 2. FAO, Rome.

Conover, D. A. (1985). Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: The Atlantic silverside *Menidia menidia*. *Fish. Bull.* **83,** 331–341.

Davis, T. L. O. (1995). Size at first maturity of southern bluefin tuna. Commission for the Conservation

of Southern Bluefin Tuna Scientific Meeting, 11–19 July 1995, Shimizu, Japan. Report CCSBT/SC/95/9, Far Seas Fish. Res. Lab., Shimizu.

Davis, T. L. O., Jenkins, G. P., and Young, J. W. (1990). Patterns of horizontal distribution of the larvae of southern bluefin (*Thunnus maccoyi*) and other tuna in the Indian Ocean. *J. Plankton Res.* **12,** 1295–1314.

Davis, T. L. O., Farley, J. H., and Bahar, S. (1998). Size partitioning by depth of southern bluefin tuna on the spawning grounds. Commission for the Conservation of Southern Bluefin Tuna Scientific Meeting, 23–31 July 1998, Shimizu, Japan. Report CCSBT/SC/98/5, Far Seas Fish. Res. Lab., Shimizu.

De Vlaming, V. L. (1983). Oocyte development patterns and hormonal involvements among teleosts. *In* "Control Processes in Fish Physiology" (Rankin, J. C., Pitcher, T. J., and Duggan, R., Eds.), pp. 176–199. Wiley, New York.

De Vlaming, V., Grossman, G., and Chapman, F. (1982). On the use of the gonosomatic index. *Comp. Biochem. Physiol.* **73,** 31–39.

Diana, J. S. (1983a). An energy budget for northern pike (*Esox lucius*). *Can. J. Zool.* **61,** 1968–1975.

Diana, J. S. (1983b). Growth, maturation and production of northern pike in three Michigan lakes. *Trans. Am. Fish. Soc.* **112,** 38–46.

Dickerson, T. L., Macewicz, B. J., and Hunter, J. R. (1992). Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus,* during 1985. *Calif. Coop. Oceanic Fish. Invest., Rep.* **33,** 130–140.

Farley, J. H., and Davis, T. L. O. (1998). Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii. Fish. Bull.* **96,** 223–236.

Ferraro, S. P. (1980). Daily time of spawning of 12 fishes in the Peconic Bays, New York. *Fish. Bull.* **78,** 455–464.

Fitzhugh, G. R., and Hettler, W. F. (1995). Temperature influence on postovulatory follicle degeneration in Atlantic menhaden, *Brevoortia tryannus. Fish. Bull.* **93,** 568–572.

Fonteneau, A., and Marcille, J., Eds. (1988). Ressources, peche et biologie des thonides tropicaux de l'Atlantique centre-est. *FAO Doc. Tech. Peches* **292.**

Goldberg, S. R., Alarcon, V. H., and Alheit, J. (1984). Postovulatory follicle histology of the Pacific sardine, *Sardinops sagax,* from Peru. *Fish. Bull.* **82,** 443–445.

Goldberg, S. R., and Au, D. W. K. (1986). The spawning of skipjack tuna from southeastern Brazil as determined from histological examination of ovaries. *In* "Proceedings of the ICCAT Conference on the International Skipjack Year Program" (Symons, P. E. K., Miyake, P. M., and Sakagawa, G. T., Eds.), pp. 277–284. ICCAT, Madrid, Spain.

Grier, H. J. (1981). Cellular organization of the testis and spermatogenesis in fishes. *Am. Zool.* **21,** 345–357.

Grier, H. J. (1993). Comparative organization of Sertoli cells including the Sertoli cell barrier. *In* "The Sertoli Cell" (Russell, L. D., and Griswold, M. D., Eds.). Cache River Press, Clearwater, FL.

Gunn, J. S., Davis, T. L. O, Farley, J. H., Clear, N. P., and Haskard, K. (1996). Preliminary estimations of the age structure of the SBT spawning stock (including a revised estimate of age at first spawning). Council for the Conservation of Southern Bluefin Tuna Scientific Meeting, 26 August–5 September 1996. Rep. CCSBT/SC/96/10. CSIRO, Hobart, Australia.

Harada, T., Murata, O., and Oda, S. (1980). Rearing and morphological changes in larvae and juveniles of yellowfin tuna. *Mem. Fac. Agric. Kinki Univ.* **13,** 33–36.

Harder, W. (1975). "Anatomy of Fishes" (Trans. by S. Sokoloff). E. Schweizerbar"tsche Verlagsbuchandlung (Nuagele V. Obermiller), Stuttgart.

Helfman, G. S. (1986). Fish behaviour by day, night and twilight. *In* "The Behaviour of Teleost Fishes" (T. J. Pitcher, Ed.), pp. 366–387. Croom Helm, London.

Hirschfield, M. F. (1980). An experimental analysis of reproductive effort and cost in the Japanese medaka, *Oryzias latipes. Ecology* **61,** 282–292.

Hisada, K. (1979). Relationship between water temperature and maturity status of bigeye tuna caught by longline in the central and eastern tropical Pacific Ocean. *Bull. Far Seas Fish. Res. Lab.* **17,** 159–175.

Hislop, J. R. G., Robb, A. P., and Gauld, J. A. (1978). Observations on the effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. *J. Fish Biol.* **13,** 85–98.

Hoar, W. S. (1969). Reproduction. *In* "Fish Physiology" (Hoar, W. S., and Randall, D. J., Eds.), Vol. 3, pp. 1–72. Academic Press, New York.

Hoar, W. S., Randall, D. J., and Donaldson, E. M., Eds. (1983). "Fish Physiology," Vol. 9. "Reproduction." Academic Press, New York.

Hunter, J. R., and Goldberg, S. R. (1980). Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax. Fish. Bull.* **77,** 641–652.

Hunter, J. R., and Leong, R. (1981). The spawning energetics of female northern anchovy, *Engraulis mordax. Fish. Bull.* **79,** 215–230.

Hunter, J. R., and Macewicz, B. J. (1985a). Measurement of spawning frequency in multiple spawning fishes. *U.S. Nat. Mar. Fish. Serv., Nat. Oceanic Atmos. Adm., Tech. Rep.* **36,** 79–94.

Hunter, J. R., and Macewicz, B. J. (1985b). Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax. Fish. Bull.* **83,** 119–136.

Hunter, J. R., and Mitchell, C. T. (1967). Association of fishes with flotsam in the offshore waters of Central America. *Fish. Bull.* **66,** 13–29.

Hunter, J. R., Lo, N. C. H., and Leong, R. J. H. (1985). Batch fecundity in multiple spawning fishes. *U.S. Nat. Mar. Fish. Serv., Nat. Oceanic Atmos. Adm., Tech. Rep.* **36,** 67–78.

Hunter, J. R., Macewicz B. J., and Sibert, J. R. (1986). The spawning frequency of skipjack tuna, *Katsuwonus pelamis,* from the South Pacific. *Fish. Bull.* **84,** 895–903.

Hunter, J. R., Macewicz, B. J., Lo, N. C. H., and Kimbrell, C. A. (1992). Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus,* with an evaluation of assumptions and precision. *Fish. Bull.* **90,** 101–128.

Idyll, C. P., and de Sylva, D. (1963). Synopsis of biological data on the blackfin tuna *Thunnus atlanticus* (Lesson) 1830 (western Atlantic). *FAO Fish. Rep.* **6,** 761–770.

Itano, D. G. (2000). The reproductive biology of yellowfin tuna (*Thunnus albacares*) in Hawaiian waters and the western tropical Pacific Ocean: Project summary. PFRP, JIMAR, UH, HI. JIMAR Contribution 00-328.

Iverson, R. T. B., Nakamura, E. L., and Gooding, R. M. (1970). Courting behavior in skipjack tuna, *Katsuwonus pelamis. Trans. Am. Fish. Soc.* **99,** 93.

Jobling, M. (1994). "Fish Bioenergetics." Chapman and Hall, London.

Juarez, M. (1978). Distribution de las larvas de la familia Scombridae en aguas adyacentes a las Bahamas. *Rev. Cuba Invest. Pesq.* **3,** 69–77.

Juarez, M., and Montolio, M. (1975). Distribucion espacial y cuantificacion de las larvas de la familia Scombridae en el Golfo de Mexico entre los meses de Mayo y Junio de 1974. INP/CIP, Cuba. *Res. Invest.* **2,** 128–129.

Kikawa, S. (1962). Studies on the spawning activity of Pacific tunas, *Parathunnus mebachi* and *Neothunnus macropterus,* by the gonad index examination. *Nankai Reg. Fish. Res. Lab., Occas. Rep.* **1,** 43–56.

Kikawa, S. (1966). The distribution of maturing bigeye and yellowfin and an evaluation of their spawning potential in different areas in the tuna longline grounds in the Pacific. *Rep. Nankai Reg. Fish. Res. Lab.* **23,** 131–208.

Klawe, W. L. (1963). Observations on the spawning of four species of tuna (*Neothunnus macropterus, Katsuwonus pelamis, Auxis thazard* and *Euthynnus lineatus*) in the eastern Pacific Ocean, based on the distribution of their larvae and juveniles. *Inter-Am. Trop. Tuna Comm., Bull.* **6,** 447–540.

Klawe, W. L., Pella, J. J., and Leet, W. S. (1970). The distribution, abundance and ecology of larval tunas from the entrance to the Gulf of California. *Inter-Am. Trop. Tuna Comm., Bull.* **14,** 505–544.

Klingbeil, R. A. (1978). Sex ratios of the northern anchovy, *Engraulis mordax,* off southern California. *Calif. Fish Game* **64,** 200–209.

Koido, T., and Suzuki, Z. (1989). Main spawning season of yellowfin tuna, *Thunnus albacares,* in the western tropical Pacific Ocean based on the gonad index. *Bull. Far. Seas Fish. Res. Lab.* **26,** 153–163.

Kume, S. (1967). Distribution and migration of bigeye tuna in the Pacific Ocean. *Rept. Nankai Reg. Fish. Res. Lab.* **25,** 75–80.

Labelle, M., Hampton, J., Bailey, K., Murray, T., Fournier, D. A., and Sibert, J. R. . (1993). Determination of age and growth of South Pacific albacore (*Thunnus alalunga*) using three methodologies. *Fish. Bull.* **91,** 649–663.

Laevastu, T., and Larkins, H. A. (1981). "Marine Fisheries Ecosystem: Its Quantitative Evaluation and Management." Fishing News Books, Farnham.

Lambert, T. C., and Ware, D. M. (1984). Reproductive strategies of demersal and pelagic spawning fish. *Can. J. Fish. Aquat. Sci.* **41,** 1565–1569.

Laroche, J. L., and Richardson, S. L. (1980). Reproduction of northern anchovy, *Engraulis mordax,* off Oregon and Washington. *Fish. Bull.* **78,** 603–618.

Lauth, R. R., and Olson, R. J. (1996). Distribution and abundance of larval scombridae in relation to the physical environment in the northwestern Panama Bight. *Inter-Am. Trop. Tuna Comm., Bull.* **21,** 125–167.

Lee, C. L. (1998). "A Study on the Feasibility of the Aquaculture of the Southern Bluefin Tuna, *Thunnus maccoyii,* in Australia." Agriculture Fisheries and Forestry, Australia, Canberra ACT.

Leis, J. M., Trnski, T., Harmelin-Vivien, M., Renon, J. P., Dufour, V., El Moudni, M. K., and Galzin, R. (1991). High concentrations of tuna larvae (Pisces: Scombridae) in near-reef waters of French Polynesia (Society and Tuamotu islands). *Bull. Mar. Sci.* **48,** 150–158.

Levitus, S., and Boyer, T. (1994). "World Ocean Atlas 1994," Vol. 4. "Temperature." NOAA Atlas NESDIS 4, U.S. Department of Commerce.

Magnuson, J. J., and Prescott, J. H. (1966). Courtship, locomotion, feeding and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). *Anim. Behav.* **14,** 54–67.

Magnuson, J. J., Block, B. A., Deriso, R. B., Gold, J. R., Grant, W. S., Quinn, T. J., Saila, S. B., Shapiro, L., and Stevens, E. D. (1994). "An Assessment of Atlantic Bluefin Tuna." National Academy Press, Washington, DC.

Marchal, E. (1963). Expose synoptique des donnees biologiques sur la thonine *Euthynnus alleteratus* (Rafinesque) 1810 (ouest Atlantique et Mediterranee). *FAO Fish. Rep.* **6,** 647–662.

Masui, Y., and Clarke, H. J. (1979). Oocyte maturation. *Int. Rev. Cytol.* **57,** 185–282.

Masuma, S., Tezuka, N., Teruya, K., Oka, K., Kanematu, M., and Nikaido, H. (1993). Maturation and spawning of reared yellowfin tunas at Yaeyama. In "Abstracts of the Annual Meeting of the Japanese Society of Scientific Fisheries," Tokyo, Japan; 2–5 April 1993.

Matsumoto, W. M. (1958). Description and distribution of larvae of four species of tuna in central Pacific waters. *Fish. Bull.* **58,** 31–72.

Matsumoto, W. M. (1966). Distribution and abundance of tuna larvae in the Pacific Ocean. *In* "Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu-Hilo, February 28–March 12, 1966" (Manar, T. A., Ed.), pp. 221–230. State of Hawaii, Honolulu.

Matsumoto, W. M., Skillman, R. A., and Dizon, A. E. (1984). Synopsis of biological data on skipjack tuna, *Katsuwonus pelamis.* U.S. Nat. Mar. Fish. Serv., Nat. Oceanic Atmos. Adm., Tech. Rep. NMFS Circ., Vol. 451, U.S. Department of Commerce.

McGowan, M. F., and Richards, W. J. (1989). Bluefin tuna, *Thunnus thynnus,* larvae in the Gulf Stream off the southeastern United States: Satellite and shipboard observations of their environment. *Fish. Bull.* **87,** 615–631.

McPherson, G. R. (1991). Reproductive biology of yellowfin tuna in the eastern Australian fishing zone, with special reference to the north-western Coral Sea. *Aust. J. Mar. Freshwater Res.* **42,** 465–477.

Miyabe, N. (1994). A review of the biology and fisheries for bigeye tuna, *Thunnus obesus*, in the Pacific Ocean. *FAO Fish. Tech. Pap.* **336**(2), 207–243.

Miyabe, N., and Bayliff, W. H. (1998). A review of the biology and fisheries for bigeye tuna, *Thunnus obesus,* in the Pacific Ocean. *Inter-Am. Trop. Tuna Comm., Spec. Rep.* **9,** 129–170.

Murray, T. (1994). A review of the biology and fisheries for albacore, *Thunnus alalunga*, in the South Pacific Ocean. *FAO Fish. Tech. Pap.* **336**(2), 188–206.

Nagahama, Y. (1983). The functional morphology of teleost gonads. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Donaldson, E. M., Eds.), Vol. 9A, pp. 223–275. Academic Press, New York.

Ng, T. B., and Idler, D. R. (1983). Yolk formation and differentiation in teleost fishes. *In* "Fish Physiology" (Hoar, W. S., Randall, D. J., and Donaldson, E. M., Eds.), Vol. 9A, pp. 373–404. Academic Press, New York.

Nikaido, H., Miyabe, N., and Ueyanagi, S. (1991). Spawning time and frequency of bigeye tuna. *Thunnus obesus. Nat. Res. Inst. Far Seas Fish., Bull.* **28,** 47–73.

Nishikawa, Y., and Ueyanagi, S. (1991). Morphological development of larvae of longtail tuna. *Bull. Nat. Res. Inst. Far Seas Fish.* **28,** 1–13.

Nishikawa, Y., Honma, M., Ueyanagi, S., and Kikawa, S. (1985). Average distribution of larvae of oceanic species of scombroid fishes, 1956–1981. *Far Seas Fish. Res. Lab., S Ser.* **12.**

Okiyama, M. (1974). Occurrence of the postlarvae of bluefin tuna, *Thunnus thynnus*, in the Japan Sea. *Japan Sea Reg. Fish. Res. Lab., Bull.,* **25,** 89–97.

Okiyama, M. (1979). Successful spawning of some holoepipelagic fishes in the Sea of Japan and zoogeographical implications. *Jpn.-Soviet Joint Symp. Aquaculture* **7,** 223–233.

Olson, R. J., and Boggs, C. H. (1986). Apex predation by yellowfin tuna (*Thunnus albacares*): Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Can. J. Fish. Aquat. Sci.* **43,** 1760–1775.

Orange, C. J. (1961). Spawning of yellowfin tuna and skipjack in the eastern tropical Pacific, as inferred from studies of gonad development. *Inter-Am. Trop. Tuna Comm., Bull.* **5,** 457–526.

Otsu, T., and Hansen, R. (1962). Sexual maturity and spawning of the albacore in the central south Pacific Ocean. *Fish. Bull.* **62,** 151–162.

Otsu, T., and Sumida, R. F. (1968). Distribution, apparent abundance, and size composition of albacore (*Thunnus alalunga*) taken in the longline fishery based in American Samoa, 1954–65. *Fish. Bull.* **67,** 47–69.

Pallarés, P., Pereira, J., Miyabe, N., and Fonteneau, A. (1998). Atlantic bigeye tuna: Overview of present knowledge (November 1996). *Inter-Am. Trop. Tuna Comm., Spec. Rep.* **9,** 20–80.

Pauly, D. (1994). "On the Sex of Fish and the Gender of Scientists." Chapman and Hall, London.

Quinn, T. J., and Deriso, R. B. (1999). "Quantitative Fish Dynamics." Oxford Univ. Press, New York.

Raju, G. (1960). A case of hermaphroditism and some other gonadal abnormalities in the skipjack *Katsuwonus pelamis* (Linnaeus). *J. Mar. Biol. Assoc. India* **2,** 95–102.

Ramon, D., and Bailey, K. (1996). Spawning seasonality of albacore, *Thunnus alalunga*, in the south Pacific Ocean. *Fish. Bull.* **94,** 725–733.

Ratty, F., Kelly, R., and Laurs, M. (1990). Gonad morphology, histology and spermatogenesis in the South Pacific albacore tuna, *Thunnus alalunga* (Scombridae). *Fish. Bull.* **88,** 207–216.

Richards, W. J., and Simmons, D. C. (1971). Distribution of tuna larvae (Pisces, Scombridae) in the northwestern Gulf of Guinea and off Sierra Leone. *Fish. Bull.* **69,** 555–568.

Richards, W. J., Simmons, D. C., Jensen, A., and Mann, W. C. (1969a). Tuna larvae (Pisces, Scombridae) collected in the northwestern Gulf of Guinea, *Geronimo* cruise 3, 10 February to 26 April 1964. *U.S. Fish Wildl. Serv., Data Rep.* **36.**

Richards, W. J., Simmons, D. C., Jensen, A., and Mann, W. C. (1969b). Larvae of tuna and frigate mackerel (Pisces, Scombridae) collected in the northwestern Gulf of Guinea, *Geronimo* cruise 4, 5 August to 13 October 1964. *U.S. Fish Wildl. Serv., Data Rep.* **37.**

Richards, W. J., Simmons, D. C., Jensen, A., and Mann, W. C. (1970). Larvae of tuna and frigate mackerel (Pisces, Scombridae) in the northwestern Gulf of Guinea and off Sierra Leone, *Geronimo* cruise 5, 10 February to 19 April 1965. *U.S. Fish Wildl. Serv., Data Rep.* **40.**

Richards, W. J., Jossi, J. W., and McKenney, T. W. (1974). Interim report on the distribution and abundance of tuna and billfish larvae collected during MARMAP operational test phase cruises I and II., 1972–1973. MARMAP Program Office, NMFS, Washington, DC.

Richards, W. J., Pothoff, T., and Kim, J. (1990). Problems identifying tuna larvae species (Pisces: Scombridae: *Thunnus*) from the Gulf of Mexico. *Fish. Bull.* **88,** 607–609.

Rodriguez-Roda, J. (1967). El atun, *Thunnus thynnus* (L.) del sur de Espana, en la campana almadrabera del ano 1966. *Invest. Pesq.* **31,** 349–359.

Roff, D. A. (1983). An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.* **40,** 1395–1404.

Rothschild, B. J. (1965). Hypotheses on the origin of exploited skipjack tuna (*Katsuwonus pelamis*) in the eastern and central Pacific Ocean. *U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish.* **512.**

Schaefer, K. M. (1987). Reproductive biology of black skipjack, *Euthynnus lineatus,* an eastern Pacific tuna. *Inter-Am. Trop. Tuna Comm., Bull.* **19,** 169–260.

Schaefer, K. M. (1996). Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares,* near Clipperton Atoll in the eastern Pacific Ocean. *Fish. Bull.* **94,** 98–112.

Schaefer, K. M. (1998). Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Inter-Am. Trop. Tuna Comm., Bull.* **21,** 201–272.

Schaefer, K. M. (1999). Comparative study of some morphological features of yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tunas. *Inter-Am. Trop. Tuna Comm., Bull.* **21,** 489–528.

Schaefer, K. M. (2001). Assessment of skipjack tuna (*Katsuwonus pelamis*) spawning activity in the eastern Pacific Ocean. *Fish. Bull.* **99,** 343–350.

Schaefer, M. B., and Orange, C. J. (1956). Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the eastern Pacific Ocean, by examination of gonads. *Inter-Am. Trop. Tuna Comm., Bull.* **1,** 281–349.

Shingu, C. (1978). Ecology and stock of southern bluefin tuna. Japan Association of Fishery Resources Protection. *Fish. Study* **31.**

Shomura, R. S., Majkowski, J., and Langi, S., Eds. (1994). Interactions of Pacific tuna fisheries. Vol. 2: Papers on biology and fisheries. *FAO Fish. Tech. Pap.* **336**(2).

Stéquert, B., and Marsac, F. (1986). La peche de surface des thonides tropicaux dans l'ocean Indien. *FAO Doc. Tech. Peches* **282.**

Stéquert, B., and Ramcharrun, B. (1996). Reproduction of skipjack tuna (*Katsuwonus pelamis*) from the western Indian Ocean. *Aquat. Living Resources* **9,** 235–247.

Stobberup, K. A., Marsac, F., and Anganuzzi, A. A. (1998). A review of the biology of bigeye tuna, *Thunnus obesus,* and the fisheries for this species in the Indian Ocean. *Inter-Am. Trop. Tuna Comm., Spec. Rep.* **9,** 81–128.

Suzuki, Z. (1994). A review of the biology and fisheries for yellowfin tuna, *Thunnus albacares,* in the western and central Pacific Ocean. *FAO Fish. Tech. Pap.* **336**(2), 108–137.

Suzuki, Z., Tomlinson, P. K., and Honma, M. (1978). Population structure of Pacific yellowfin tuna. *Inter-Am. Trop. Tuna Comm., Bull.* **17,** 273–441.

Takemura, A., and Oka, M. (1998). Immunochemical sexing of living yellowfin tuna, *Thunnus albacares* (Bonnaterre), using a vitellogenin-like protein. *Aquaculture Res.* **29,** 245–249.

Timohina, O. I., and Romanov, E. V. (1996). Characteristics of ovogenesis and some data on maturation and spawning of skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758), from the western part of the equatorial zone of the Indian Ocean. *In* "Proceedings of the Expert Consultation on Indian

Ocean Tunas, 6th session" (Anganuzzi, A. A., Stobberup, K. A., and Webb, N. J., Eds.), pp. 247–257. IPTP Coll. Vol. 9.

Tyler, C. R., and Sumpter, J. P. (1996). Oocyte growth and development in teleosts. *Rev. Fish. Biol. Fish.* **6,** 287–318.

Uchida, R. N. (1961). Hermaphroditic skipjack. *Pac. Sci.* **15,** 294–296.

Uchida, R. N. (1981). Synopsis of biological data on frigate tuna, *Auxis thazard*, and bullet tuna, *A. rochei*. *NOAA Tech. Rep. NMFS Circ.* **436.**

Ueyanagi, S. (1957). Spawning of the albacore in the western Pacific. *Nankai Reg. Fish. Res. Lab. Rep.* **6,** 113–124.

Ueyanagi, S. (1969). Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. *Bull. Far Seas Fish. Res. Lab.* **2,** 177–256.

Wallace, R. A., and Selman, K. (1981). Cellular and dynamic aspects of oocyte growth in teleosts. *Am. Zool.* **21,** 325–343.

Warashina, L., and Hisada, K. (1970). Spawning activity and discoloration of meat and loss of weight in the southern bluefin tuna. *Bull. Far Seas Fish. Res. Lab.* **3,** 147–165.

Ware, D. M. (1982). Power and evolutionary fitness of teleosts. *Can. J. Fish. Aquat. Sci.* **39,** 3–13.

Ware, D. M. (1984). Fitness of different reproductive strategies in teleost fishes. *In* "Fish Reproduction: Strategies and Tactics" (Potts, G. W., and Wootton, R. J., Eds.), pp. 349–366. Academic Press, London.

Watson, J. J., Priede, I. G., Witthames, P. R., and Owori-Wadune, A. (1992). Batch fecundity of Atlantic mackerel, *Scomber scombrus* L. *J. Fish Biol.* **40,** 591–598.

West, G. (1990). Methods of assessing ovarian development in fishes: A review. *Aust. J. Mar. Freshwater Res.* **41,** 199–222.

Wild, A. (1986). Growth of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean based on otolith increments. *Inter-Am. Trop. Tuna Comm., Bull.* **18,** 423–482.

Wild, A. (1994). A review of the biology and fisheries for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean. *FAO Fish. Tech. Pap.* **336**(2), 52–107.

Wootton, R. J. (1979). Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symp. Zool. Soc. Lond.* **44,** 133–159.

Wootton, R. J. (1982). Environmental factors in fish reproduction. *In* "Proceedings of the International Symposium on Reproductive Physiology of Fish" (Richter, C. J. J., and Goos, H. J. Th., Eds.), Wageningen, The Netherlands, 2–6 August 1982, pp. 210–219.

Wootton, R. J. (1985). Energetics of reproduction. *In* "Fish Energetics New Perspectives" (Tyler, P., and Calow, P., Eds.), pp. 231–254. Croom Helm, London.

Wootton, R. J. (1990). "Ecology of Teleost Fishes." Chapman and Hall, New York.

Yamada, T., Aoki, I., and Mitani, I. (1998). Spawning time, spawning frequency and fecundity of Japanese chub mackerel, *Scomber japonicus*, in waters around the Izu Islands, Japan. *Fish. Res.* **38,** 83–89.

Yamamoto, K., and Yoshioka, H. (1964). Rhythm of development in the oocyte of the medaka, *Oryzias latipes*. *Bull. Fac. Fish., Hokkaido Univ.* **15,** 5–19.

Yesaki, M. (1994a). A review of the biology and fisheries for kawakawa (*Euthynnus affinis*) in the Indo-Pacific region. *FAO Fish. Tech. Pap.* **336**(2), 388–408.

Yesaki, M. (1994b). A review of the biology and fisheries for longtail tuna (*Thunnus tonggol*) in the Indo-Pacific region. *FAO Fish. Tech. Pap.* **336**(2), 370–387.

Yesaki, M., and Arce, F. (1994). A review of the *Auxis* fisheries of the Philippines and some aspects of the biology of frigate (*A. thazard*) and bullet (*A. rochei*) tunas in the Indo-Pacific region. *FAO Fish. Tech. Pap.* **336**(2), 409–439.

Yoshida, H. O. (1966). Skipjack tuna spawning in the Marquesas Islands and Tuamotu Archipelago. *Fish. Bull.* **65,** 479–488.

Yoshida, H. O. (1979). Synopsis of biological data on tunas of the genus *Euthynnus*. *U.S. Nat. Oceanic Atmos. Adm., Tech. Rep. Nat. Mar. Fish. Serv., Circ.* **429.**

Yuen, H. S. H. (1955). Maturity and fecundity of bigeye tuna in the Pacific. *U.S. Fish. Wildl. Serv., Spec. Sci. Rep.* **150,** 1–30.

Yukinawa, M. (1987). Report on 1986 research cruise of the R/V *Shoyu Maru*. Distribution of tuna and billfishes larvae and oceanographic observation in the eastern Indian Ocean January–March, 1985. *Rep. Res. Div., Fish. Agency Jpn.* **61,** 1–100.

7

MECHANICAL DESIGN FOR SWIMMING: MUSCLE, TENDON, AND BONE

MARK W. WESTNEAT
STEPHEN A. WAINWRIGHT

I. Introduction
II. External Morphology: Body Form and Fin Shape
III. Axial Muscle: Myomeres and Myosepta
IV. Axial Muscle: Red Muscle Morphology
V. Axial Connective Tissues: Main Horizontal Septum
VI. Muscle Function: Tendon Linkages in the Horizontal Septum
VII. Muscle Function: Principles of Hydrostatic Pressure
VIII. Mechanical Design of the Caudal Fin Muscles and Tendons
IX. The Backbone and Vertical Septum
X. Summary and Future Research

The muscle, tendon, and bone of tunas and mackerels form a mechanical system specialized for both high-performance swimming and long-distance cruising. The axial musculature, connective tissues, and skeleton of scombrid fishes exhibit modifications of the basic actinopterygian design for swimming that highlight mechanisms for the generation and transmission of force from muscle to caudal fin. This chapter illustrates the axial morphology of scombrids and analyzes the mechanics of thunniform locomotion. The external body shape and tail morphology are described for a variety of scombrid fishes. We review the complex shapes of myomeres and myosepta in the mackerels and tunas and reveal the orientation of two major systems of collagen fibers in myosepta and horizontal septa with respect to points of attachment to skeleton and skin. Locomotor muscle is arranged in serially nested cones that are associated with complex arrays of connective tissue. The collagen fibers of myosepta, horizontal septa, and skin are the tensile elements that transfer locomotor forces from the contraction of myomeres to the backbone and caudal fin during locomotion. Locomotor muscle pulls against a three-dimensional structure of tendons, septa, and skin that is kept in tension by the radial expansion of the contracting muscle. The main horizontal

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

septum is formed by the convergence of myosepta and is likely to be the major transmitter of muscle force to the axial skeleton. The vertical septum is formed from the serial neural spines and a fabric of collagen fibers connecting them. We propose a biomechanical model for the function of the neural spines and vertical septum in energy storage and return in scombrids. A posterior system of muscles and tendons operates the lunate caudal fin in tunas and mackerels. A new mechanical model is proposed for the function of the caudal muscles in fine tuning the shape and motion of the caudal fin. The construction of biomechanical models allows the identification of several musculoskeletal mechanisms of locomotion in scombrid fishes that direct future research on muscle function. Key features of the locomotor design of tunas, mackerels, and outgroups are highlighted on a phylogeny to identify the major evolutionary stages in the functional morphology of scombrid locomotion.

I. INTRODUCTION

The locomotor system of fishes has emerged as a primary focus for the study of vertebrate biomechanics because investigators are combining studies of muscle physiology, comparative morphology, hydrodynamics, and behavior to answer central questions about the mechanics of swimming. The morphology of fish locomotor systems plays a key role in our understanding of the mechanisms of propulsion in fishes. From body shape to the anatomy of fins, muscles, and vertebrae, the mechanical design of fishes has generated many of the central hypotheses now being tested in fish locomotion. This is particularly true for scombrid fishes (mackerels, tunas, and relatives) with their streamlined bodies, propeller-like tails, and the unique structure and function of tuna muscle and connective tissues. Thus, this chapter presents the comparative morphology of tunas and their relatives from the perspective of mechanical designs that contribute to swimming performance. Tracing the evolution of key structural features on a phylogenetic hypothesis (Figure 1) reveals several stages in the modification of the high-performance scombroid locomotor design.

All scombrid fishes swim by generating waves of undulation along the length of the body and producing lateral thrusts of the tail. Studies of the kinematics of mackerel indicate that mackerels swim by body undulation in which significant body bending occurs. Tailbeat frequency is relatively high (up to 15 Hz), length-specific wavelength is about 1.0, and wavelength is longer than stride length, the distance traveled in one tailbeat cycle (Videler and Hess, 1984; Wardle and Videler, 1993). Tuna swimming is performed with tailbeat frequencies and amplitude ranges that are similar to other scombrids, but with significantly longer propulsive wavelength and maximum stride length values (Dewar and Graham, 1994). These behavioral studies suggest that tunas are stiffer and bend their ver-

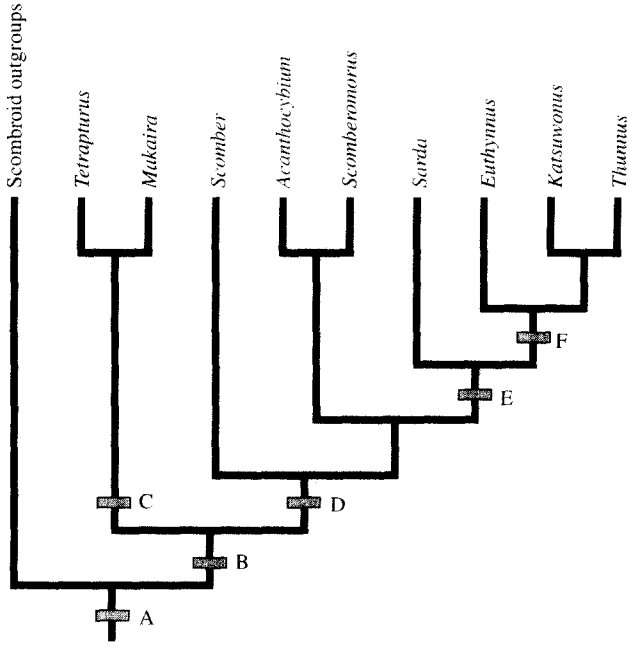


Fig. 1. Phylogenetic hypothesis of relationships for some of the scombroid fishes for which we have data on locomotor morphology. Changes in characters of locomotor structure and swimming mode are indicated on the tree. Tree is for a subset of taxa reviewed by Collette (1997). (A) Characteristics of most fishes: myomeres arranged in nested cones, slow oxidative red muscle laterally positioned, horizontal and vertical septa function as force transmission systems, and caudal fin forked or paddle shaped. (B) Anterior-pointing cones (APCs) elongate, main horizontal septum (MHS) hypertrophied, great lateral tendon (GLT) hypertrophied, increase in aspect ratio (AR) of forked and lunate tails, and caudal fin with rays modified as flaps. (C) Undulatory locomotion, highest AR caudal fins, neural spines platelike, and extremely elongate muscle cones. (D) Carangiform locomotion, and neural spines strongly curved posteriorly. (E) Thickened body, internalized red muscle, and reduction of hypochordal longitudinalis (HL) muscle. (F) Thunniform locomotion, high-AR caudal fin, fully internal red muscle, elongate APCs, endothermy, long, low-angled posterior oblique tendons, hypural plate fused, caudal keel with joint, and HL ligamentous.

tebral columns less than mackerels while attaining similar high-performance locomotion. Biomechanical analyses indicate that scombrid locomotion depends critically on the transmission of forces from locomotor muscle to the backbone via connective tissues, including the myosepta, the horizontal and vertical septa, and the skin (Wainwright, 1983; Westneat *et al.*, 1993). These hypotheses have received support from recent physiological studies that correlated muscular con-

traction patterns with the kinematics of tunas during swimming (Knower *et al.*, 1999; Shadwick *et al.*, 1999).

A detailed understanding of the mechanisms of swimming in tunas requires additional study of the functional morphology of axial muscle, connective tissue, and skeletal support. Previous research on the locomotor morphology of scombrid fishes (Collette, 1978; Fierstine and Walters, 1968; Graham *et al.*, 1983; Kafuku, 1950; Kishinouye, 1923; Nursall, 1956; Westneat *et al.*, 1993) identified the key components of the musculature, connective tissues, vertebral column, and caudal skeleton that are involved in high-performance swimming of tunas. The position of slow oxidative or "red" muscle has been a strong focus of this research due to its role in thermogenesis in tunas (Altringham and Block, 1997; Block, 1991; Carey, 1981; Graham, 1975; Rayner and Keenan, 1967). However, biomechanical explanations of red muscle position and caudal fin musculoskeletal design have not been proposed, and further research on myomere shape, connective tissue linkages, and vertebral mechanics will be necessary to develop a testable theory for the mechanical design of tunas and mackerels.

This chapter contributes to a theory of scombrid locomotor mechanics by summarizing recent work on morphology and modeling of scombrid fishes and presenting new data on the functional morphology of myomeres, horizontal and vertical septa, and the caudal fin. We review the literature on the structure of muscle in scombrid fishes and use morphometrics of myomere shape to make predictions about the generation and transmission of force during swimming. Linked with the study of muscle are the key anatomical features of the horizontal septum, including the robust system of tendons that connect myomeres to backbone and tail. To complement work on the horizontal septum, we describe the connective tissues of the vertical septum and propose a mechanism of energy storage and return involving the bending and twisting of neural spines. Also, we present new information on the muscles, tendons, and bone of the caudal fin and develop a biomechanical model of caudal fin function in scombrids. Finally, we trace the distribution of some of the major locomotor features onto a phylogeny of scombroid fishes to explore evolutionary patterns in the design for swimming.

II. EXTERNAL MORPHOLOGY: BODY FORM AND FIN SHAPE

The degree of streamlining of body shape, cross-sectional profile, and design of the caudal and pectoral fins are key features of the locomotor mechanism in tunas (Collette, 1978; Fierstine and Walters, 1968; Magnuson, 1978). Body profile and surface area are central to calculations of drag, and caudal fin shape is a key determinant of thrust. Scombrids range from anteriorly thickened bodies with nar-

row caudal peduncles and highly lunate tails, such as tunas, to more streamlined and slender bodies with relatively thicker peduncles and forked tails, such as the Spanish mackerels. No detailed study of morphometrics on body shape or fin shape has been performed for scombrids, although the methods of landmark morphometrics and shape analysis (Bookstein, 1991) would apply nicely to functional questions of body profile and fin shape.

Fortunately, several authors have published data on aspects of external morphology that are functionally relevant. Magnuson (1978) published a table of fineness ratios (length/thickness) that are used as a metric of streamlining. Fineness ratios ranged from about 4.5 in *Thunnus* and *Euthynnus* to 4.8 in *Auxis,* 5.6 in *Sarda,* 6.2 in *Scomber,* and 8.4 in *Acanthocybium.* Magnuson and Weininger (1978) estimated external shape and surface area by tracing photographs of seven species of tuna and applying a geometric model based on length, width, depth, and a positional estimate for maximum depth. Their results showed that body surface area was roughly proportional to the square of length, but that fin areas were proportional to the cube of length. A preliminary comparison suggested that for fish of the same length, the surface area of a mackerel was significantly lower than that of a bonito and a bigeye tuna, suggesting that direct measurements of surface areas and body profiles will be a critical data set for future hydrodynamic modeling. A phylogenetic perspective (Figure 1) reveals that most basal scombroid groups (Gempylids, Trichiurids, and the billfishes) tend to have elongate bodies, as do the mackerels (e.g., *Scomber, Scomberomorus*), and there is a trend toward anterior thickening of the body and narrowing of the caudal peduncle in the bonitos (*Sarda*) and tunas (*Euthynnus, Thunnus*).

Morphometrics of the caudal fin of scombrids have focused on aspect ratio, an estimate of the degree to which a fin is winglike. Aspect ratio (AR) is calculated as the fin span squared, divided by area. Aspect ratios were calculated by Fierstine and Walters (1968) and Nursall (1956), and Magnuson (1978) summarized available data. The aspect ratios of scombrids range from about 4 to 9, with the closely related billfishes such as the marlin (*Makaira*) reaching an AR of 10 or above (Figure 2). In general the mackerels (*Scomber, Scomberomorus*) have AR values at the lower end of the scale, although the wahoo (*Acanthocybium*) is part of the mackerel tribe Scomberomorini but has a higher AR of about 6. The bonitos (Sardini) such as *Sarda* tend to have intermediate ARs, and the tunas (*Auxis, Euthynnus,* and *Thunnus*) have slender caudal fins with relatively high spans, giving them ARs between 6 and 9. Some diversity is apparently present within each scombrid lineage, as Magnuson (1978) lists the AR of the bluefin tuna, *Thunnus thynnus,* as low, around 5.5. Phylogenetic comparison (Figure 1) indicates that high-AR tails have evolved at least three times in the scombroids—in the billfishes, the wahoo, and the tunas.

A complete survey of caudal fin shape variation in scombrids would contrib-

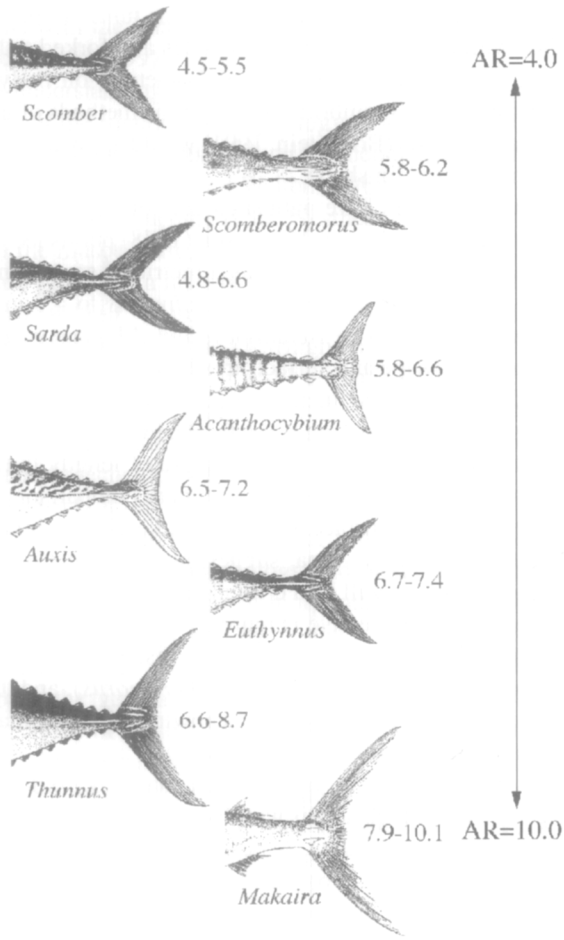


Fig. 2. Caudal fin shapes and aspect ratios (AR) ranging from low in the mackerels to high in the tunas and in the blue marlin. Caudal fin drawings adapted from Collette and Nauen (1983).

ute significantly to our knowledge of locomotor morphology. In addition to aspect ratio, there is clear variation in the angle of dorsal and ventral caudal fin lobes, and in the distribution of area of the fin. We discuss below the mechanisms of caudal fin musculature, which allow dynamic changes in fin shape during the tail stroke. As additional kinematic studies and swimming performance tests are done with living tunas, analyses of the hydrodynamics around the flapping caudal fin foil will reveal mechanisms of thrust production.

III. AXIAL MUSCLE: MYOMERES AND MYOSEPTA

Research on locomotor morphology in fishes has provided a basis for generating and testing hypotheses of mechanical design for swimming (Alexander, 1969; Dickson, 1996; Mos and Van der Stelt, 1982; Nursall, 1956; Wainwright, 1983; Westneat *et al.*, 1993; Willemse, 1959). A central goal of these studies has been to develop mechanical hypotheses for muscle function. Alexander (1969) considered the function of muscle segments (myomeres) by calculating muscle fiber trajectories from the myoseptum to the vertebral column. Modeling of the shortening of the fiber trajectories enabled calculation of the relative efficiency and power output of several different muscle fiber arrangements. The model of Mos and Van der Stelt (1982) predicted "infinitesimal" undulation movements through consideration of a horizontal strip of muscle, but this model excluded consideration of myomere geometry and the horizontal septum. Nursall (1956) insightfully treated the myomeres as providing the force for a lever system that bends the body due to serially arranged "flexures" of the myomeres. Although Nursall's model of bending did not consider the mechanism of force transfer through the complex morphology of myomeres and septa, the model included a means of calculating the mechanical advantage of the lateral tendons in the tail of a tuna. Wainwright (1983) considered the roles of many of the components (muscle, tendon, skin, and skeleton) likely to contribute to the mechanism of force transfer from muscle through tendon and skin to vertebrae and caudal fin. This work highlighted the need to include in the model the tendons and other tissues that contain collagen fibers and transmit forces. Finally, several Russian authors published work on the muscle tendon systems of the locomotor apparatus of fishes, including the Scombridae (Koval and Butuzov, 1986; Vronskii and Nikolaichuk, 1988).

Segmentally arranged myomeres with collagenous myosepta are present in all fishes, but in most scombroid fishes these structures are hypertrophied masses of muscle with stout connective tissues. These systems of oriented collagen fibers play a critical role in force transmission during swimming (Long *et al.*, 1996; Wainwright *et al.*, 1978; Westneat *et al.*, 1993). Connective tissue morphology in the axial locomotor system of scombroid fishes was described by Kishinouye (1923), Kafuku (1950), Fierstine and Walters (1968), and Westneat *et al.* (1993). Each of these studies identified connective tissues leading from the musculature to the backbone, and related these tissues to locomotion. Kafuku (1950) referred to a "sliding mechanism of two tendons" that attaches to the medial red muscle of tunas, and Fierstine and Walters (1968) described the structure of the caudal tendons, including the "great lateral tendon" of the tunas. Westneat *et al.* (1993) demonstrated that the collagen fibers forming the myosepta and the connective tissues of the horizontal septum, described below, are critical to the mechanism of

undulatory locomotion in scombrid fishes. This study showed that the connective tissues of the main horizontal septum are the mechanical center for transduction of muscle contraction into bending moments of the backbone. Below, we survey the complex shapes of myomeres and myosepta of scombroid fishes in relation to their connections to vertebrae and skin, and focus on the orientation of two sets of collagen fibers, the anterior and posterior oblique tendons, that are integrated into a single system for transmission of locomotor force.

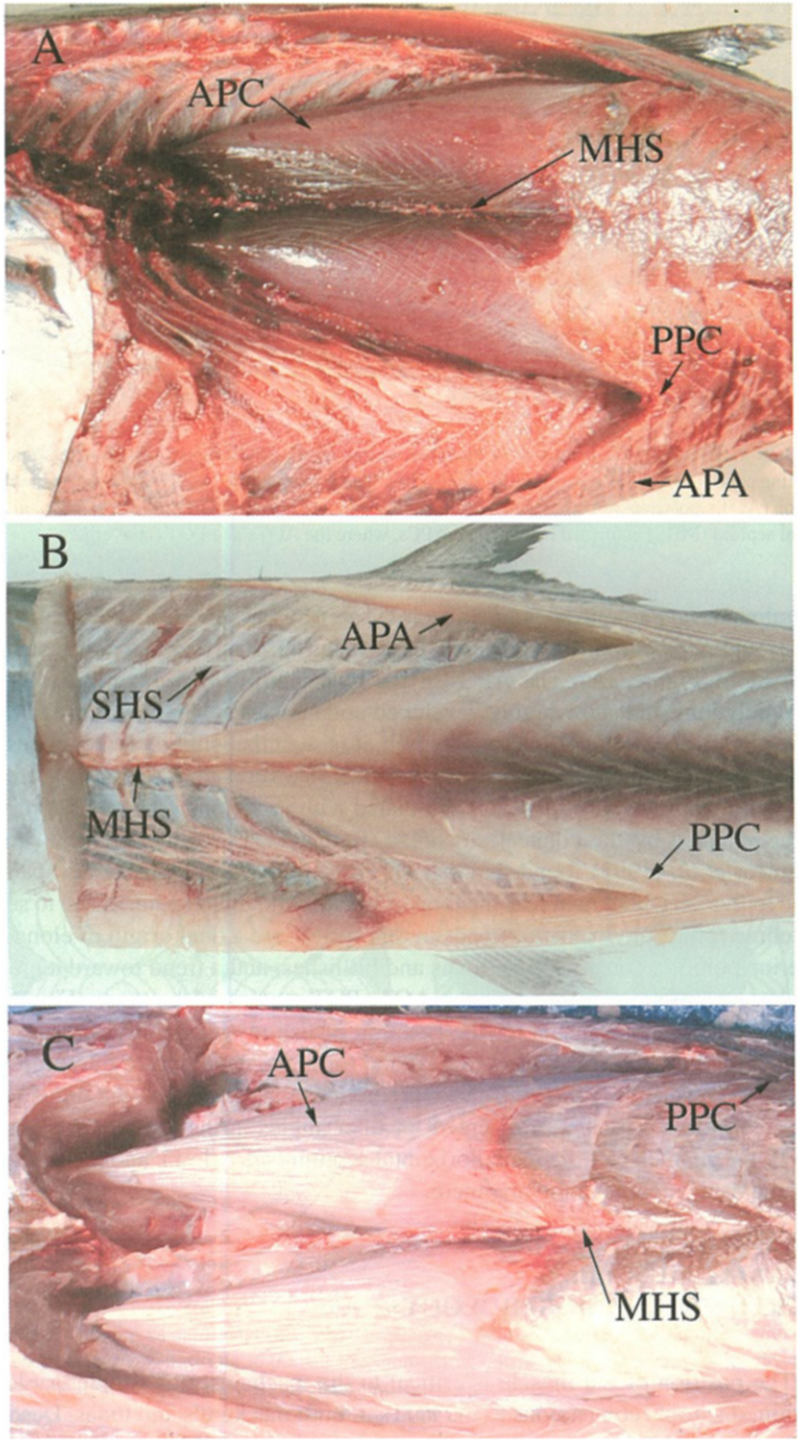
The basic design of myomeres and tendinous septa in the locomotor system is present in virtually all fishes (Nursall, 1956; Gemballa and Britz, 1998; Patterson and Johnson, 1995). A myomere is a set of muscle fibers that attach anteriorly to one myoseptum and posteriorly to the next myoseptum. Muscle fibers are generally oriented longitudinally, but their fiber angle with respect to the long axis of the fish varies across species and within a myomere (Alexander, 1969). In scombrid fishes a portion of each myomere is composed of red, slow-twitch aerobic muscle, and the rest of the myomere is fast-twitch anaerobic muscle (Hochachka *et al.,* 1978). Each myoseptum is a collagenous sheet separating two myomeres (Figures 3 and 4) that attaches to the backbone, vertical septum, and skin. The myoseptum of scombrid fishes is formed of four major connective tissue cones. Two of these point forward: one dorsal and one ventral to the horizontal septum. These are the anterior-pointing cones (APCs; Figures 3 and 4). The myoseptum has two large posterior-pointing cones (PPCs): one dorsal and one ventral to the APCs. The dorsalmost and ventralmost elements of the PPCs extend forward as the anterior-pointing arms (APAs; Figures 3 and 4).

Each myoseptum is a fabric of two tracts of collagen fibers, each tract having different orientations (Figures 3 and 4). One tract of myoseptal fibers is oriented generally longitudinally. A fiber starting near the tip of the anterior-pointing cone will either merge with the skin or converge medially between the APCs to form the posterior oblique tendon (POT; Figures 3–6). All POTs lie within the main horizontal septum. In the other tract of myoseptal collagen fibers, the fibers loop around the long axis of the APC at its base, where it meets the other APC. These fibers continue medially where they attach to vertebral centra as anterior oblique tendons (AOTs; Figures 3–6), forming a second component of the main horizontal septum. AOTs loop over the posterior half of the APCs and the anterior half of the PPCs and attach to the vertical septum as secondary horizontal septa. Both the longitudinal and circumferential tracts of fibers attach to the skin along the line of the skin's intersection with the APCs.

The cones and the connective tissues of the myoseptum that are visible in

---

Fig. 3. Lateral dissections of the left side of (A) *Euthynnus alletteratus,* (B) *Scomberomorus maculatus,* and (C) *Makaira nigricans,* showing the shape of a myomere in the midbody region. Anterior is to the left. APC, anterior-pointing cone; PPC, posterior-pointing cone; APA, anterior-pointing arm; MHS, main horizontal septum; SHS, secondary horizontal septum.


A
APC
MHS
PPC
APA
B
APA
SHS
MHS
PPC
C
APC
PPC
MHS

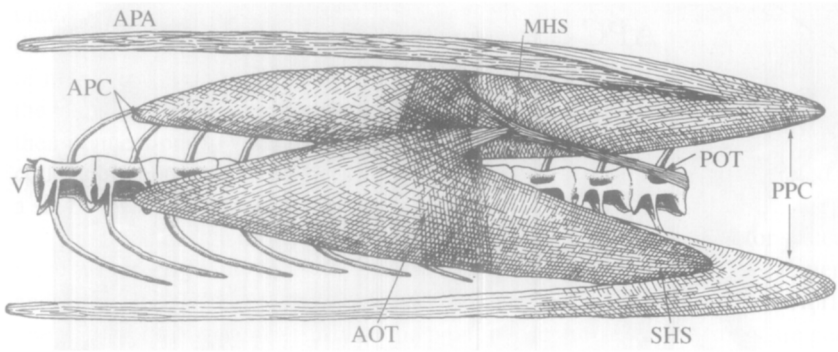


Fig. 4. Drawing of a myomere of *Scomberomorus cavalla* in oblique view showing anterior-pointing cones (APC), posterior-pointing cones (PPC), anterior-pointing arms (APA), anterior oblique tendon (AOT), posterior oblique tendon (POT), and secondary horizontal septa (SHS). The main horizontal septum (MHS) is formed between the APCs, where the AOTs and POTs converge.

lateral view vary among scombrid species. The APCs of *Scomber* (Westneat *et al.*, 1993) and *Scomberomorus* (Figure 3B) are shorter than those of tunas such as *Euthynnus* (Figure 3A). The APCs of the blue marlin (*Makaira nigricans*) are extremely long and show highly developed collagen sheets that converge to form strong POTs (Figure 3C). In cross-section, it is seen that slightly fewer cones are nested within a single transverse section of a mackerel than a tuna (Figure 5). Differences in myomere shape are associated with variation in the number of vertebrae spanned by the connections of AOTs and POTs to the vertebral centra. Westneat *et al.* (1993) found that the AOT–POT "loop" of mackerels spanned three to five vertebrae, whereas the loop of bonitos and tunas spanned five to seven vertebrae. Thus, phylogenetic trends in this system are a dual origin of elongated anterior-pointing cones, in both tunas and billfishes, and a trend toward a greater number of vertebrae spanned by the AOT–POT system in the tunas (Figure 1). Current quantitative models for the function of fish myomeres in exerting force through tendons (Westneat *et al.*, 1993) and through generation of intramuscular pressure (Westneat *et al.*, 1998) make predictions that depend on the dimensions of the muscle cones, the arrangement of fiber angles in the muscle (Alexander, 1969), the geometry of the main horizontal septum (see below), and the positions of red muscle regions in the myomere.

IV. AXIAL MUSCLE: RED MUSCLE MORPHOLOGY

The position of red muscle is critical to the mechanism of undulatory locomotion, due to its connections to the POTs in both mackerels and tunas. Descrip-

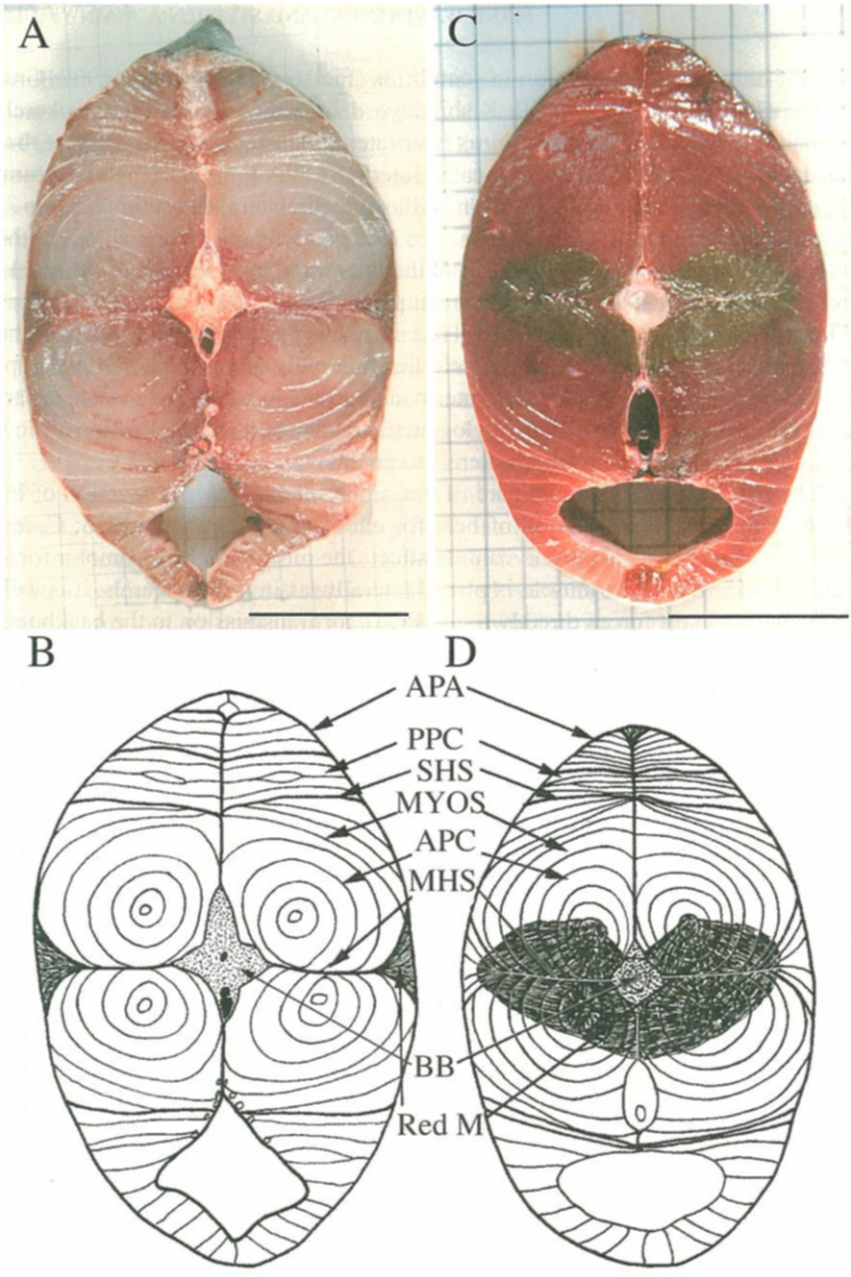


Fig. 5. Transverse sections of the body of a mackerel and a tuna (A and B, *Scomberomorus cavalla*, 770 mm (standard length); C and D, *Euthynnus alletteratus*, 630 mm SL). Drawings below each photograph illustrate important locomotor structures. Note the convergence of myosepta of anterior-pointing cones to form the main horizontal septum. APA, anterior-pointing arms; APC, anterior-pointing cones; BB, backbone; MHS, main horizontal septum; MYOS, myosepta; PPC, posterior-pointing cones; SHS, secondary horizontal septa.

tions of red muscle distribution in scombrids (Fierstine and Walters, 1968; Graham *et al.*, 1983; Kafuku, 1950; Kishinouye, 1923) have shown that mackerels such as *Scomber* and *Scomberomorus* have laterally placed red muscle tissue, but that tunas have their red muscle located internally, along the horizontal septum. This difference in red muscle position is illustrated in lateral dissection (Figure 3) in which the red muscle of the tuna is seen located along the medial slopes of the anterior-pointing cones (Figure 3A) and the lateral red muscle cone of the mackerel is visible close to the skin attachment point (Figure 3B). Transverse sections (Figure 5) also show that the mackerel red muscle is placed at the lateral tip of the horizontal septum, and tuna red muscle lies internally along the horizontal septum. Interestingly, *Sarda* shows an intermediate state, in which red muscle is partially internalized, so that a clear phylogenetic trend toward internalization of slow oxidative muscle is seen from mackerels to bonitos to tunas (Figure 1).

The red muscle of the myomere of tunas plays a dual role: production of locomotor forces and production of heat for endothermy (Graham, 1975; Carey, 1981). Placement of red muscle volume affects the mechanics of locomotor force transmission. When red muscle is placed laterally, as in the mackerels, it is well positioned to exert forces directly to the POTs for transmission to the backbone. Internal red muscle in tunas is always centered around the horizontal septum, and often has a significant volume located laterally. Thus, it is positioned to pull directly on the long tendons (AOTs and POTs) of the horizontal septum. The mechanical advantage of internal red muscle is less than that of lateral muscle due to its proximity to the backbone and due to the change in angle of insertion on the POTs. However, Altringham and Block (1997) showed that the internally placed red muscle generates significantly more power due to its warmth, suggesting a possible trade-off between force from mechanical advantage and force from contractile properties. Also, it is possible that internal red muscle in the posterior half of a tuna may partially bypass the POT system and exert force directly on the great lateral tendon that crosses the caudal peduncle and inserts on the hypural plate. Shadwick *et al.* (1999) suggested that there may be shear between red and white muscle components of the myomere due to the transmission of contraction forces posteriorly to the caudal fin. A comparative approach to red muscle design, twitch properties, and motor patterns is required to address questions of red muscle function in its various configurations.

V. AXIAL CONNECTIVE TISSUES: MAIN HORIZONTAL SEPTUM

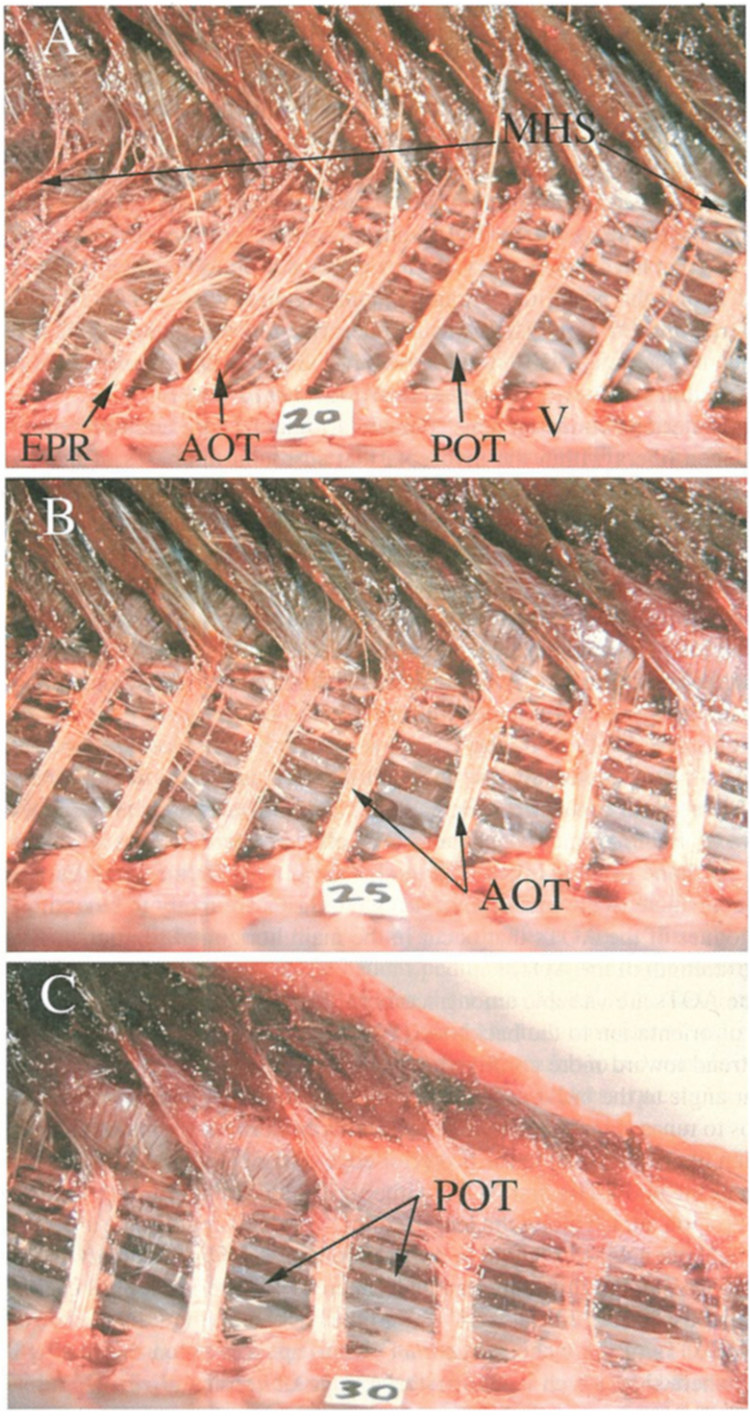
The horizontal septum of scombroid fishes is a spectacular fabric of stout tendons that is unparalleled among fishes. The main horizontal septum (MHS; Figures 3 and 5) is a layer of connective tissue that attaches to the backbone along the

midline, and extends laterally toward the skin between the anterior-pointing cones. The horizontal septum is formed by the convergence of myosepta from the APCs. The sheet of myosepta dives medially and attaches to the backbone (Figures 6 and 7). The MHS is the most conspicuous connective tissue structure, and is composed of sturdy white bands of parallel collagen fibers (Figures 6 and 7). These collagen fibers of the MHS come from two prominent connective tissue structures that have different orientations: the anterior oblique tendons (Figures 4, 6, and 7) and the posterior oblique tendons (Figures 4, 6, and 7). This crossed-fiber array of AOTs and POTs was first described by Kishinouye (1923) in tunas and then by Kafuku (1950) in mackerels. A comparative and mechanical analysis of this tendon system was presented in Westneat *et al.* (1993).

The anterior oblique tendons (Figures 4, 6, and 7) are circumferential bands of collagen fibers within the myosepta that surround the bases of the APC and PPC. The AOT fibers attach to the vertical septum and the neural and hemal spines, contributing to the secondary horizontal septa. Medial AOT fibers form discrete tendons that angle anteriorly as they dive to the backbone. The anterior oblique tendons are specialized, hypertrophied versions of epipleural and epicentral tendons that are present in a broad diversity of teleostean fishes. Patterson and Johnson (1995) surveyed these tendons and their ossifications as intermuscular bones in teleosts (incorrectly referring to the connective tissues as ligaments), and Gemballa and Britz (1998) added information to that survey by the use of polarized light. The AOTs in the horizontal septum are often closely associated with epipleural ribs. Epipleural ribs, when present in a particular segment, articulate with the vertebral centrum and extend laterally within the main horizontal septum (Figure 6). Every epipleural rib has AOT collagen fibers running along its edges. When the bone of an epipleural rib ends laterally, AOT fibers continue from its tip to contribute to the myoseptum. Epipleural ribs are likely to be ossified serial homologues of the AOTs that occur in the main horizontal septum, and increase tensile strength of the AOT.

The AOTs are variable among scombrid fishes in their number, structure, and angle of orientation to the backbone (Westneat *et al.*, 1993). There is a phylogenetic trend toward more cordlike and robust AOTs that insert at a more perpendicular angle to the backbone as one moves up the phylogeny from mackerels to bonitos to tunas (Figure 1). In *Scomber* and *Scomberomorus,* an AOT is a band of collagen fibers attaching to the posterior edge of the epipleural ribs in the anterior region of the body. The first AOTs without ribs, located in the anterior half of the caudal region, attach along the lengths of the vertebral centra. The anterior AOTs insert at about a 45°–55° angle to the backbone in *Scomber, Scomberomorus,* and *Acanthocybium,* but this angle gradually increases posteriorly, until each AOT is a continuous sheet of fibers at 75°–80° to the backbone (Figure 7).

The AOTs of the wahoo (*Acanthocybium*) are narrow on the first 9–11 vertebrae where they attach to the posterior edge of epipleural ribs (Figure 7). On

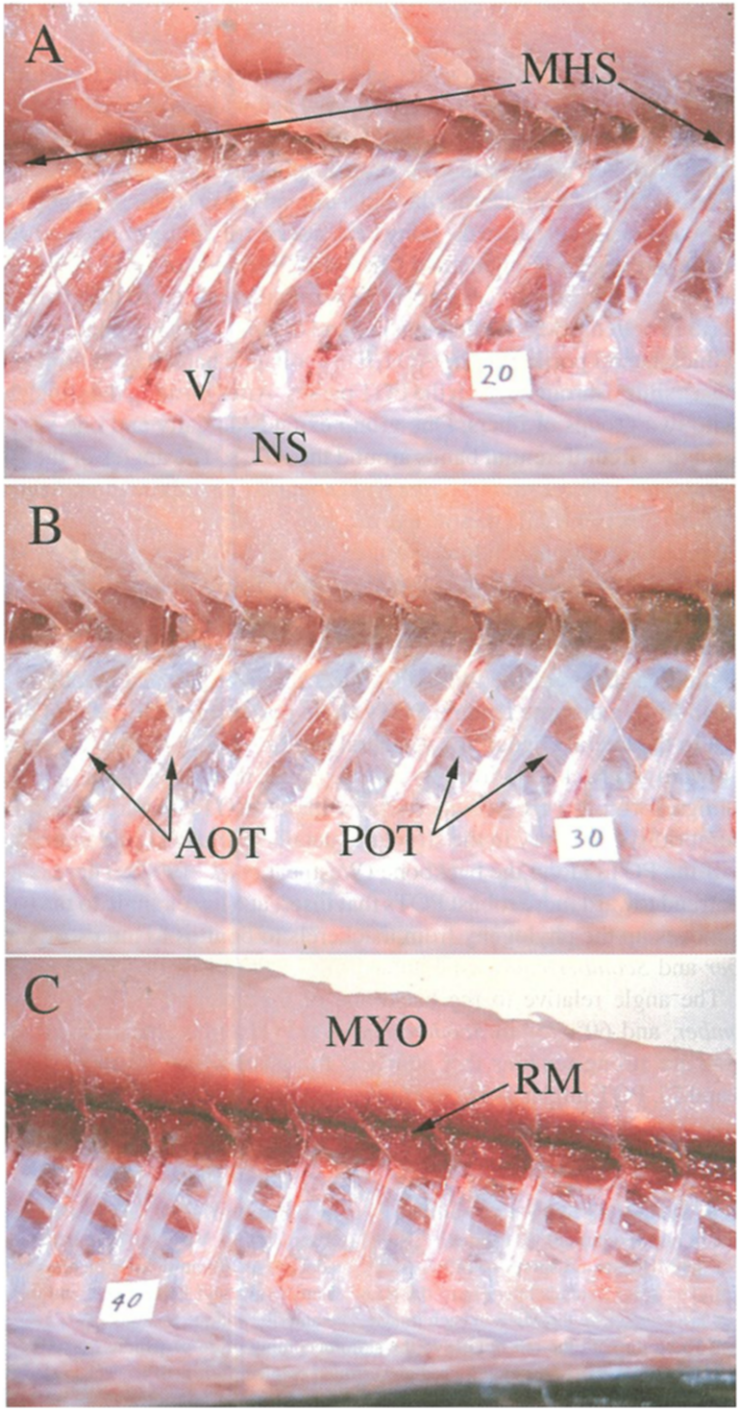

A
MHS
EPR
AOT
20
POT
V
B
25
AOT
C
POT
30

vertebrae 32–48, the AOTs are wider and insert on ½ to ¾ of the centrum length. At vertebrae 49–54, the AOTs become narrow again, correlated with broad insertions of POTs. The AOTs of *Sarda, Euthynnus,* and *Thunnus* (Figure 6) differ from those of the mackerels and wahoo in several ways. Most AOTs in these taxa surround epipleural ribs. Epipleural ribs and associated AOTs are present on the first 32 vertebrae, but are absent on the bony keel, a series of tightly connected vertebrae in the peduncle region (Collette and Chao, 1975). Bands of AOT fibers occur on both the posterior and the anterior edge of each epipleural rib. At the tip of each epipleural rib in both mackerels and tunas, a band of stout collagen fibers splays out to form a thick lateral portion of the AOT. This collagen band passes around a POT, forming a "sling" through which the POT passes. After forming the sling, the AOT splits into two groups of fibers. One group extends dorsally and one ventrally as they form the circumferential bands around the APCs. The angles of the AOTs of *Sarda, Euthynnus,* and *Thunnus* range from about 50° to the backbone anteriorly to about 80°–90° near the tail (Westneat *et al.,* 1993).

The posterior oblique tendons (Figures 4, 6, and 7) are a second set of robust bands of collagen in the main horizontal septum. These tendons are formed from the longitudinal collagen fibers of the myosepta of anterior-pointing cones as these fibers converge posteriorly and laterally. In the mackerels, the POTs start where the longitudinal fibers of the two APCs meet midlaterally, just medial to the red muscle, to form a discrete tendon. POTs angle posteromedially, within the MHS, to attach to the lateral edge of the vertebral centra. As a POT extends posteromedially toward the backbone from its lateral origin, it passes through the series of AOT slings, forming a crossed fiber array with the AOTs (Figures 6 and 7).

Scombrid species vary in the structural details of the POT and in the insertion points of the POTs along the backbone (Westneat *et al.,* 1993). There is a phylogenetic trend toward more robust POTs that insert at a lower angle to the backbone as one moves up the phylogeny from mackerels to bonitos to tunas (Figure 1). In *Scomber* and *Scomberomorus* the anterior-most POT is a thin band of collagen fibers. The angle relative to the backbone of the anterior POTs is around 45° in *Scomber,* and 60°–75° in *Scomberomorus.* POTs that attach to the posterior vertebrae are strong tendons that attach to the posterior ⅓ of the centrum (Figures 6 and 7). POT angles are acute in this region in the mackerels, ranging from

Fig. 6. Morphology of the main horizontal septum (MHS) in *Thunnus obesus* (845 mm SL) in the region of (A) vertebra 20, (B) vertebra 25, and (C) vertebra 30. View is of the right side, dorsal surface of the MHS (neural spines point toward the reader at the bottom of each picture). Anterior is to the left. The MHS extends laterally to the point where AOTs and POTs meet, and the reflected myomeres are seen above the MHS in each image. The anterior oblique tendons (AOT) run from the vertebrae (V) up through the red muscle to the skin, becoming more perpendicular to the vertebral column posteriorly. AOTs in the anterior region surround epipleural ribs (EPR). The posterior oblique tendons (POT) have a shallower angle of insertion on the vertebrae posteriorly.


A
MHS
V
20
NS
B
AOT
POT
30
C
MYO
RM
40

a minimum of 12° in *Scomberomorus* to around 20° in *Scomber*. The wahoo (*Acanthocybium*) POTs are similar in angle and position to those of the mackerels, although POTs in the wahoo often insert on more than one vertebral centrum, and posterior POTs are wide at the vertebral insertion, sending some fibers to the centra anterior and posterior of the main attachment point.

The POTs of *Sarda, Euthynnus,* and *Thunnus* are different in several ways from those of the mackerels. Tuna POTs have a low angle to the backbone, ranging from about 40° anteriorly down to 10°–15° posteriorly. Tuna POTs are long, spanning five or six AOTs. All POTs in the tunas have branching of the main bands of collagen fibers into smaller tendons (Figure 6). The anterior POTs insert on the centrum and on the ventral surface of an epipleural rib. The POTs that attach mainly to vertebrae 18–25 have up to four branches (Figure 6A). The effect of POT branching in tunas is that each segment of the axial skeleton is inserted upon by the connective tissues of multiple myomeres and each myomere pulls on multiple centra. Horizontal septum geometry and the lengths and angles of insertion of the AOTs and POTs are central components of biomechanical models of locomotor function in the Scombridae.

VI. MUSCLE FUNCTION: TENDON LINKAGES IN THE HORIZONTAL SEPTUM

Hypotheses regarding locomotor mechanics in fishes must include an explanation of the transfer of muscle force through the complex connective tissues of the myosepta and horizontal septum. Myosepta and horizontal septa are the tissues that transfer forces from the contraction of myomeres to the backbone and caudal fin during locomotion in scombrids (Fierstine and Walters, 1968; Wainwright, 1983; Westneat *et al.*, 1993). The geometry of the myomeres, the position of red muscle, and particularly the geometric conformation of crossed-fiber arrays of collagen in the main horizontal septum suggest three complementary mechanisms that contribute to body bending in scombrid fishes: (1) direct pull upon the array of posterior oblique tendons in the horizontal septum by myomeres, (2) increase in the tension of the connective tissue system by hydrostatic pressure created by

Fig. 7. Morphology of the main horizontal septum (MHS) in *Acanthocybium solandri* (1120 mm SL) in the region of (A) vertebra 20, (B) vertebra 0, and (C) vertebra 40. View is of the right side, dorsal surface of the MHS [neural spines (NS) point toward the reader at the bottom of each picture]. Myomeres (MYO) are reflected above the MHS. Anterior is to the left. The anterior oblique tendons (AOT) run from the vertebrae (V) up through the red muscle (RM) to the skin, becoming more perpendicular to the vertebral column posteriorly. Both AOTs and POTs are flatter and broader in the wahoo than in the tuna.

the swelling of contracting muscles, and (3) muscles that exert force directly onto the caudal fin. Quantitative models of these mechanisms permit calculations of mechanical advantage of muscle and can account for locomotor specializations occurring in scombrid fishes.

The mechanism of force transfer through the MHS via the POTs may be modeled as a lever system for exerting forces on the backbone to cause bending (Westneat *et al.,* 1993). The amount of force from contracting muscle that is applied to the backbone in a bending moment is determined by the length of the POT, the angle of the POT to the backbone, and the lateral distance from the backbone of the AOT–POT sling. A quantitative model of the main horizontal septum (Figure 8) makes it possible to predict the action of a muscle segment in terms of the amount of force or displacement moment applied to the vertebrae by the AOTs and POTs.

The mechanics of mackerel and tuna myomeres can be compared by using the velocity ratio (the reciprocal of the mechanical advantage) as a measure of the transmission of motion through the POTs (Westneat *et al.,* 1993). The velocity ratio is the ratio of output motion to input motion of the system, and lateral displacement is the sine of the AOT–backbone angle times the length of the backbone segment. The geometry of the system at rest is two-dimensional (Figure 8A), allowing calculation of the angles and distances involved in the force transmission system.

Shortening of red muscle pulls on the POT and draws it through the AOT slings (Figure 8B). The model calculates the total angular rotation of the backbone at the joint between vertebrae posterior to the insertion of an AOT (Figure 8B). If the total angular rotation over all joints is divided evenly over the three intervertebral joints spanned by the AOT and POT, the model can predict total angular rotation due to a single unit of muscle. Westneat *et al.* (1993) simulated 10% muscle contractions in a mackerel (*Scomberomorus cavalla*) and a tuna (*Euthynnus alletteratus*). For the mackerel, a muscle contraction of 5.5 mm caused a total angle change of about 10° distributed over three intervertebral joints, or an angle of about 3.3° at each intervertebral joint to produce the bent backbone. The lateral displacement of the backbone at the point of attachment of the POT was calculated to be 11.3 mm. The velocity ratio of the system is the ratio of output motion (11.3 mm) to input motion (5.5 mm), which equals 2.05.

In the *Euthynnus* horizontal septum, the POT is longer and has a lower angle to the vertebrae, and the effective bending force of the tendons spans more intervertebral joints (5–7) than does the mackerel (3). A 10% muscle shortening produces a total angle change among intervertebral joints of 18.2°. Distributed over five intervertebral joints, this results in a rotation at each joint of 3.6°. Displacement at the posterior end of the tuna POT is 25.8 mm, over twice the displacement result of the mackerel. The velocity ratio is also larger: 25.8 mm/7.5 mm = 3.4. Thus, the tuna has a displacement advantage that is one-third greater than the

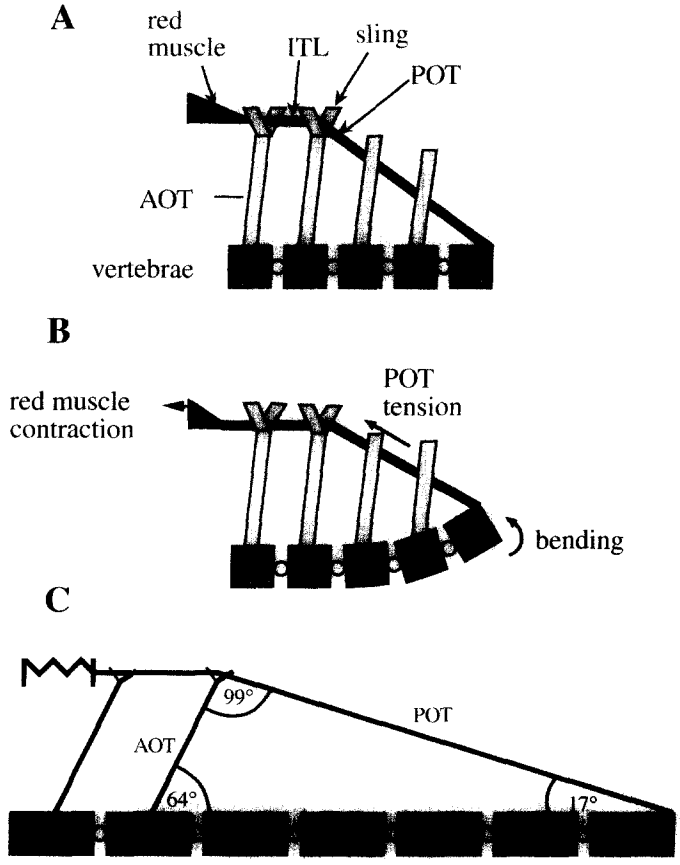


Fig. 8. Mechanical diagrams of the biomechanical model of the AOT–POT mechanism for vertebral bending in scombrid fishes. Anterior is to the left. (A) Geometric position of the mechanism of *Scomberomorus cavalla* at rest. (B) Contraction of red muscle through the AOT slings causes the backbone to bend. (C) The geometry of the MHS mechanism of *Euthynnus alletteratus* at rest. Morphometrics and angle calculations can be used in the model to calculate bending at each intervertebral joint.

mackerel. The mechanical (force) advantages of the two designs are the inverse of the velocity advantage (about 0.5 for the mackerel and 0.3 for the tuna).

Research on the mechanical properties of bending in backbones has shown that the angular stiffness of the backbone around the intervertebral joints determines the amount of mechanical work (force times distance) that muscle must do over a complete cycle of bending (Long, 1992). Because the backbones of scombrids, and particularly tunas, have many features that contribute to their flexural

stiffness, we suggest that undulation of the backbone in scombrids requires high force advantage rather than velocity advantage. The higher angle of the mackerel POT to the backbone is better suited to a forceful lateral pull than that of tunas. The long, low angled POT of tunas is perhaps better suited for energy storage in elastic recoil, because elastic recoil length is proportional to length of the tendon (Alexander, 1988). The angle of the POTs is variable from head to tail in scombrid fishes, starting high anteriorly and ending low posteriorly. This geometry suggests design for force advantage anteriorly, smoothly transforming to a displacement advantage posteriorly. Future research on this force transmission system might focus on quantitative analysis of the AOT–POT system in a broader range of scombrid fishes and other taxa. Equipped with biomechanical models, such research could predict the functional role of variation in connective tissue design, and the model could be tested with direct measurement of body bending and forces in the tendons of the posterior region of the fish.

VII. MUSCLE FUNCTION: PRINCIPLES OF HYDROSTATIC PRESSURE

In current models of myomere function and the mechanics of the horizontal septum (Figure 8), an important mechanism is that of maintaining the lateral position of the POT. This is the moment arm of force application to the backbone. The sling mechanism of the AOTs (Figure 8) functions as a tensile standoff that maximizes the mechanical advantage of the POT's lateral pull. By holding the AOT–POT junction away from the backbone, the sling prevents mediad displacement of the cradled POT during bending. This system is analogous to a "jib" mechanism used in mechanical engineering. A jib is an extra strut, usually with a pulley on the end, that is added perpendicular to the direction of force to increase the length of the effort arm of a lever (Vogel, 1988). The role of the AOT sling is thus to increase the moment arm of the force from the muscle applied to the backbone. In order for the AOT to hold the POT away from the backbone like a jib it is necessary to put the AOT into tension. The mechanism of production of tensile forces in the AOT involves hydrostatic pressure.

Hydrostatic pressure is generated for the purpose of putting connective tissues in tension by a mechanism involving the anterior-pointing cones of white muscle (Figures 3 and 4). The term "muscular hydrostat" (Kier and Smith, 1985) refers to muscular systems of constant volume that can exert lateral pressure forces when they contract. Kier and Smith (1985) demonstrated that decrease in length of a constant volume cylinder inevitably results in an increase in radius, and vice versa. This fact is used by organisms in numerous mechanisms for force transmission without rigid skeletal elements (Smith and Kier, 1989).

The same principle can be applied to the structure of myomeric cones, substi-

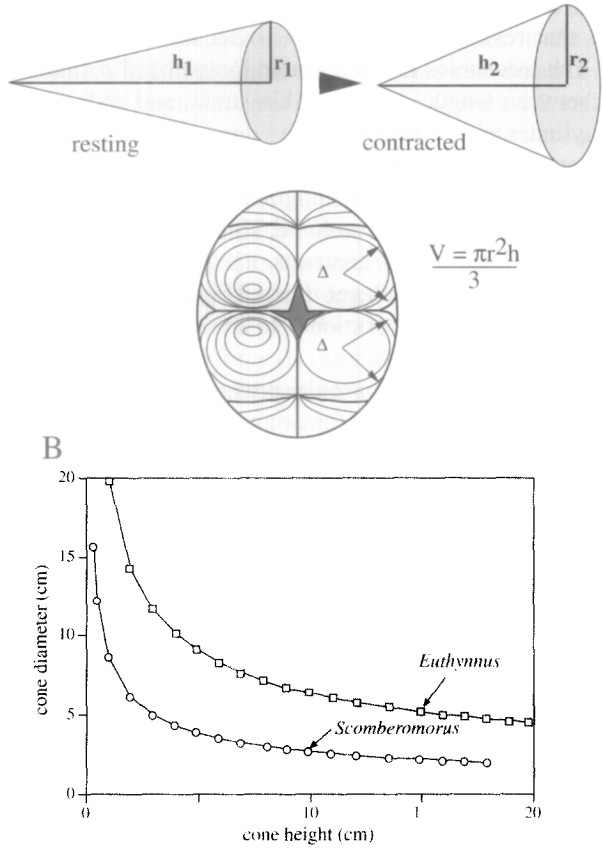


Fig. 9. (A) Mechanical diagram of the mechanism of generation of intramuscular pressure. Pressure changes by contraction and radial expansion of muscle cones. A cone of length (height) h and radius r_1 shortens, causing a local increase in radius to r_2. The radial swelling of the cones (shown in cross-section) causes an increase in hydrostatic pressure (P) in the space bounded by backbone, septa, and skin because these structures resist the expansion. (B) The relation between length and diameter for a cone of constant volume. Curves for actual cone volumes of *Scomberomorus cavalla* and *Euthynnus alletteratus* are shown, with the resting dimensions of real myomeric cones indicated.

tuting the equation for the volume of a cone for that of a cylinder (Figure 9A). When a cone of muscle contracts, the fact that the volume remains constant causes the cone to swell, increasing the radius of the cone's base (Figure 9). Westneat *et al.* (1993) used morphometric data on cone geometry to model the contraction of the anterior-pointing cone of *Scomberomorus cavalla* and *Euthynnus alletteratus*. Their calculations showed that a 10% muscle shortening for both species resulted in a 5% increase in radius.

Muscular hydrostats will stiffen as they contract if they are wrapped with high-tension fibers that resist radial expansion (Kier and Smith, 1985; Wainwright *et al.*, 1976). The mechanics of fiber-wound, pressurized cylinders depend upon the relations between length, diameter, skin stress, and wall thickness (Quillen, 1998). For a cylinder, circumferential stress due to internal pressure is twice longitudinal skin stress (Wainwright *et al.*, 1976). For a cone, the relationship between internal muscle pressure expanding laterally depends on total longitudinal muscle force, cone shape, and cone volume. This is so because when the constant-volume longitudinal muscle cone contracts, it expands radially and increases the stress of the circumferential collagen fibers (Figure 9; Westneat *et al.*, 1993). Internal muscle pressure is proportional to the degree of radial expansion of the cone.

A quantitative model of intramuscular pressure generation in fish muscle was developed by Westneat *et al.* (1998) for two nonteleostean actinopterygian fishes, *Polypterus* and *Amia*. Here we apply that model to mackerel and tuna muscle, in which the muscle cone of *Scomberomorus maculatus* has a volume of 19.5 cm^3 (h = 9.5 cm, r = 1.4 cm) and the cone of *E. alletteratus* a volume of 106.2 cm^3 (h = 15.0 cm, r = 2.6 cm). The model starts with the relationship between the length (h) and radius (r) of a cone-shaped, constant-volume muscular hydrostat (Figure 9). The volume of a cone is

$$V = \frac{\pi r^2 h}{3} \tag{1}$$

For a muscle cone of constant volume V, the relation between height and radius of the cone is

$$r = \sqrt{\frac{3V}{\pi h}} \tag{2}$$

This equation, when solved for a range of cone shapes with the volume of the scombrid cones (Figure 9B), reveals that changes in cone length, due to muscle contraction, translate into substantial radial expansion over a limited range of cone geometries. The resting geometries of the mackerel and tuna muscle cones are both positioned in the region of the curve where muscle shortening begins to be transmitted into increasing radial force, but before the exponentially increasing slope of radial expansion (Figure 9B). Thus, changes in intramuscular pressure occur without large changes in cone dimensions.

To calculate longitudinal muscle force, we used the equation of Calow and Alexander (1973) for a muscle whose fibers are at an angle to the primary direction of force,

$$F_l = \frac{V}{d} \cdot \delta \sin 2\alpha \tag{3}$$

where V = volume, d = diameter, δ = muscle fiber force, and α = muscle fiber angle to the long axis of the muscle. We used Altringham and Johnston's (1982)

estimate of muscle fiber force per unit area in fish white muscle: 200 kN/m^2, and Alexander's (1969) measurements of muscle fiber angles in the myomeres of *Scomber scombrus* (30°). Longitudinal muscle forces calculated using this equation for the cones of *S. maculatus* and *E. alletteratus* were 1.2 and 3.5 N (newtons), respectively. Muscle force and fiber angle will likely vary among species and affect the force of muscle contraction.

In a cone-shaped muscular hydrostat, changes in longitudinal force are transmitted to radial force by the relationship between cone length and cone diameter (Figure 9B). Kier and Smith (1985) suggested that this mechanism in cylindrical muscular hydrostats is similar to that of a lever system, where the dimensions of the hydrostat determine lever mechanics. For a lever, the output force transmission (F_o) equals the product of input force (F_i) and in-lever length (L_i) divided by out-lever length (L_o). We propose that the transmission of force from longitudinal to radial is proportional to the change in cone dimensions during a muscle contraction. We calculated radial force by the equation

$$F_r = F_l \cdot \frac{\Delta h}{\Delta d} \tag{4}$$

Radial muscle forces for the average cones of *S. maculatus* and *E. alletteratus* were 7.6 and 18.8 N. These data illustrate that longitudinal shortening forces can be magnified by the properties of a fiber-wound, constant-volume, hydrostatic muscle, similar to the properties of fiber-wound cylinders (Wainwright *et al.*, 1976). The force transmission advantage ($\Delta h/\Delta d$) of *S. maculatus* was 6.2, whereas that of *E. alletteratus* was 5.3.

To compute pressure in kilopascals (kilonewtons per square meter), we divided radial force by the surface area of the curved portion of the cone:

$$SA = \pi r l, \text{ where } l = \sqrt{r^2 + h^2} \tag{5}$$

Pressures calculated using the model for the average cones of *S. maculatus* and *E. alletteratus* were 156 and 130 kPa (slightly over 1 atm of pressure). These estimates depend upon little or no collagen fiber extension, in which the Young's modulus (E = stress/strain) is high. These predicted values are in the range of intramuscular pressures measured in sharks (Wainwright *et al.*, 1978) and in basal actinopterygian fishes (Westneat *et al.*, 1998).

The functional role of intramuscular pressure is to expand radially and increase the stress of the circumferential AOT fibers (Figures 3–6). Modeling results are consistent with the hypothesis that the AOT must be put into tension to act as a jib for the action of the POT, thus maximizing the amount of lateral force applied to the backbone. The amount of tension required in the AOT during locomotion is likely to be affected by the degree of support given by epipleural ribs, and by the relative force or velocity advantage of the POT (i.e., POT angle). If, however, only red muscle fibers contract during locomotion, then the mechanism of the anterior-pointing cones will function somewhat differently. In mackerels,

most red muscle lies laterad of the APC, in a separate region along the lateral midline (Figure 5). Contraction of this muscle would contribute little to increased pressure in the APC. The red muscle of tunas, on the other hand, is located medially within the boundary of the APC myosepta (Figure 5). Contraction of tuna red muscle will cause increased pressure within the APCs and increased tensile forces in the AOT. This may contribute to the higher apparent stiffness of the anterior portion of the tuna's body during locomotion.

An additional physical principle influences the way in which oriented collagen fibers of AOTs and those within the skin can be put into useful tension by hydrostatic pressure created by contracting muscle. The skin of a pressurized, constant volume cylinder reinforced by a crossed helical fiber array and inflated circumferentially will decrease in length with a force that is the circumferential force multiplied by the tangent of the fiber winding angle (Wainwright *et al.*, 1978). The crossed helical collagen fiber array in the skin of scombrids, with angles of 55° to the long axis and higher, ensures that longitudinal strains will be larger than circumferential strains. Because this fiber arrangement constrains extension of the radius of the main APCs and of the muscle mass in general, the swelling of the contracting muscle is responsible for putting the entire connective tissue array, including horizontal septa and skin, into tension.

Phylogenetic analysis of the mechanisms by which fish muscular hydrostats function must await further testing of the model and survey of cone shapes among taxa. Further study of muscle pressure variation and myomere morphology will reveal the effects of cone geometry on intramuscular pressure mechanisms across taxa and help to refine mechanical models of pressurized vertebrate musculoskeletal systems. To test hypotheses of this model, subdermal pressure measurements similar to those recorded for sharks (Wainwright *et al.*, 1978) and for basal actinopterygians (Westneat *et al.*, 1998) should be recorded among scombrid species.

VIII. MECHANICAL DESIGN OF THE CAUDAL FIN MUSCLES AND TENDONS

The functional morphology of fish caudal fins has been studied in a variety of fish taxa (Bainbridge, 1963; Nursall, 1963; Videler, 1975; Lauder, 1989), but few studies have considered the role of internal caudal structure for the mechanisms of propulsion in scombrids (Fierstine and Walters, 1968; Gibb *et al.*, 1999). In scombrid fishes, large tendons from the myomeres attach in the caudal region, and there is a set of muscles in the caudal peduncle and the fin that are separate from the serial myomeres. There are thus two systems controlling caudal fin propulsion—myomeric tendons powered from body muscle, and the mechanical design of intrinsic caudal muscles and their tendinous insertions on the fin.

In the caudal peduncle of both mackerels and tunas, the terminal five to six myosepta lack POTs, AOTs, and circumferential fibers. Nevertheless, the conver-

gence of myosepta to form locomotor tendons is particularly striking in the caudal region, where three robust collagenous structures are present: (1) the subdermal sheath (SDS), (2) the great lateral tendon (GLT), and (3) the medial caudal tendon (MCT; Figures 10–12). The subdermal sheath is a thick layer of collagen fibers underlying the skin. The SDS is particularly thick in the area beneath the fleshy, lateral keel. The SDS is formed from a fusion of cross-fibered collagen fibers at the posterior end of the septa of the anterior-pointing arms, one epaxial and one hypaxial. The SDS attaches to the hypural plate medially, and onto the caudal fin rays ventrally and dorsally.

The great lateral tendon (Figures 10–12) is made of nested myosepta of anterior-pointing cones, the bulk of which are derived from the last five to six myosepta. Longitudinal fibers are predominant in this tendon. Each cone that contributes to the GLT is a long tube of collagen attaching to the hypural plate of the caudal fin (Figure 10). These collagen fibers in the GLT are likely homologous to POTs that have shifted insertion to the caudal skeleton. The GLT attaches medially to the hypural plate, and has a broad aponeurosis onto the bases of the caudal fin rays (Figures 11 and 12). A second set of caudal tendons is formed where the collagen fibers of the posterior PPCs fuse, as a continuation of the SHS, to become the medial caudal tendon (MCT), which underlies the GLT (Figure 10). The MCT inserts on the hypural plate medial and anterior to insertion of the GLT.

Nomenclature of caudal muscles is now relatively stable, although previous work on fish caudal fin musculature has used a variety of names for the same muscles. Videler (1975) included a table of synonyms of caudal muscles, but used names for muscles of *Tilapia* that are not now in use. Other authors (Lauder, 1989; Gibb *et al.*, 1999) have followed Winterbottom's (1974) synonymy, and that convention is followed here. Scombrid fishes have a reduced number of intrinsic caudal fin muscles relative to other percomorph fishes, and other muscles have been reduced in size. Gibb *et al.* (1999) described just two caudal muscles in *Scomber japonicus* (the hypochordal longitudinalis and interradialis), but in dissections of both *Scomber scomber* and *S. japonicus,* we found six nonmyomeric muscles that attach to or are intrinsic to the caudal fin. Present in all mackerels and tunas we have examined (*Scomber, Scomberomorus, Acanthocybium, Sarda, Euthynnus,* and *Thunnus*) are the hypochordal longitudinalis, flexor dorsalis, flexor ventralis, infracarinalis, supracarinalis, and interradialis (Figures 11–12).

The hypochordal longitudinalis (HL; Figures 11 and 12) is an unpaired structure on both sides of the caudal fin that originates on the hypurapophysis, a lateral hooklike process of the parhypural (Figure 13), and inserts on the bases of the sturdy central fin rays of the dorsal caudal fin lobe. In tunas, the muscle fibers are greatly reduced or absent, leaving the structure as a hypochordal longitudinalis ligament in *Thunnus* (HLL; Figure 11B). Note that the structure is not technically a "tendinous remnant" as described by Fierstine and Walters (1968), because connective tissues without muscle, extending from bone to bone, are ligaments. In mackerels and other scombrids, the muscle fibers are more robust, and may be

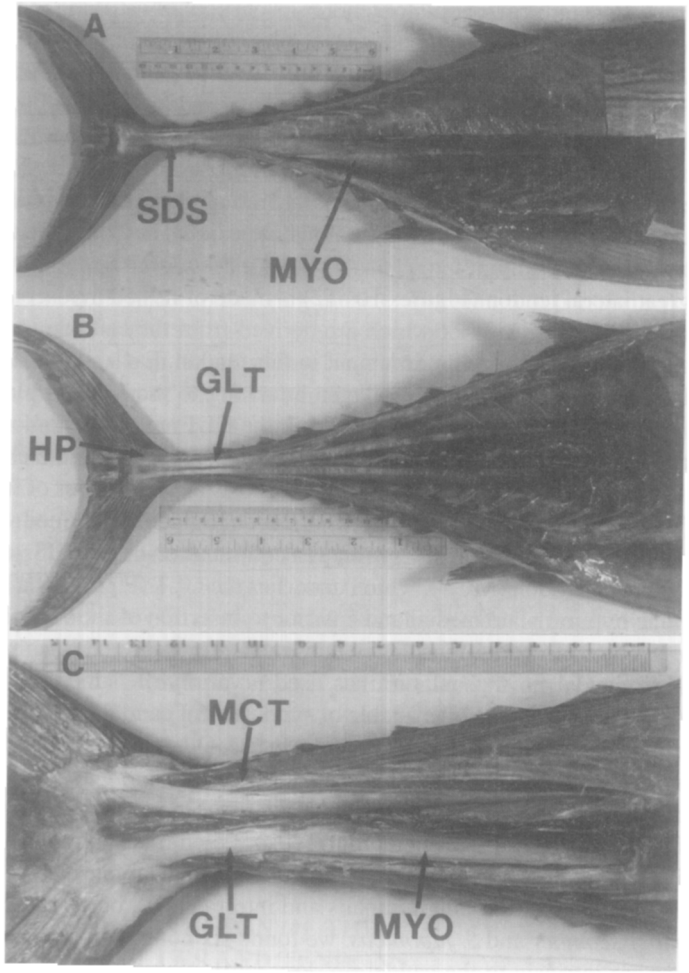


Fig. 10. Modified posterior myomeres in *Euthynnus alletteratus* (550 mm SL) including (A) the subdermal sheath (SDS) and the tendinous attachments from myomeres (MYO) to the caudal skeleton and (B) the anterior-most myomere in which the POT contributes to the great lateral tendon (GLT) that attaches to the hypural plate (HP). Note the elongated shape of the anterior-pointing cones. (C) Modified posterior myomeres (MYO), great lateral tendon (GLT), and medial caudal tendon (MCT) in *Scomberomorus cavalla,* 620 mm SL. Adapted from Westneat *et al.* (1993).

functionally implicated in asymmetry of the fin beat, in which the dorsal lobe of the caudal fin leads the ventral lobe (Gibb *et al.,* 1999).

The flexors ventralis and dorsalis together form a pair of muscles on each side of the caudal fin that originate on the vertebral centra of preural vertebrae 2 and 3 (including the "keel" region in tunas) and insert via a tendon onto the posterior

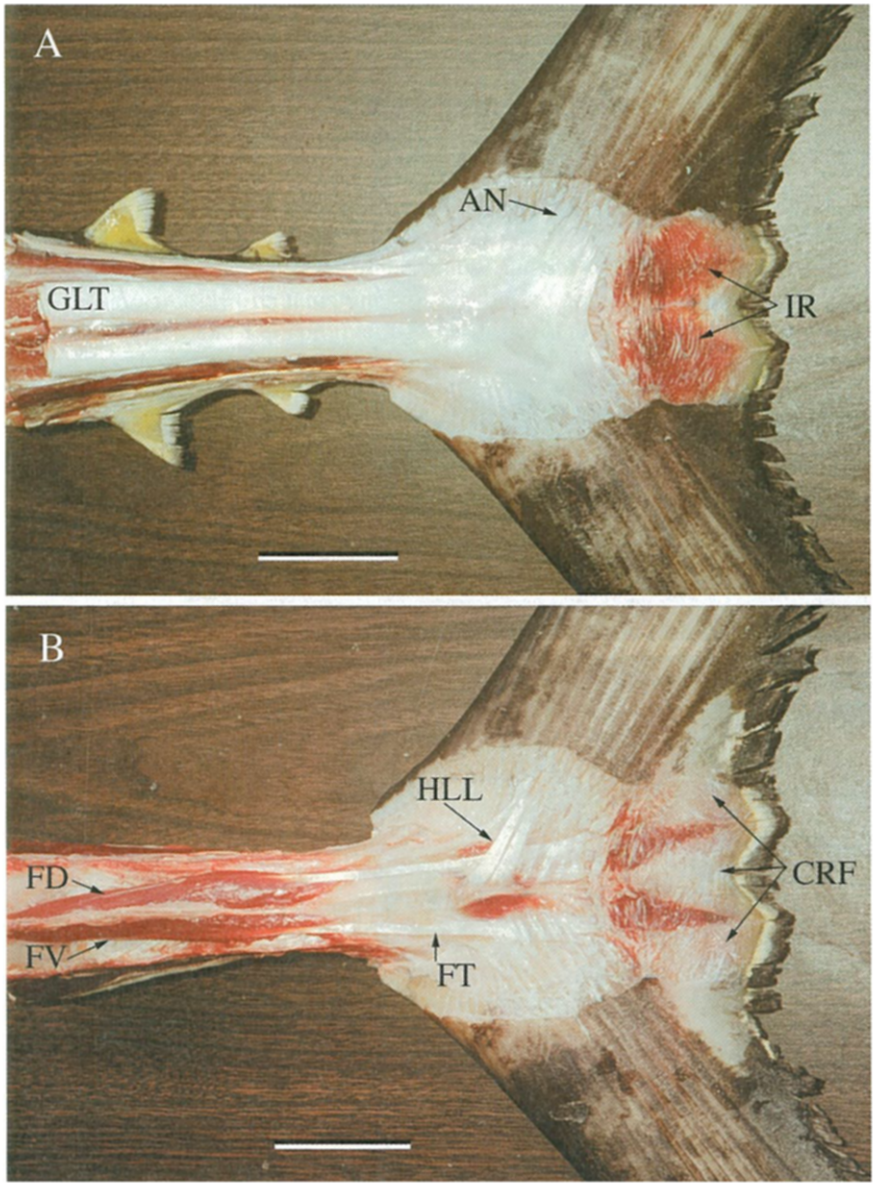
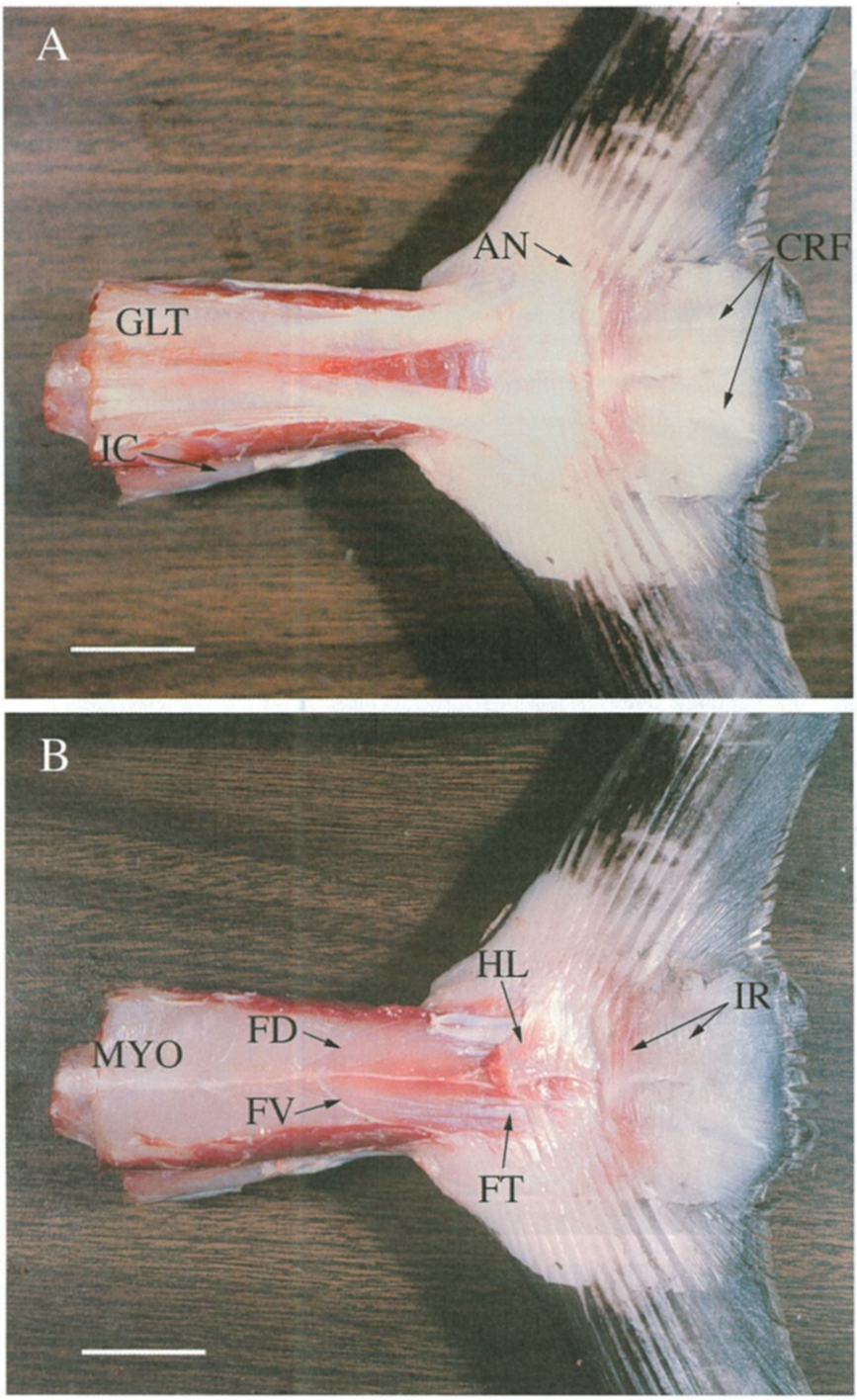


Fig. 11. Caudal fin musculature of yellowfin tuna, *Thunnus albacares*, in (A) superficial dissection with skin removal, and (B) deep dissection after removal of great lateral tendon and aponeurosis. AN, aponeurosis; CRF, modified caudal ray flaps; FD, flexor dorsalis muscle; FT, flexor tendon; FV, flevor ventralis muscle; GLT, great lateral tendon; HLL, hypochordal longitudinalis ligament; IR, interradialis muscle. Scale bar = 5 cm.


A
AN
CRF
GLT
IC
B
HL
IR
FD
MYO
FV
FT

hypural plate and onto the bases of the fan-shaped central caudal fin rays (here named caudal ray flaps—Figures 11–13). Their function in scombrids has not been studied, but based on positional information, they are responsible for abducting (not flexing, despite their names) the caudal fin flaps from side to side to increase or decrease the camber of the caudal fin during the propulsive stroke (Figure 14).

The infracarinalis posterior and supracarinalis posterior originate on the posterior-most pterygiophores supporting the last anal and dorsal finlets and insert on the anterior-most caudal fin rays of the ventral and dorsal fin lobes. The functional role of these muscles remains unexplored, but contraction of these muscles is likely to "flare" the tail, protracting the dorsal and ventral caudal fin lobes, thereby increasing the aspect ratio.

The interradialis is a muscle complex that invests the caudal fin rays in the posterocentral region of the fin, attaching the caudal ray flaps to one another and to the more fused dorsal and ventral lobes of the caudal fin (Figures 11–13). Gibb *et al.* (1999) discovered that the caudal fin of *Scomber japonicus* undergoes cycles of dorsoventral expansion and contraction, with the fin maximally contracted at maximal lateral excursion, and expanded as the fin crosses the midline. The position and fiber directions of the interradialis in mackerels and tunas support their suggestion that the muscle is a retractor or depressor that decreases the dorsoventral span of the tail. The interradialis and posterior infra- and supracarinales muscles thus form an antagonistic set of muscles for control of fin aspect ratio (Figure 14).

The evolution of the caudal muscles and their functional roles in body–caudal fin locomotion in fishes was outlined by Lauder (1989). Lauder's review and synthesis identifies the lines of action of the caudal muscles in a diversity of fishes, from basal taxa with heterocercal tails to teleosts with homocercal tails. Lauder's (1989) study highlights the need for functional studies of the intrinsic caudal muscles, focusing on the role of the hypochordal longitudinalis in creating an asymmetrical tail stroke by the homocercal tail. For scombrid fishes, a similar approach is warranted, in which mechanical hypotheses for the caudal fin are tested with kinematic data analysis of muscular motor patterns, and framed within a phylogenetic hypothesis of scombrid relationships.

Hypotheses for the role of caudal muscles in scombrids are proposed based on their origins and insertions on the caudal skeleton (Figures 13 and 14). The primary action of sweeping the high aspect-ratio tail is driven by the axial musculature and force transmission via the AOT–POT system and by the great lateral

Fig. 12. Caudal fin musculature of wahoo, *Acanthocybium solandri*, in (A) superficial dissection with skin removal, and (B) deep dissection after removal of great lateral tendon and aponeurosis. AN, aponeurosis; CRF, modified caudal ray flaps; FD, flexor dorsalis muscle; FT, flexor tendon; FV, flevor ventralis muscle; GLT, great lateral tendon; HL, hypochordal longitudinalis muscle; IC, infracarinales muscle; IR, interradialis muscle; MYO, myomeric muscle. Scale bar = 5 cm.

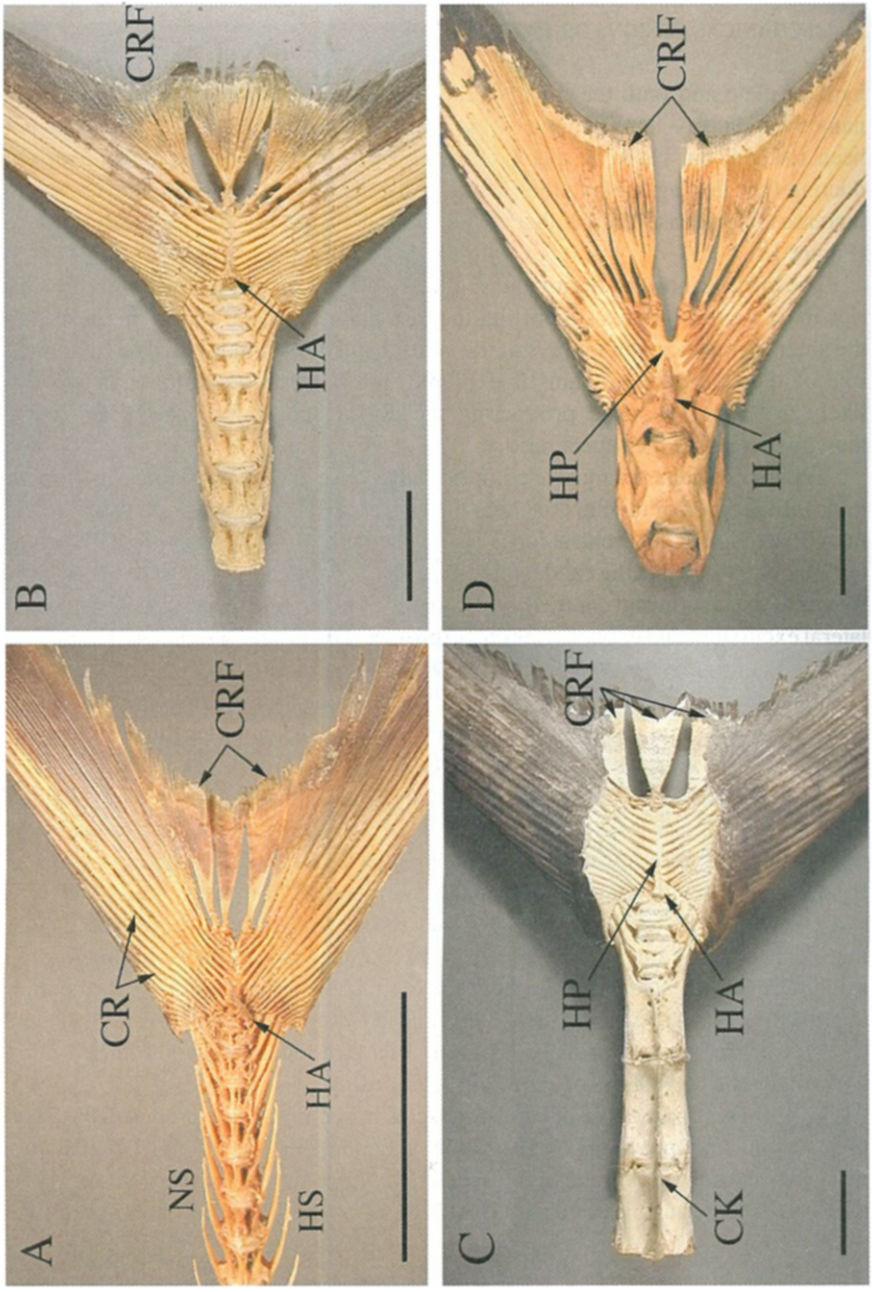


Fig. 13. Morphology of the caudal fin skeleton in (A) *Scomberomorus maculatus,* (B) *Acanthocybium solandri,* (C) *Thunnus albacares,* and (D) *Tetrapturus angustirostris.* Scombroid fishes are variable in the morphology of neural and hemal spines, the caudal keel, and the modified caudal fin ray flaps on the trailing edge of the fin. CK, caudal keel; CR, caudal rays; CRF, caudal ray flaps; HA, hypurapophysis; HP, hypural plate; HS, hemal spines; NS, neural spines.

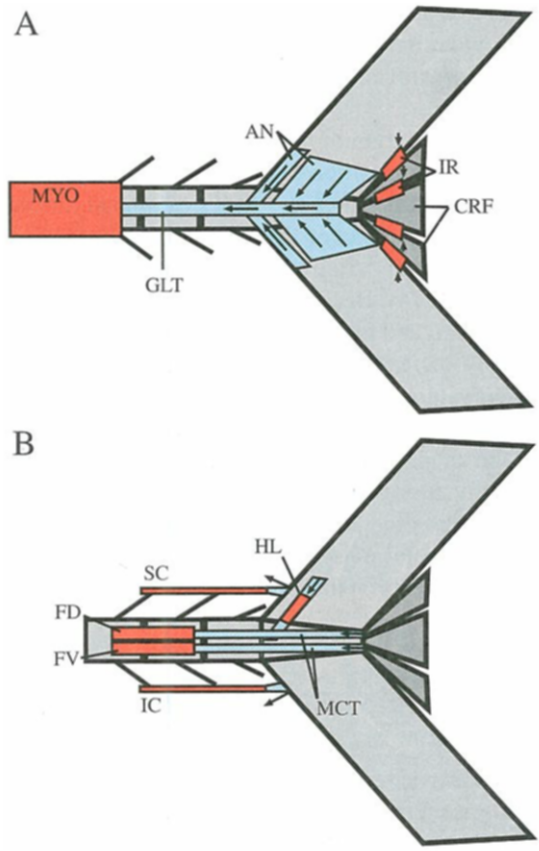


Fig. 14. Mechanical diagram of the function of the caudal fin musculature of scombroid fishes. This is a generalized model for tunas, mackerels, and billfishes (red = muscle; blue = tendon). (A) The major force transmission pathway for tail thrust is from myomere (MYO) to great lateral tendon (GLT), to tendinous aponeurosis (AN), to the hypural plate and leading edge of the caudal fin. Also shown is the mechanism of interradialis (IR) control of the spread of the caudal ray flaps (CRF). (B) The mechanisms of tail fin control by intrinsic caudal musculature. The dorsal and ventral flexors (FD, FV) pull on the medial caudal tendons (MCT) to control the angle of attack of the caudal ray flaps (CRF). The supracarinalis (SC) and infracarinalis (IC) insert tendinously on the leading edge and protract (flare) the tail. The hypochordal longitudinalis (HL) controls the dorsal leading edge, likely functioning to control tail stroke asymmetry.

tendons and medial caudal tendons (Figure 14A). The large forces transmitted through the GLT are distributed broadly to the hypural plate by large tendinous aponeuroses (AN; Figure 14A). We suggest that mackerels and tunas have considerable control over fin shape through action of the caudal muscles. The fin span and vertical profile of the fin can be dynamically altered during the caudal stroke

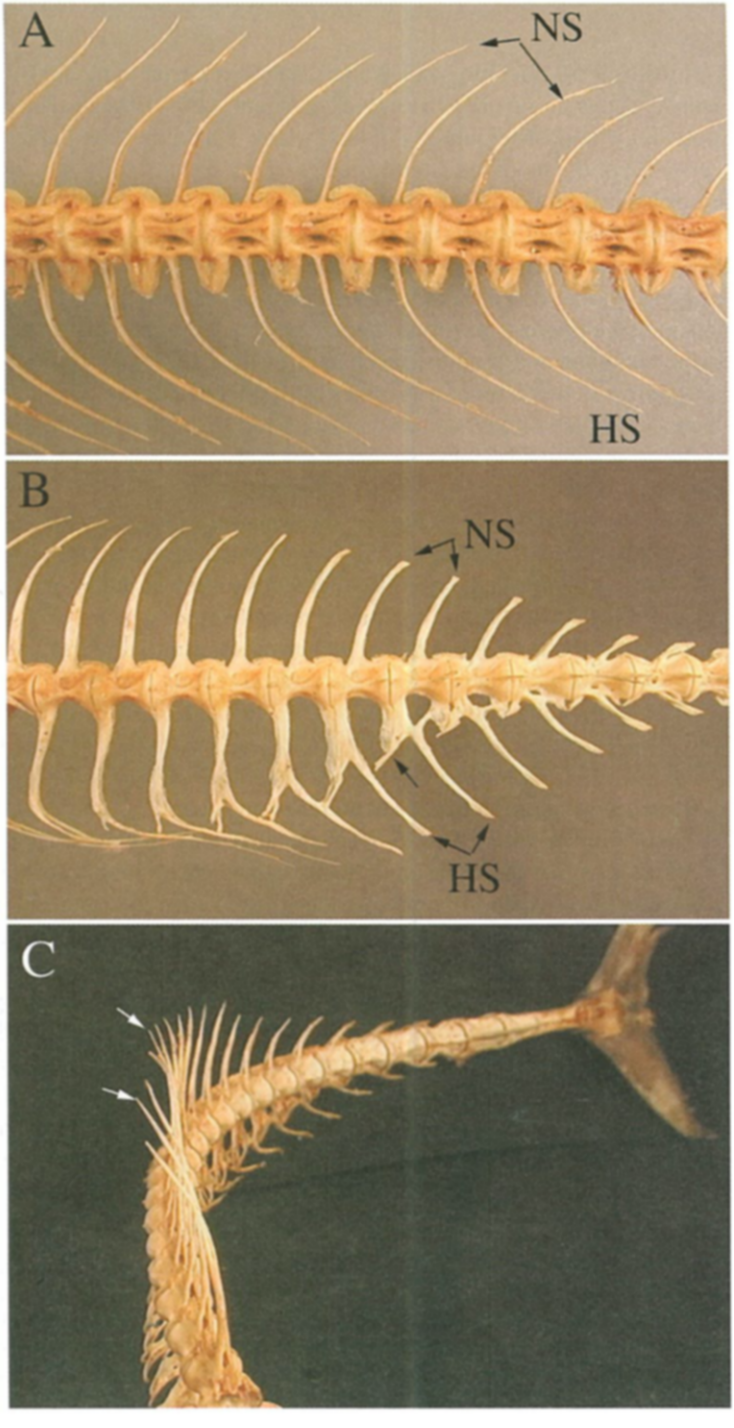
by the carinales muscles and interradialis antagonists (Figure 14). This mechanical design likely provides a means for changing the aspect ratio of the caudal fin with swimming speed or with tail position during the stroke, as observed in *Scomber* (Gibb *et al.*, 1999).

The central, posterior margin of the fin is formed by modified caudal fin rays that are similar in shape and position to the "flaps" on the rear margin of aircraft wings (Figures 11–14). In all scombroid fishes examined, the dorsal and ventral flexor muscles can alter the angle of these caudal ray flaps. In an aircraft wing, flaps are located on the aft or "trailing edge" of the wing and increase both lift and drag (McCormick, 1974). Because of the increased drag, flaps are only partially extended on takeoff, and fully extended on landing. Flaps extend downward and rearward, thereby increasing both camber and wing area. The greater the wing's camber, or curvature, the better the wing will perform at slow air speeds, due to the greater lift generated. Tunas and mackerels may adjust the camber and the lift vectors of the caudal fin in a similar manner, during changes in forward velocity or dynamically during the fin stroke as angles of attack change relative to the water flow. Testing hypotheses of caudal fin muscle function will require data on EMG profiles of locomotor muscles (Jayne and Lauder, 1995; Shadwick *et al.*, 1999) and force measurements on the large tendons that transmit locomotor forces (Knower *et al.*, 1993).

IX. THE BACKBONE AND VERTICAL SEPTUM

The mechanics of vertebral function in fishes have been analyzed from the perspective of energy storage, dynamic oscillation, and the properties of stiffness and damping that influence the transmission of waves of bending during swimming (Hebrank *et al.*, 1990; Hebrank, 1982; Long, 1992; Long and Nipper, 1996). The vertebral column of scombrid fishes possesses enlarged neural and hemal spines, and zygapophyses that articulate from one vertebra to the next, suggesting that scombrid backbones may have a relatively high stiffness (Figure 15). Tunas have bony processes extending between hemal spines that may also increase stiffness (Figure 15B), and the hypural plates are completely fused in tunas, providing a solid attachment point for robust tendons. Hebrank (1982) found that skipjack (*Katsuwonus*) backbones had high stiffness relative to nonscombrids, and other

Fig. 15. Morphology of the backbone, including neural and hemal spines in the posterior body region of (A) the mackerel *Scomberomorus maculatus* and (B) the tuna *Euthynnus alletteratus*. Mackerel spines are slender and more angled posteriorly, whereas tuna spines are more robust and more vertical, and have bony struts (arrow in B) that increase backbone stiffness. In (C) the wet backbone of *E. alletteratus* is bent, showing the tendency for the neural and hemal spines to extend out of the plane of the vertical septum (arrows) in the absence of connective tissue fibers.

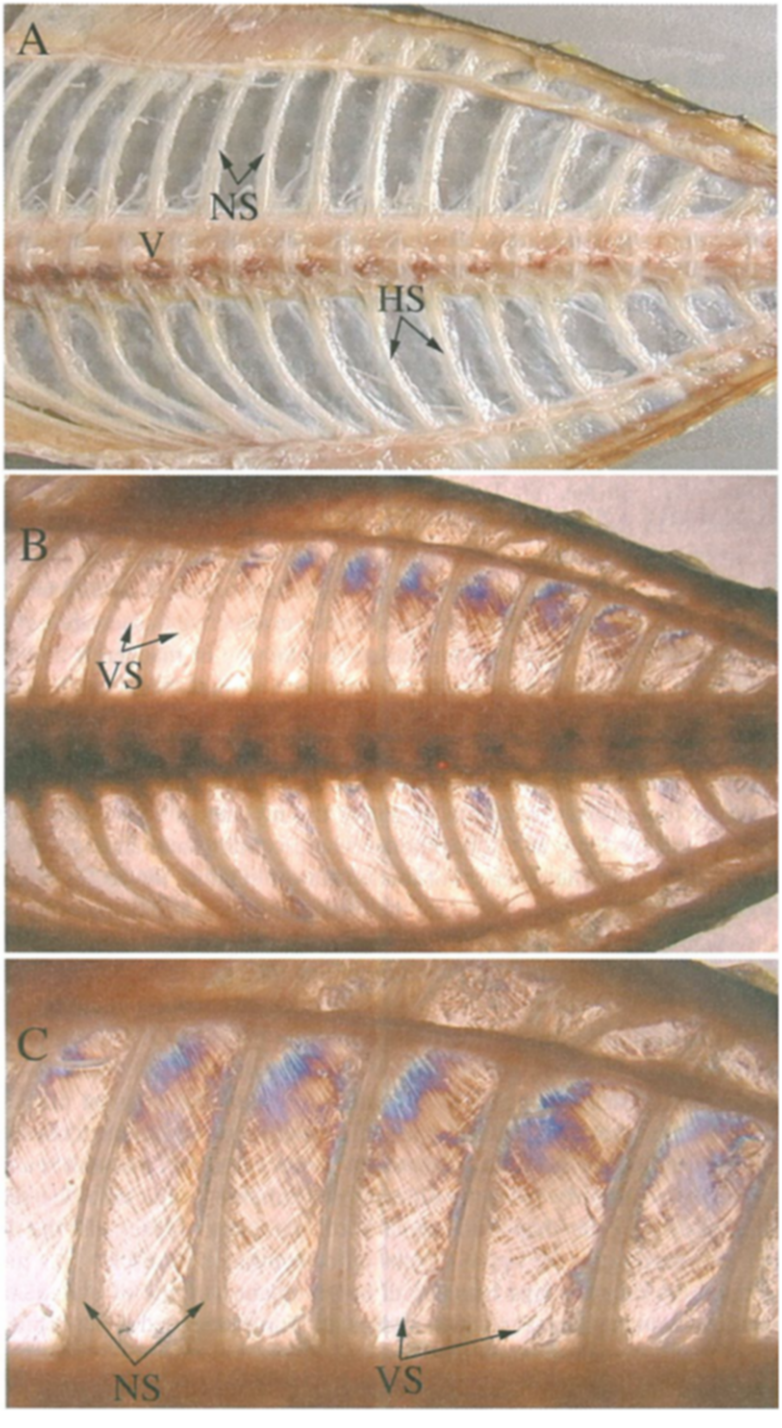

A
NS
HS
B
NS
HS
C

studies (Nursall, 1956; Fierstine and Walters, 1968) referred to the high stiffness of the caudal peduncle of tunas. However, Hebrank (1982) found that stiffness was lowest in the caudal region of skipjack where a flexible joint is present between vertebrae of the modified lateral keel.

The mechanical properties of whole backbones and intervertebral joints have been measured in several scombroid taxa. The lateral stiffness of the backbone of blue marlin (*Makaira nigricans*) is lower than that of scombrids (Hebrank *et al.*, 1990), suggesting that it is a more undulatory swimmer than tunas. Long (1992) used dynamic bending tests to reveal the stiffness and damping properties of the blue marlin backbone and used the mechanics of the intervertebral joints to calculate the total work that a set of myomeres must do over the complete locomotor cycle. Increased axial stiffness can also be achieved by contraction of axial musculature (Long and Nipper, 1996), so that the waveform of the body of an undulatory swimmer is determined in part by the stiffness contributions of vertebral column, myomeres, and the horizontal and vertical septa. There is a phylogenetic trend from lower vertebral stiffness in billfishes and mackerels to increasing stiffness in the tunas, suggesting the need for a broader survey of mechanical properties to integrate with other data on functional morphology.

In most fishes, the neural and hemal spines of adjacent vertebrae are tightly bound by a set of collagen fibers to form the vertical septum (Figure 16). In scombroid fishes, the vertical septum is hypertrophied, with strong arrays of collagen, and likely plays a role in force transmission and energy storage in locomotion. Biomechanical models of the vertical septum developed at the BioDesign Studio (Duke University) were presented at a conference on aquatic locomotion in Plymouth England (Wainwright, 1991). A mechanical model of the vertical septum begins with the fact that the neural and hemal spines are angled posteriorly, extending rearward beyond the intervertebral joint (Figures 15A and 15B). This morphology causes the distal portions of the neural and hemal spines to tend toward rotation out of the vertical plane during bending (Figure 15C). However, a woven fabric of collagen fibers binds the spines of adjacent vertebrae together, preventing distal spine rotation out of the plane of the septum (Figure 16). The collagen fiber matrix is a crossed-fiber array, in which the fibers are oriented in two primary directions, ranging from 45° to 55° to the vertebral axis (Figure 16C). If the collagen fibers prevent motion of the spines out of the vertical plane, then the spines will twist along their lengths.

Fig. 16. The vertical septum of the yellowfin tuna, *Thunnus albacares*. (A) Freshly dissected backbone, including neural spines, hemal spines, and intact collagen fiber matrix of the vertical septum. (B) Vertical septum viewed through polarized light. Note the crossed-fiber array of collagen in the vertical septum that binds the spines together. (C) Magnified view of highly oriented cross-fiber array of collagen in the vertical septum. Fiber angles range from 45° to 55° for those that extend upward and rearward, and 60° to 70° for those that course downward and rearward.


A
NS
V
HS
B
VS
C
NS
VS

Physical models of this design showed strong strain energy storage under bending (Wainwright, 1991), suggesting that strain energy may be stored in the twisted neural and hemal spines and the crossed-fiber matrix during axial undulation. Videler (1993) illustrated a strikingly similar model of the vertical septum, but refers to septal fibers that run "primarily in one direction." Collagen fibers in vertebrate axial septa are rarely, if ever, organized in a single direction, highlighting the need for use of polarized light in the examination of collagen fibers (Figure 16). Gemballa and Britz (1998) recently used this approach in a broader survey of intermuscular tendons in a diversity of fishes. Use of this technique and study of freshly dissected backbones with the vertical septum intact in dynamic vertebral bending tests (Long, 1992) will refine and test hypotheses of backbone and vertical septum function.

X. SUMMARY AND FUTURE RESEARCH

The myomeres, the mechanical design of skeletal elements in backbone and tail, and particularly the intricate design of axial connective tissues are key indicators of pathways of force transfer during locomotion in mackerels and tunas. Morphometric data on these structures, combined with physical models of the anatomy, have produced several insights into the function of the locomotor systems of scombrid fishes. The main horizontal septum is formed by the convergence of myosepta. One set of tendons in the septum, the POTs, collect the longitudinal forces created by shortening of the myomeres and transmits them posteriorly and medially to the backbone, where bending moments occur at the intervertebral joints. The other set of tendons in the septum, the AOTs, resist radially expansive hydrostatic pressure, thus stiffening the anterior-pointing cones and the skin. The AOTs thus supply tension to the slings that maintain the lateral position of the POTs, giving POTs a large moment arm with which to bend the backbone.

The model of force and velocity transmission by the POTs shows that the geometry of the myosepta determine their ability to transmit force and motion to the backbone. A steeply angled POT system, such as that of most mackerels, transmits bending force to the backbone at the expense of displacement advantage. Tunas, with their long POTs at a low angle to the vertebrae, transmit relatively high velocity posteriorly from the anterior musculature to the tail. The second model, that of the cone-shaped muscular hydrostat, demonstrates that the AOTs are put into tension by the radial expansion of contracting muscle. This model, based upon the relationships between dimensions and volume of cylinders and cones, shows that the degree to which hydrostatic forces are used to put connective tissues of the horizontal septum into tension depends upon the initial geometry of the cones and the degree to which the cones change geometry during muscle con-

traction. The predictions regarding force transmission in both of these models need to be tested through analyses of kinematics, mechanical properties of tissues, internal pressure profiles, and patterns of muscle activity in the locomotor muscle.

The models we propose raise several questions about axial locomotor morphology and force transmission. What is the effect of slow oxidative muscle position on locomotor biomechanics? The distribution of the aerobic red muscle fibers within the myomere is of paramount importance to the long-range cruising locomotion typical of scombrid fishes. Previous studies (e.g., Fierstine and Walters, 1968; Graham *et al.*, 1983) found extensive variation in morphology and position of red muscle in the myomeres of scombrids. The red muscle of mackerels that is positioned laterally will exert force primarily on the POTs to exert force directly on the vertebrae. The red muscle of tunas also lies along the horizontal septum and is connected to the POTs, but this internal muscle may also function to exert radial tensile forces in the AOT through the hydrostatic cone model. Recent analyses of the *in vitro* contractile properties of individual red muscle fibers (Altringham and Block, 1997; Rome *et al.*, 1992) and the motor patterns of red muscle in swimming tunas (Shadwick *et al.*, 1999) may contribute the physiological data on muscular input that is necessary to test these models.

The mechanisms of caudal fin function in scombrids are of clear functional relevance due to the high aspect ratio of the tail and the powerful thrust during swimming for which these fishes are famous. The serially homologous myomeres in the caudal region are modified to contribute to the great lateral tendon and the medial caudal tendon for transmitting force to the tail (Figure 10). We suggest a basic mechanical design for force transmission in the caudal fin that begins to answer the question, how does the essentially separate mechanism involving the posterior segments, caudal musculature, and the GLT interact with the more anterior mechanisms of backbone undulation? Further testing of a biomechanical model of the caudal region may reveal how muscular forces are transferred through the caudal tendons to the caudal fin during the power stroke. The vertical septum is an additional functional complex in fishes that has received little attention but may play an important role in the biomechanics of aquatic locomotion.

A complete phylogenetic analysis of functional characters is not yet possible, as we still need morphological and functional data sets for most taxa. However, preliminary phylogenetic mapping of key locomotor characters (Figure 1) reveals that a number of functional modifications occur at the transition from bonitos (Sardini) to tunas (Thunnini). Thunniform locomotion (Figure 1, node F) is accompanied by a high-aspect-ratio caudal fin, fully internal red muscle, elongate anterior-pointing cones, regional endothermy, long, low-angled posterior oblique tendons, a fused hypural plate, a modified caudal keel with a flexible joint, and reduction of the hypochordal longitudinalis muscle to a ligament. The functional implications of longer cones and low-angled POTs can be explored using mechanical models proposed here, but many of the unique features of tunas await

further experimental testing and comparison to other scombroid fishes. Also of note is the apparent independent evolution in the billfishes and tunas of high-AR caudal fins, long APCs, and extremely heavy, cordlike systems of collagen in the main horizontal septum.

In summary, the two major goals to strive for in future research are (1) a broad comparative approach to locomotor morphology that will allow the integration of mechanical models with the rapidly increasing knowledge of scombrid phylogeny (Block *et al.*, 1993; Block and Finnerty, 1994; Collette, 1978, 1997; Johnson, 1986) and (2) experimental testing of models of mechanical design of the myomeres, horizontal septa, vertical septum, and caudal fin in the context of research on tuna behavior and physiology (Altringham and Block, 1997; Block, 1991; Brill, 1987; Carey, 1981; Dewar and Graham, 1994; Graham *et al.*, 1989; Shadwick *et al.*, 1999). The locomotor mechanisms of scombrid fishes will only be understood when we adopt an approach that combines information from phylogeny and physiology with the testing of mechanical models through measurement of kinematics, muscular motor patterns, and the mechanical properties of axial tissues.

ACKNOWLEDGMENTS

Many thanks to B. Block and D. Stevens for coordinating this volume and for their help with the manuscript. Special thanks to J. W. Nursall for his insightful comments on the chapter. The ideas in this chapter were aided and abetted in many ways by C. A. Pell, J. H. Long, Jr., and D. A. Pabst. Funded by ONR Grant N00014-99-0184 and NSF Grant DEB-9815614 to M. W. Westneat.

REFERENCES

Alexander, R. McN. (1969). The orientation of muscle fibers in the myomeres of fishes. *J. Mar. Biol. Assoc. U.K.* **49,** 263–290.

Alexander, R. McN. (1988). "Elastic Mechanisms in Animal Movement." Cambridge Univ. Press, Cambridge.

Altringham, J. D., and Block, B. A. (1997). Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200,** 2617–2627.

Altringham, J. D., and Johnston, I. A. (1982). The pCa-tension and force-velocity characteristics of skinned fibers isolated from fish fast and slow muscles. *J. Physiol. Lond.* **333,** 421–449.

Bainbridge, R. (1963). Caudal fin and body movement in the propulsion of some fish. *J. Exp. Biol.* **40,** 23–56.

Block, B. A. (1991). Endothermy in fish: Thermogenesis, ecology, and evolution. *In* "Biochemistry and Molecular Biology of Fishes" (Hochachka, P., and Mommsen, T., Eds.), Vol. 1, pp. 269–311. Elsevier, New York.

Block, B. A., and Finnerty, J. R. (1994). Endothermy in fishes: A phylogenetic analysis of constraints, predispositions, and selection pressures. *Environ. Biol. Fishes* **40,** 283–302.

Block, B. A., Finnerty, J. R., Stewart, A. F. R., and Kidd, J. (1993). Evolution of endothermy in fish: Mapping physiological traits on a molecular phylogeny. *Science* **260,** 210–214.

Bookstein, F. L. (1991). "Morphometric Tools for Landmark Data: Geometry and Biology." Cambridge Univ. Press, New York.

Brill, R. W. (1987). On the standard metabolic rates of tropical tunas, including the effects of body size and acute temperature change. *Fish. Bull., U.S.* **85,** 25–35.

Calow, L. J., and Alexander, R. McN. (1973). A mechanical analysis of a hind leg of a frog (*Rana temporaria*). *J. Zool. Lond.* **171,** 293–321.

Carey, F. G. (1981). Warm fish. *In* "A Companion to Animal Physiology" (Taylor, C. R., Johansen, K., and Bolis, L., Eds.), pp. 216–233. Cambridge University Press, Cambridge.

Collette, B. B. (1978). Adaptations and systematics of the mackerels and tunas. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp.7–40. Academic Press, New York.

Collette, B. B. (1997). Mackerels, molecules, and morphology. *In* "Proc. 5th Indo-Pac. Fish Conf., Noumea" (Seret, B., and Sire, J. Y., Eds.), pp. 149–164. Société Française d'Ichtyologie & Institut de Recherche pour le Développement, Paris.

Collette, B. B., and Chao, L. N. (1975). Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae: Sardini). *Fish. Bull., U.S.* **73,** 516–625.

Collette, B. B., and Nauen, C. E. (1983). "FAO Species Catalogue. Vol. 2. Scombrids of the World. An Annotated and Illustrated Catalogue of Tunas, Mackerels, Bonitos and Related Species Known to Date." FAO Fish. Synop. 125, Vol. 2. FAO, Rome.

Dewar, H., and Graham, J. B. (1994). Studies of tropical tuna swimming performance in a large water tunnel. III. Kinematics. *J. Exp. Biol.* 192, 45–59.

Dickson K. A. (1996). Locomotor muscle of high-performance fishes: What do comparisons of tunas with ectothermic sister taxa reveal? *Comp. Biochem. Physiol.* **113,** 39–49.

Fierstine, H. L., and Walters, V. (1968). Studies in locomotion and anatomy of scombroid fishes. *Mem. South. Cal. Acad. Sci.* **6,** 1–31.

Gemballa, S., and Britz, R. (1998). Homology of intermuscular bones in acanthomorph fishes. *Am. Mus. Novitates (N. Y.)* **3241,** 1–25.

Gibb, A. C., Dickson, K. A., and Lauder, G. V. (1999). Tail kinematics of the chub mackerel *Scomber japonicus:* Testing the homocercal tail model of fish propulsion. *J. Exp. Biol.* **202,** 2433–2447.

Graham, J. B. (1975). Heat exchange in the yellow-fin tuna, *Thunnus albacares,* and skipjack tuna, *Katsuwonus pelamis,* and the adaptive significance of elevated body temperatures in scombrid fishes. *Fish. Bull., U.S.* **73,** 219–229.

Graham, J. B., Koehrn, F. J., and Dickson, K. A. (1983). Distribution and relative proportions of red muscle in scombrid fishes: Consequences of body size and relationships to locomotion and endothermy. *Can. J. Zool.* **61,** 2087–2096.

Graham, J. B., Lowell, W. R., Lai, N. C., and Laurs, R. M. (1989). O_2 tension, swimming velocity, and thermal effects on the metabolic rate of the Pacific albacore, *Thunnus alalunga*. *J. Exp. Biol.* **48,** 89–94.

Hebrank, M. R. (1982). Mechanical properties of fish backbones in lateral bending and in tension. *J. Biomech.* **15,** 85–89.

Hebrank, J. H., Hebrank, M. R., Long, J. H., Jr., Block, B. A., and Wainwright, S. A. (1990). Backbone mechanics of the blue marlin, *Makaira nigricans* (Pisces, Istiophoridae). *J. Exp. Biol.* **148,** 449–459.

Hochachka, P. W., Hulbert, W. C., and Guppy, M. (1978). The tuna power plant and furnace. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 153–174. Academic Press, New York.

Jayne, B. C., and Lauder, G. V. (1995). Red muscle motor patterns during steady swimming in largemouth bass: Effects of speed and correlations with axial kinematics. *J. Exp. Biol.* **198,** 1575–1587.

Johnson, G. D. (1986). Scombroid phylogeny: An alternative hypothesis. *Bull. Mar. Sci.* **39,** 1–41.

Kafuku, T. (1950). "Red muscles" in fishes. I. Comparative anatomy of the scombroid fishes of Japan. *Jpn. J. Ichthyol. Gyoruigaka Zasshi* **1,** 89–100.

Kier, W. M., and Smith, K. K. (1985). Tongues, tentacles and trunks: The biomechanics of movement in muscular hydrostats. *Zool. J. Linn. Soc.* **83,** 307–324.

Kishinouye, K. (1923). Contributions to the comparative study of the so-called scombroid fishes. *J. Coll. Agric. Tokyo Imp. Univ.* **8,** 293–475.

Knower, T., Shadwick, R. E., Biewener, A. A., Korsmeyer, K., and Graham, J. B. (1993). Direct measurement of tail tendon forces in swimming tuna. *Am. Zool.* **33,** 30A.

Knower, T., Shadwick, R. E., Katz, S. L., Graham, J. B., and Wardle, C. S. (1999). Red muscle activation patterns in yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas during steady swimming. *J. Exp. Biol.* **202,** 2127–2138.

Koval, A. P., and Butuzov, S. V. (1986). Features of the structure of the internal tendon system in some Scombridae species. *Vestnik Zoologii* **6,** 59–65.

Lauder, G. V. (1989). Caudal fin locomotion in ray-finned fishes: Historical and functional analyses. *Am. Zool.* **29,** 85–102.

Long, J. H., Jr. (1992). Stiffness and damping forces in the intervertebral joints of blue marlin (*Makaira nigricans*). *J. Exp. Biol.* **162,** 131–155.

Long, J. H., Jr., and Nipper, K. S. (1996). The importance of body stiffness in undulatory propulsion. *Am. Zool.* **36,** 678–694.

Long, J. H., Jr., Hale, M. E., McHenry, M. J., and Westneat, M. W. (1996). Functions of fish skin: Flexural stiffness and steady swimming of longnose gar (*Lepisosteus osseus*). *J. Exp. Biol.* **199:** 2139–2151.

Magnuson, J. J. (1978). Locomotion of scombrid fishes. *In* "Fish Physiology," Vol. 7. "Locomotion" (Hoar, W. S., and Randall, D. J., Eds.), pp. 239–313. Academic Press, New York.

Magnuson, J. J., and Weininger, D. (1978). Estimation of minimum sustained speed and associated body drag of scombrids. *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 293–312. Academic Press, New York.

McCormick, B. W. (1974). "Aerodynamics, Aeronautics, and Flight Mechanics," 2nd ed. Wiley, New York.

Mos, W., and Van der Stelt, A. (1982). Efficiency in relation to the design of the segmented body musculature in *Brachydanio verio*. *Neth. J. Zool.* **32,** 123–143.

Nursall, J. R. (1956). The lateral musculature and the swimming of fish. *Proc. Zool. Soc. Lond.* **126,** 127–143.

Nursall, J. R. (1963). The caudal musculature of *Hoplopagrus guntheri* Gill (Perciformes: Lutjanidae). *Can. J. Zool.* **41,** 865–880.

Patterson, P., and Johnson, G. D. (1995). The intermuscular bones and ligaments of teleostean fishes. Smithson. Contrib. Zool. no. 559. Smithsonian Institution Press.

Quillen, K. J. (1998). Ontogenetic scaling of hydrostatic skeletons: Geometric, static stress and dynamic stress scaling of the earthworm *Lumbricus terrestris*. *J. Exp. Biol.* **201,** 1859–1870.

Rayner, M. D., and M. J. Keenan. (1967). Role of red and white muscles in the swimming of skipjack tuna. *Nature* **214,** 392–393.

Rome, L. C., Choi, I., Lutz, G., and Sosnicki, A. A. (1992). The influence of temperature on muscle function in fast swimming scup. I. Shortening velocity and muscle recruitment during swimming. *J. Exp. Biol.* **163,** 259–274.

Shadwick, R. E., Katz, S. L., Korsmeyer, K. E., Knower, T., and Covell, J. W. (1999). Muscle dynamics in skipjack tuna: Timing of red muscle shortening in relation to activation and body curvature during steady swimming. *J. Exp. Biol.* **202,** 2139–2150.

Smith, K. K., and Kier, W. M. (1989). Trunks, tongues, and tentacles: Moving with skeletons of muscle. *Am. Sci.* **77,** 28–35.

Videler, J. J. (1975). On the interrelationships between morphology and movement in the tail of the cichlid fish *Tilapia nilotica*. *Neth. J. Zool.* **25,** 144–194.

Videler, J. J. (1993). "Fish Swimming." Chapman & Hall, London.

Videler, J. J., and Hess, F. (1984). Fast continuous swimming of two pelagic predators, saithe (*Pollachius virens*) and mackerel (*Scomber scombrus*): A kinematic analysis. *J. Exp. Biol.* **109,** 209–228.

Vogel, S. (1988). "Life's Devices: The Physical World of Animals and Plants." Princeton Univ. Press, Princeton.

Vronskii, A. A., and Nikolaichuk, L. A. (1988). A comparative anatomy of lateral musculature myomeres in teleostean fish with different levels of motor activity communication. *Vestnik Zoologii* **3,** 63–68.

Wainwright, S. A. (1983). To bend a fish. *In* "Fish Biomechanics" (Webb, P., and Weihs, D., Eds.), pp. 68–91. Praeger, New York.

Wainwright, S. A. (1991). Design for swimming. *J. Mar. Biol. Assoc. U.K.* **71,** 725.

Wainwright, S. A., Biggs, W. D., Currey, J. D., and Gosline, J. M. (1976). "Mechanical Design in Organisms." Wiley, New York.

Wainwright, S. A., Vosburgh, F., and Hebrank, J. H. (1978). Shark skin: Function in locomotion. *Science* **202,** 747–749.

Wardle, C. S., and Videler, J. J. (1993). The timing of the emg in the lateral myotomes of mackerel and saithe at different swimming speeds. *J. Fish Biol.* **42,** 347–359.

Westneat, M. W., Hoese, W., Pell, C. A., and Wainwright, S. A. (1993). The horizontal septum: Mechanisms of force transfer in locomotion of scombrid fishes (Scombridae; Perciformes). *J. Morphol.* **217,** 183–204.

Westneat, M. W., Hale, M. E., McHenry, M. J., and Long, J. H. (1998). Mechanics of the fast-start: Muscle function and the role of intramuscular pressure in the escape behavior of *Amia calva* and *Polypterus palmas*. *J. Exp. Biol.* **201,** 3041–3055.

Willemse, J. J. (1959). The way in which flexures of the body are caused by muscle contractions. *Koninkl. Nederl. Akad. van Wetens. Proc. Ser. C* **62,** 589–593.

Winterbottom, R. (1974). A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Philadelphia* **125,** 225–317.

8

SWIMMING AND MUSCLE FUNCTION

JOHN D. ALTRINGHAM
ROBERT E. SHADWICK

I. Introduction
II. Swimming Performance
III. External Body Form
IV. Swimming Kinematics and Hydrodynamics
V. Muscle Structure and Physiology
VI. Endothermy
VII. Slow Muscle and Sustained Swimming Performance
VIII. Muscle Function during Swimming
IX. Modeling Muscle Function
X. Forces Generated by the Muscle
XI. Do Caudal Tendons Function as Springs?
XII. The Uncoupling of Slow Muscle Strain from Body Bending
XIII. Variations within Scombrids
XIV. Summary
XV. Directions for Future Research

Scombrids stand out from most other fish by their ability to cruise at relatively high speeds and migrate long distances. This chapter briefly describes the morphological adaptations that have equipped tuna for continuous, fast, efficient swimming, and their unique body kinematics and hydrodynamics. The emphasis, however, is on recent work on muscle function. The distribution of slow muscle in the body, and the way in which it is used to generate thrust, can be seen as a complex continuum in fish, and tuna lie at one extreme. Slow muscle in tunas is concentrated near the midpoint of the body, and forms a large internal mass. In each half tailbeat, rapid muscle activation on one side of the body leads to a brief pulse of power generation that appears to be transmitted directly to the caudal fin by the long posterior oblique tendons. This generates a strong vortex at the caudal fin to provide thrust. Internalization of slow muscle and its concentration half way along the body are seen in ectothermic scombrids and may have been a preadaptation for endothermy. The internal slow muscle of tuna shows signs of physiolog-

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

ical adaptation for improved function at stable, elevated temperatures. To highlight the ways in which tuna are similar or different to other fish, comparisons are made wherever possible with other scombrids, and with nonscombrid fish.

I. INTRODUCTION

This chapter addresses the challenging problem of how tunas use their muscle to swim. Tunas are high-speed pelagic predators that spend their entire lives swimming. To sustain fast, continuous locomotion, tunas have evolved a suite of morphological specializations that distinguish them from other fishes. Here we summarize recent research on body kinematics and muscle mechanics of tunas and other scombrids which has provided a quantitative basis for understanding the unique features of thunniform swimming. To highlight the similarities and differences with other fishes, our discussion is put into context of data from other species of scombrid and nonscombrid fish.

II. SWIMMING PERFORMANCE

In his 1978 review, John Magnuson noted that "scombrids are astounding bundles of adaptations for efficient and rapid swimming. . . . The entire biology of scombrids is tightly linked to swimming as a way of life." It is from this point of view that we have begun to analyze the mechanical design and function of locomotor muscle in these fish.

Scombrids stand out from most other fish by their ability to cruise at relatively high speeds and migrate long distances. Most swim continuously at speeds ranging from 0.33 BL s^{-1} (body lengths per second) to over 2 BL s^{-1}, and few cruise at less than 1 BL s^{-1} (Magnuson, 1978). The slowest recorded species is the wahoo, *Acanthocybium solandri,* which has an elongated body form unusual in scombrids. *Thunnus* species are typically faster at about 1 BL s^{-1}, and *Euthynnus* often exceed 2 BL s^{-1}. Large, mature specimens of *Thunnus thynnus* have high absolute speeds, but are slower in terms of body lengths per second (0.3–1 BL s^{-1}; Wardle *et al.*, 1989). Against this trend, it should be said that species with the fastest recorded cruising speeds include skipjack (*Katsuwonus pelamis*), bullet mackerel (*Auxis rochei*), and Atlantic bonito (*Sarda sarda*). Cruising speed does appear to be related to the presence or absence of a swim bladder. In general, the more negatively buoyant species without swim bladders swim faster to generate sufficient lift to avoid sinking. Speed is also inversely related to the area of the pectoral fins used to generate lift (Magnuson, 1978). Few nonscombrid teleosts are continuous undulatory swimmers: exceptions include migrating salmon, which can swim at speeds of 1–2 BL s^{-1} for several hundred kilometers (Johnson and Groot, 1963; Neave, 1964; Beamish, 1978).

Burst speeds in scombrids are less variable than sustained speed (Magnuson, 1978), ranging from 12 to 15 BL s^{-1}. The highest recorded speed was for *Acanthocybium*, which is not surprising given its elongated body. The high-speed, high-efficiency "design" of tunas has led to compromises: they are much less maneuverable than most other fish (Blake *et al.*, 1995). What are the important features of this design? Tuna differ from other fish in their external and internal anatomy, swimming kinematics, and physiology, and in the way their locomotor muscle functions. Only recently have these properties been investigated quantitatively by kinematic analyses of tunas swimming at steady speeds and by *in vitro* and *in vivo* investigations of muscle dynamics.

III. EXTERNAL BODY FORM

There is a long-standing appreciation that scombrids, particularly the tunas, have biomechanical specializations that give them superior swimming ability among the teleosts (e.g., Lindsey, 1978; Magnuson, 1978). Indeed, some of these features, such as the high-aspect-ratio lunate tail, streamlined body, elongate myotomes, and internalized and endothermic slow muscle, are also found in the fast-swimming lamnid sharks, and are generally considered to represent the most highly evolved adaptations for efficient, and relatively fast, sustained swimming. In terms of streamlining, the body thickness to length ratio is close to the optimum for minimum drag (Hertel, 1966). *Thunnus, Euthynnus, Katsuwonus,* and *Auxis* could not be nearer the optimum, *Sarda* and *Scomber* are very close, and only *Acanthocybium* among species studied is too slender to have a minimum drag : volume ratio. Flow over a body is likely to be laminar, even at high speeds, up to the point when the body begins to taper toward the tail. The position of maximum body thickness should therefore be well back on the body and in scombrids is around 0.4–0.5 BL from the snout. There are no significant differences within the scombrids (Magnuson, 1978), but the position of maximum body thickness in nonscombrids is generally further forward. The rounded body profile of scombrids also increases swimming efficiency (Weihs, 1989). However, the body is not circular in section, but ellipsoidal, to limit lateral movement of the body (Lighthill, 1969). The narrow caudal peduncle reduces kinetic energy losses due to movement of water (Lighthill, 1969). Lateral keels on the peduncle reduce turbulence (Webb, 1975) and possibly provide some lift (Magnuson, 1970). Another anatomical specialization in scombrids is the presence of finlets, small nonretractable fins that occur in pairs along the dorsal and ventral midlines anterior to the caudal fin. In tunas there are 6–10 pairs. These appear to direct cross flow between the two sides of the body toward the tail, which may help to maintain laminar flow over the tail and augment lift (Magnuson, 1970; Webb, 1975), prevent boundary layer separation, and reduce drag (Lindsey, 1978), or even prevent roll (Walters, 1962). In a kinematic study of finlets in the chub mackerel *Scomber*

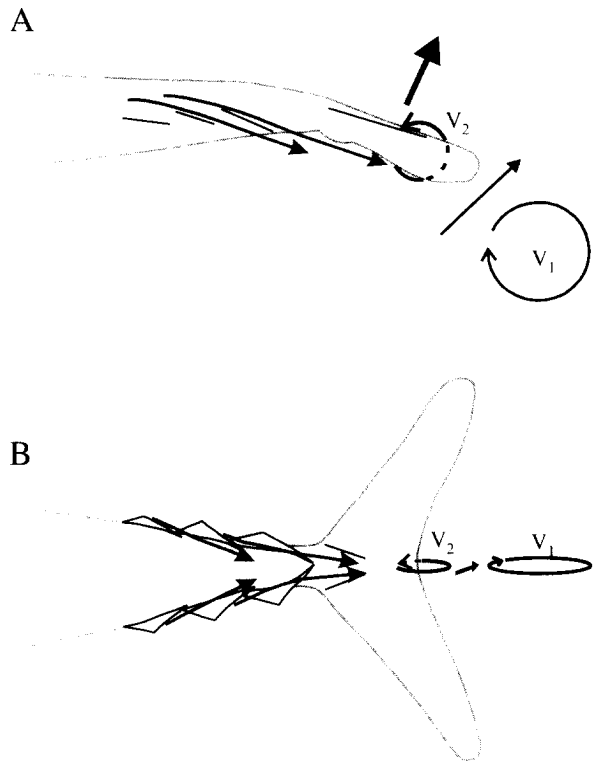


Fig. 1. Vorticity enhancement hypothesis proposed by Nauen and Lauder (2000). (A) dorsal view; (B) lateral view. In both views the tail is decelerating toward one lateral extreme position (large arrow in A). A possible path of water flow is indicated by the small arrows. The water flowing over the peduncle is directed into the developing vortex V_2, adding to forward thrust (from Nauen and Lauder, 2000, with permission from Company of Biologists, Ltd.).

japonicus, Nauen and Lauder (2000) proposed that water flow is directed longitudinally along the keels as the tail fin is decelerating at the extreme of its lateral stroke, thereby enhancing the development of a caudal fin vortex and the resulting thrust (Figure 1).

Prominent scales are rarely found in tuna, but some species have a scaled zone called the corselet just behind the operculum. It has been suggested that it may be a drag reduction device: the corselet could prevent breakaway, by introducing microturbulence to the boundary layer, thereby reducing the velocity gradient (Walters, 1962). Webb (1975) suggests it serves as a fairing for the pectorals, which are held against the side during burst swimming. The second dorsal fin also fits into a slot during burst swimming, as do the pelvic and first dorsal fins, which

are only opened during maneuvering. The second dorsal and anal fins reduce lateral body movement (Magnuson, 1978). The body is extremely smooth, even around the eyes, opercula, and so on. Finally, the caudal (and pectoral) fins of scombrids are typically lunate and have a high aspect ratio, both increasing the lift:drag ratio (e.g., Lighthill, 1969). Aspect ratios of >10 for pectoral fins and up to 8 for caudal fins in scombrids are the highest recorded in fish, although sailfish and marlin are comparable. *Thunnus, Euthynnus, Katsuwonus,* and *Auxis* have the highest aspect ratios, and *Scomber, Sarda,* and *Acanthocybium* some of the lowest, although some *Thunnus* fall into the latter group (Magnuson, 1978).

IV. SWIMMING KINEMATICS AND HYDRODYNAMICS

Swimming in tuna is characterized by minimal lateral movement of all but the caudal region of the fish, and virtually all of the thrust comes from the caudal fin (e.g., Lighthill, 1970, 1975). For theoretical reasons reviewed at length by Magnuson (1978), the thunniform mode is believed to be a highly efficient way of swimming, a view supported by the oxygen consumption measurements of Dewar and Graham (1994a).

Breder's (1926) classification of swimming modes is clearly an oversimplification, but provides a useful framework. It places tuna at one end of a spectrum of swimming styles, in the thunniform swimming mode. At the other end are the anguilliform or eel-like swimmers that throw their entire body into a series of large-amplitude waves and generate thrust along most of their length. This mode is energetically inefficient and slow. Between these two extremes there is a continuum through subcarangiform to carangiform swimming, the latter grading into thunniform. Within those species which swim using their body musculature there are many species which do not fit into this series, for example, those designed for acceleration or high maneuverability, and then there are the many species that swim using paired and unpaired fins other than the caudal fin. We will confine our discussion in this review to the main anguilliform to thunniform series, since this allows us to describe tuna in relation to other fish without undue complexity.

Undulatory swimming is powered by a backward-traveling wave of body bending that must push against the water to generate thrust. Since the water yields as the fish pushes against it, the wave must travel backward faster (v) than the fish swims forward (u). The amplitude of the wave also increases as it travels down the body, with the lateral displacement of the tail tip (peak-to-peak) generally being about 0.2 BL in most species. The number of waves on the body at a given instant varies between approximately 0.7 and 1.7 in different species (Videler, 1993; Wardle *et al.*, 1995). Swimming speed, expressed in BL s^{-1}, is strongly correlated with tailbeat frequency (TBF), but not tail tip amplitude. Speed in-

creases are driven by increases in the propagation of the activation wave along the body, culminating in faster TBF and generally little increase in tail tip amplitude. Thus, for steady swimming the kinematics are relatively constant in terms of tail-beat period (Wardle and Videler, 1993; Wardle *et al.*, 1995). Stride length, the distance moved in a tail beat, varies from 0.4 to slightly >1.0 BL between species: u/v increases (i.e., there is less slip) as stride length increases (Videler, 1993). Stride length in tuna and other scombrids varies considerably and there are no apparent trends within the scombrids (Table I) or between them and other species (Videler and Hess, 1984; Wardle *et al.*, 1989; Wardle and Videler, 1993; Dewar and Graham, 1994b). Direct comparison is difficult because stride length varies with swimming speed and size in many species. Table I does show, however, that the highest stride lengths reported are for fish swimming unrestricted in large tanks or at sea, rather than in flumes. Videler (1993) likens the maximum stride length to the fish's "top gear" when the fish is swimming at maximum speed. Wardle and Videler (1980) proposed that the very high speeds in tunas may be accomplished by stride lengths much greater than 1.0 BL, but so far there is no evidence to support this model. It is probable that many of the published values reflect suboptimal performance. We would predict tuna to have longer maximum stride lengths and higher u/v values than most fish. However, since thrust is generated primarily at the tail, not by lateral motion of body segments, the ratio of u/v may not be important as an indicator of efficiency.

A kinematic analysis of yellowfin tuna was conducted by Dewar and Graham (1994b), who used video images of 32- to 53-cm-long fish during steady swimming in a water tunnel treadmill at speeds up to 3 BL s^{-1}. Their work described the lateral movements of the body, the yaw of the head, and the relation between swimming speed and TBF. They showed that the length-specific caudal amplitude and stride length are similar to those of other teleosts, but that the relative increase in TBF with increasing speed is less. For example, a TBF of 2 Hz was required to swim at 1 BL s^{-1}, but this increased to only 4 Hz for swimming at 3 BL s^{-1}. This situation probably occurs because the TBF is relatively high (and stride length relatively low) at low speeds near the minimum sustainable for each species. This might reflect a low swimming efficiency at the lowest speeds: the lift-based caudal thrust mechanism may not be highly effective when the tail is not moving rapidly through the water.

As mentioned above, the major kinematic feature in tunas that sets them apart from other teleosts, and even other scombrids like mackerel, is that the lateral excursions of the body are more limited to the tail region. Consequently, the amplitude envelope (a plot of the body wave amplitude as a function of axial position) is narrow in the front and midbody, and rises more steeply toward the tail, compared with other fish. Figure 2 shows such a comparison for a series of fish from eel to tuna. At 0.5 BL the wave amplitude in tunas is only about 0.1 of the amplitude measured at the trailing edge of the caudal fin, whereas the relative amplitude is 0.17 in mackerel, 0.25 in the subcarangiform group, and 0.45 in the

Table I

Comparison of Swimming Speed (U), Tailbeat Frequency (f), and Stride Length (L_s) for Tunas and Other Scombrids

Species	Common name	Water temp. (°C)	Body length (m)	U (BL s^{-1})	f (Hz)	L_s (BL)	Method	Source[a]
Scomber scombrus	Atlantic mackerel	12	0.31–0.35	5.0–18	5.4–14.9	0.76–1.04	Tank	12–14
Scomber japonicus	Chub mackerel	17–20	0.26–0.32	1.0–12.0	1.9–16	0.53–0.75	Flume	7, 8
Sarda chiliensis	Pacific bonito	22	0.57	1.5–4.0	1.8–5.5	0.72–0.83	Tank	10
		20	0.6–0.7	0.9–2.4	1.2–3.2	0.75–0.79	Tank	1, 4
Sarda sarda	Atlantic bonito	18	0.16	3.75–6.25	6.0–9.0	0.62–0.69	Flume	11
Euthynnus affinis	Kawakawa	25	0.4–0.6	3.1–8.2	7.0–14.0	0.42–0.52	Tank	5
		24	0.38	1.36	3.0	0.44	Flume	2
Thunnus alalunga	Albacore tuna	16–17	0.9	0.74–1.23	1.86–2.11	0.4–0.58	Flume	6
Thunnus thynnus	Bluefin tuna	20	2.3	0.6–1.2		0.54–0.93	Sea pen	15
Thunnus albacares	Yellowfin tuna	24–26	0.52	3.0–10.5	2.0–13.0	0.75–1.5	Open ocean	16
		24–28	0.53	0.57–2.5	1.5–3.5	0.4–0.75	Flume	3
		22–27	0.4–0.44	1.1–2.5	1.9–3.6	0.57–0.7	Tank	9
		18	0.56	1.01	1.52	0.67	Tank	1
		24	0.56	0.93	1.66	0.56	Tank	1
Katsuwonus pelamis	Skipjack tuna	24–26	0.57	3.0–10.0	3.0–21	0.57–1.2	Open ocean	16
		24–28	0.51	1–2.8	3–4.8	0.33–0.6	Flume	2
		22–27	0.38–0.41	1.5–3.7	2.8–5.2	0.53–0.71	Flume	9

[a]Sources: (1) Altringham and Block, 1997; (2) Dewar, 1993; (3) Dewar and Graham, 1994b; (4) Ellerby *et al.*, 2000; (5) Fierstine and Walters, 1968; (6) Graham *et al.*, 1989; (7) Hunter and Zweifel, 1971; (8) Katz and Shadwick, 1998; (9) Knower *et al.*, 1999; (10) Magnuson and Prescott, 1966; (11) Pyatetskiy, 1970; (12) Videler and Hess, 1984; (13) Wardle and He, 1988; (14) Wardle and Videler, 1980; (15) Wardle *et al.*, 1989; (16) Yuen, 1966.

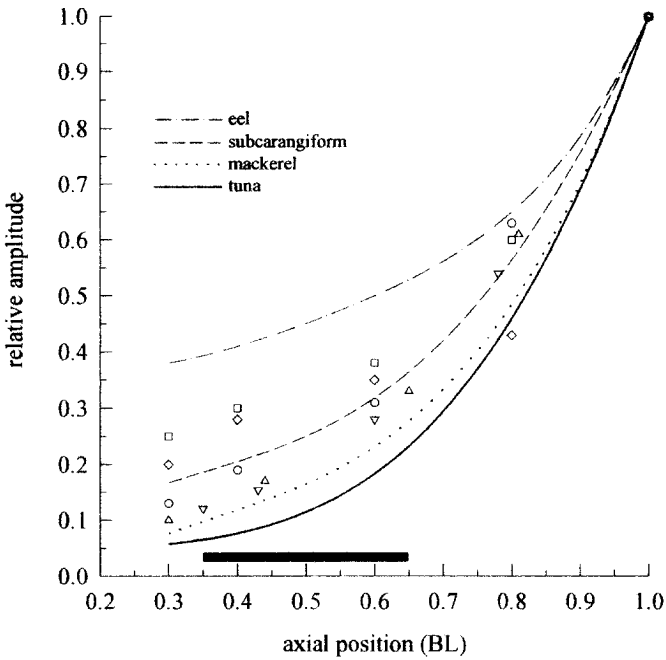


Fig. 2. Body wave amplitude (normalized to the maximum amplitude at the tail tip) as a function of axial position (BL) for a number of scombrid and nonscombrid fish during steady swimming. Polynomial curves were fit to data for eel (D'Août and Aerts, 1999), mackerel (Katz and Shadwick, 1998), and a group of subcarangiform swimmers consisting of bass (▽ Jayne and Lauder, 1995), cod (△ Videler and Wardle, 1978), saithe (○ Videler and Hess, 1984), muskie (◇), and trout (□ Webb, 1978). The tuna curve is fit to data for skipjack, *Katsuwonus pelamis*, and yellowfin, *Thunnus albacares* (Knower, 1998), and the horizontal bar represents the longitudinal position of the bulk of the internal slow muscle in those two species.

eel at the same axial location. In tunas, the body tapers fairly abruptly beyond 0.7 BL, and it is only in this posterior region where the body cross-sectional area and red muscle mass are greatly reduced that the relative amplitude rises above 0.3. As stated above, increased speed in undulatory swimming is not generally accompanied by a concomitant increase in tail tip amplitude. However, tunas may differ in this regard. A comparison of skipjack tuna swimming at low and high speeds, shown in Figure 3, suggests that the amplitude envelop may indeed be altered in sprinting, with a much larger lateral displacement seen in the posterior third of the body. Whether this kinematic change is seen only during acceleration or also at high-speed steady swimming is unknown at present.

In fish that swim by undulation of the body and caudal fins, two main approaches to describing thrust generation have been taken. One can be described

as the bulk momentum or added-mass method, and the other a lift-based method. As the body bends, and the bends travel down the fish, the body and caudal fin push against the water, increasing the momentum of the water traveling backward. The reaction to this is an equal force pushing the fish forward (see, e.g., Webb, 1978). The bending of the body also generates vortices that pass down the body and are shed by the caudal fin into the wake of the fish (Figure 4). This generates a reverse Karman vortex street. The reaction to this street pushes the fish forward. It has generally been argued that for most fish the bulk momentum method was the most appropriate description, and that only in thunniform swimmers was a lift-based, vortex wake approach appropriate. However, Triantafyllou *et al.* (1993) showed that the Strouhal numbers calculated for more than 10 fish species were in the predicted range for maximum efficiency of thrust generation from a vortex wake. The list includes fish as diverse as bream, bonito, cod, goldfish, shark, and trout. The Strouhal number *St* is defined as

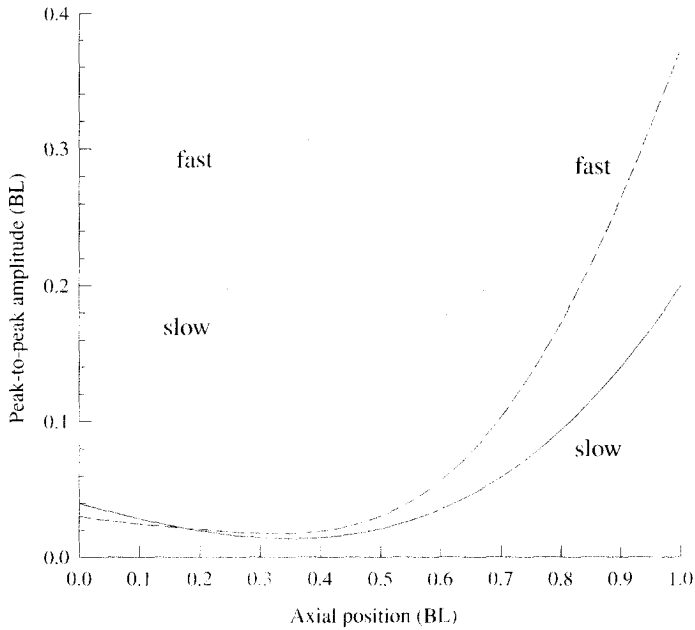


Fig. 3. Lateral displacement of the body midline (peak-to-peak), normalized to body length (BL) as a function of axial position for a slow-swimming (2.1 BL s^{-1}) *Katsuwonus pelamis* and a fast-swimming (8.2 BL s^{-1}) *Euthynnus affinis*, indicating possible kinematic differences. The tail tip amplitude is 0.2 BL at the slow speed and 0.38 BL at the fast speed. Drawn from data in Fierstine and Walters (1968) and Knower (1998).

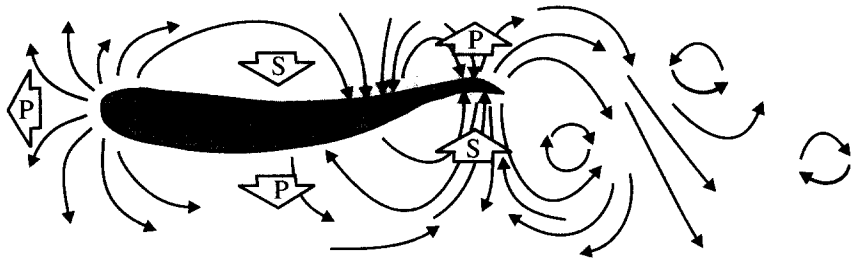


Fig. 4. Vortex structure around a mullet (*Chelon labrosus*) swimming in a straight line at constant speed. P and S are pressure and suction zones around convex and concave bends, respectively. The arrows show the main flow directions. Based on Müller *et al.* (1997).

$$St = \frac{fA}{U},$$

where f is the tailbeat frequency, A is the wake width (approximates to tailbeat amplitude), and U is the forward velocity. St is the ratio of unsteady to inertial forces, and should be in the range 0.25–0.35 for optimal thrust development. Müller *et al.* (1997) showed that a carangiform swimmer, the mullet, *Chelon labrosus,* has a Strouhal number of 0.34 and generates a strong vortex wake (Figure 4). Approximately one-third of the energy in the wake is generated by the anterior two-thirds of the body. They suggest that the undulating pump mechanism (put forward by Blickhan *et al.*, 1992) generates a circulation on the body. This circulation flows down the body, joining the bound vortex at the tail before being shed as a free vortex. Wolfgang *et al.* (1999) suggest that fish control this body-generated vorticity through body flexure and caudal fin movement to maximize the useful energy released in the vortex wake, a view supported by Müller *et al.* (1997). In the transition from carangiform to thunniform swimming, the importance of the body-generated vortex will diminish.

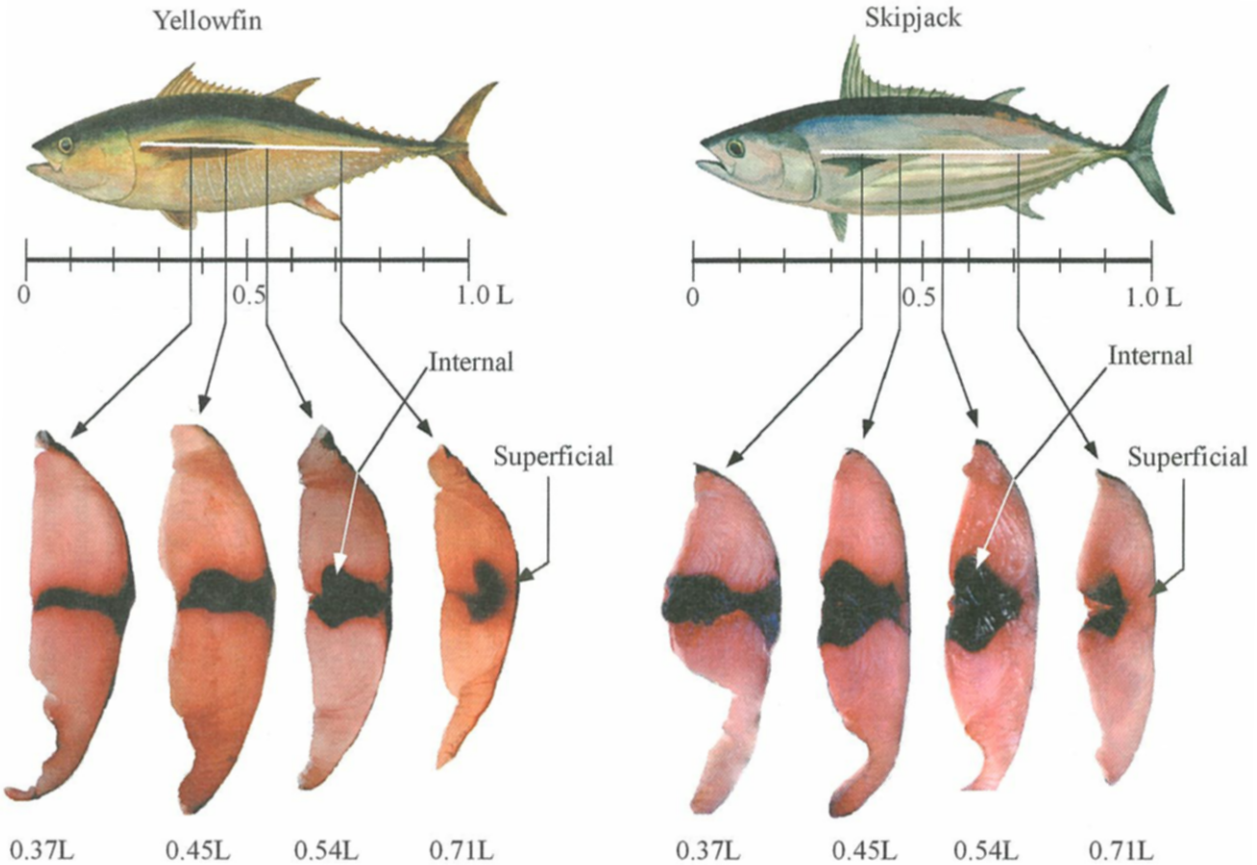
V. MUSCLE STRUCTURE AND PHYSIOLOGY

Axial muscle of fish is arranged into segmental myotomes which have a complex three-dimensional structure (reviewed by Videler, 1993). The myotomes form stacked cones in which the muscle fibers follow complex helical trajectories from one myotome to the next down the body of the fish. Myotomal and fiber arrangement follow broadly similar patterns in all fish, but there are major differences between selachians and primitive teleosts on the one hand, and more advance teleosts on the other (Alexander, 1969). Alexander proposed that this

complex arrangement enabled all fibers across the body section to undergo similar strains during body bending.

The axial muscle of fish can be divided into two major types, fast-twitch or white muscle and slow-twitch or red muscle, which are typically anatomically discrete. Some species have a thin layer of pink muscle, intermediate in properties between the fast and slow muscle (see Johnston, 1981). On the basis of histological and sometimes physiological studies, several other types have been identified (e.g., Bone, 1978; Johnston, 1981). Most of the myotomal muscle is fast and typically 90–100% of the fish cross-section at a given point, and the proportion of slow muscle is related to the ecology of the fish: constantly swimming pelagic species have more slow muscle than benthic species (Boddeke *et al.*, 1959; Videler, 1993). As a percentage of body mass, scombrids are 4–13% slow muscle (Graham *et al.*, 1983), although five of the seven species studied were between 4 and 7%. The slow muscle in most fish is confined to a zone, triangular in cross section, beneath the lateral line, and generally makes up an increasing proportion of the body cross-section toward the tail (Videler, 1993). However, some species have different distributions of slow muscle, the functional significance of which is often not known. Differences in relative slow muscle mass between scombrids are small, but the slow muscle is distributed differently. There is a tendency for some of the slow muscle to be placed deeper in the body, between the lateral line and the vertebral column. In those species which possess countercurrent heat exchangers to elevate slow muscle temperature, this internalized slow muscle component may constitute more than 50% of the slow muscle (Figure 5). However, even in ectothermic species such as the bonito, *Sarda chiliensis,* a significant proportion of the slow muscle is deep in the body (Ellerby *et al.*, 2000). Graham *et al.* (1983) showed that as a percentage of cross-sectional area, slow muscle of *Auxis, Euthynnus, Katsuwonus,* and *Thunnus* reached a maximum at 0.4–0.5 BL from the snout, in contrast to *S. chiliensis* and *Scomber japonicus,* where it was maximal at 0.7 BL. They suggested that this large difference between ectothermic and endothermic scombrids is related to differences in swimming mode. However, if expressed in terms of absolute muscle cross-sectional area, *Thunnus albacares, S. chiliensis, Scomber scombrus* (Ellerby *et al.*, 2000), and *S. japonicus* (Shadwick *et al.*, 1998) all have their slow muscle peak at 0.5 BL. The peak is broadest in *Scomber* and narrowest in *T. albacares.* In nonscombrid species, slow muscle mass shows a broader distribution along the body (Ellerby *et al.*, 2000). This suggests an increasing localization of the major power source as locomotion has become more specialized in the scombrids.

Is there a functional significance to this shift? One possible rationale is as follows. In fish that generate thrust along much of their body by means of undulatory waves, slow muscle must be present along much of their length to generate the bending wave—the presumed ancestral, metameric muscle arrangement? Evolution toward sustained, high-speed swimming, which uses only the caudal fin


Yellowfin
0
0.5
1.0 L
Internal
Superficial
0.37L
0.45L
0.54L
0.71L
Skipjack
0
0.5
1.0 L
Internal
Superficial
0.37L
0.45L
0.54L
0.71L

to generate thrust, would benefit from several "design" changes in the power source. An increase in slow muscle mass would increase the available power, as seen in most scombrids. Mechanically this muscle would be best placed in the midline, and thus internal to the existing slow muscle. Placing slow muscle closer to the backbone reduces its mechanical advantage, but the long posterior oblique tendons found in many scombrids, which make acute angles to the backbone in tuna and bonito, compensate for this placement (Westneat *et al.*, 1993; Ellerby *et al.*, 2000). Power transmission to the caudal fin in a thunniform swimmer would be mechanically more efficient from a discrete source on either side of the body, in the fish's midline, pulling directly on the caudal fin through tendons (analogous to cursorial, terrestrial vertebrates). This might explain the increasing localization of slow muscle at 0.5 BL. The disadvantage of such an arrangement is the reduced maneuverability evident in many scombrids: they are designed for fast, straight-line swimming.

At the other end of the spectrum, in eel-like swimmers, the distributed arrangement of slow muscle along the body, and the relatively slow backward-traveling wave of activation, delivers thrust gradually during a large proportion of each tailbeat cycle. In the evolution of thunniform swimming, thrust generation has become more discontinuous, occurring as more or less discrete bursts twice in each tailbeat. An increase in the electromyography (EMG) wave speed and a localization of the slow muscle around 0.5 BL (Ellerby *et al.*, 2000) will facilitate the production of discrete power bursts. We will come back to this subject later.

Fast and slow muscle types in fish are not homogeneous. There is a longitudinal slowing of the twitch from anterior to posterior in most species studied (e.g., Wardle *et al.*, 1989; Altringham *et al.*, 1993; Davies and Johnston, 1993; Davies *et al.*, 1995; Rome *et al.*, 1993; Altringham and Ellerby, 1999). Altringham and Block (1997) observed a similar trend in yellowfin tuna, *T. albacares*. They also showed that twitch contraction time decreased with increasing depth into the slow muscle. In some tuna (e.g., *T. albacares* and *Katsuwonus pelamis;* Knower *et al.*, 1999) many of the fibers in the superficial slow muscle mass take on the appearance of intermediate- or fast-twitch fibers, suggesting an increase in contraction dynamics toward the tail (Figure 5). Confirmation is required from mechanical experiments, but Knower (1998) found that posterior superficial "slow" muscle in *T. albacares* and *K. pelamis* was active only during burst swimming, suggesting faster mechanics. The significance of these regional differences in muscle properties is not understood.

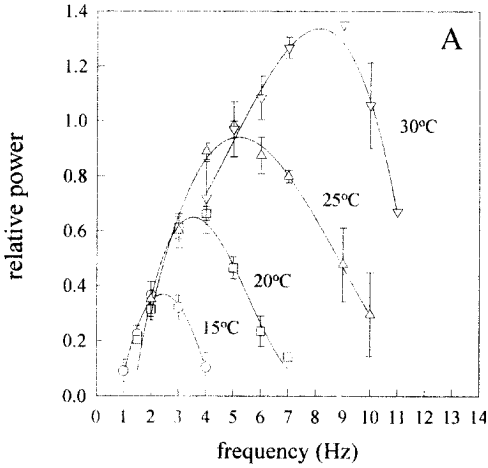
Fig. 5. Transverse sections of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tuna at different points along the body to show the distribution of the slow muscle. Note also the transition to pale fast fibers of the more superficial "slow" muscle at posterior locations. L = fork length. From Knower *et al.* (1999) with permission from Company of Biologists, Ltd.

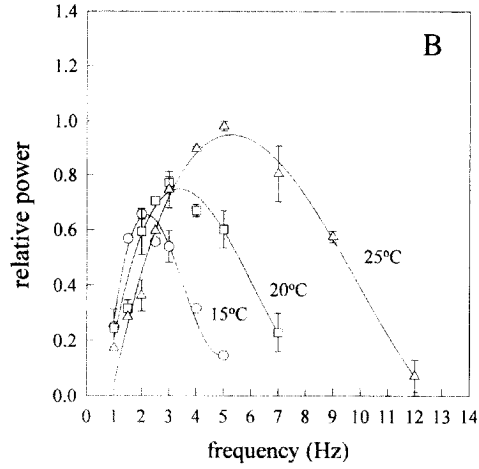
VI. ENDOTHERMY

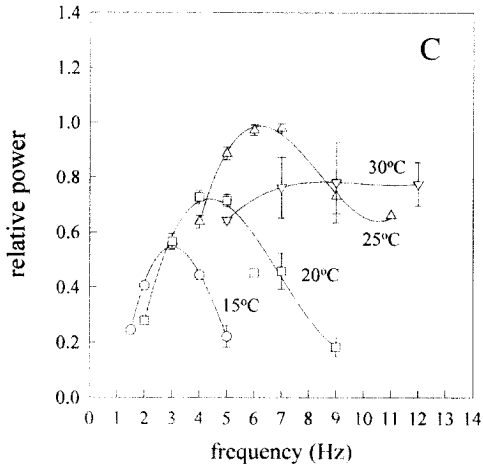
The development of a large slow muscle mass for increased mechanical power may have been an important preadaptation for the evolution of endothermy (Graham and Dickson, 2000). Significant gains in muscle power can be obtained through small increases in temperature (see below), and any adaptations that led to retention of some of the significant heat generated by active muscle would have a selective advantage.

The ability of tunas to maintain elevated internal slow muscle temperatures is well documented (e.g., Carey and Teal, 1966; Carey *et al.*, 1971; Graham, 1975; Carey, 1981). Tunas have a higher proportion of slow-twitch, relative to fast-twitch, myotomal muscle than other teleosts (Magnuson, 1978; Graham *et al.*, 1983). The heat generated by muscle contraction and metabolism is conserved by the internalization of the aerobic muscle mass and the presence of a countercurrent heat exchanger (the *rete mirabilis*) in the circulatory system, which reduce conductive and convective heat loss at the gills and body surfaces. Tunas have a high standard metabolic rate and numerous specializations associated with increased oxygen delivery to the tissues and high metabolic demands (Brill, 1987, 1996; Brill and Bushnell, this volume). In continuously swimming fish, internal muscle temperature may be maintained up to 21°C above ambient water temperature (bluefin tuna, *Thunnus thynnus;* Carey and Lawson, 1973). In *Katsuwonus,* slow-twitch muscle temperatures are 12°C above ambient, and in other *Thunnus* species the steady state muscle temperature elevation is 6°C or less (Dizon and Brill, 1979; Graham and Dickson, 1981; Holland *et al.*, 1992). Heat retention mechanisms in aerobic muscle are not unique to tuna, being found in other large, active pelagic fish: lamnid sharks (Carey *et al.*, 1971), Alopiid sharks (Carey, 1981; Bone and Chubb, 1983), blue sharks (Carey and Scharold, 1991), and swordfish (Carey, 1990). This suggests that there are strong selective pressures for warming the locomotor muscles. It has been suggested (e.g., Carey and Teal, 1966) that this system of regional endothermy has evolved to enhance the locomotory performance of the fish by increasing muscle power output, and this was recently tested by Altringham and Block (1997) in yellowfin tuna, *Thunnus albacares.* Figure 6A compares the power output of isolated deep, slow muscle fibers at different tailbeat frequencies and temperatures. *In vivo* muscle action was simulated by imposing sinusoidal strains on the fibers and timing stimulation to maximize muscle power output. This approach has been widely applied to fish swimming studies (for review see Altringham and Ellerby, 1999), and in the case of tuna, conditions which

Fig. 6. Relative power versus frequency curves for (A) deep and (B) superficial slow fibers from the yellowfin tuna, *Thunnus albacares,* and for (C) superficial slow fibers from the bonito, *Sarda chiliensis.* From Altringham and Block (1997) with permission from Company of Biologists, Ltd.


A
relative power
frequency (Hz)
30°C
25°C
20°C
15°C


B
relative power
frequency (Hz)
25°C
20°C
15°C


C
relative power
frequency (Hz)
30°C
25°C
20°C
15°C

optimize power production have been shown to match *in vivo* conditions (Shadwick *et al.*, 1999). As predicted, increasing temperature increases muscle power and the tailbeat frequency at which it is generated. This is perhaps not surprising and the same pattern might be seen in most muscles. However, comparison with more superficial slow fibers from the same species (Figure 6B), and with results from the slow muscle of the ectothermic bonito, *Sarda chiliensis* (Figure 6C), shows some revealing differences. Power output of deep slow muscle from *T. albacares* was more dependent upon temperature than both other muscle types. In deep *T. albacares* fibers there was a progressive increase in temperature sensitivity as temperature was lowered from 30 to 25°C (Q_5 = 1.31), 25 to 20°C (Q_5 = 1.40), and 20 to 15°C (Q_5 = 1.84). There was also a progressive increase in temperature sensitivity with increasing depth (three depths studied) in the slow muscle (depending upon location and temperature, Q_5 increased from 1.2 to 2.0). Finally, performance of the deep muscle of *T. albacares* did not deteriorate until temperature was raised to 35°C. Slow *S. chiliensis* muscle deteriorated above 25°C. The obvious conclusion to be drawn is that the deep slow muscle of *T. albacares* has adapted to perform best at stable, elevated temperatures. Slow *S. chiliensis* muscle is more typical of ectothermic fish: it has a low temperature dependence but is unstable at temperatures above those experienced in the wild.

The marked adaptation for optimal performance at high, stable temperatures seen in *T. albacares* deep slow muscle is perhaps a little surprising, given that this species typically maintains deep slow muscle only 6°C above ambient water temperature (Dizon and Brill, 1979). The thermal properties of the deep slow muscle of bluefin tuna, *T. thynnus*, which can be maintained 9–21°C above ambient (Carey and Lawson, 1973), should prove to be particularly interesting.

VII. SLOW MUSCLE AND SUSTAINED SWIMMING PERFORMANCE

At 25°C, *Thunnus albacares* slow muscle generates maximum power at a tailbeat frequency of 5 Hz (Figure 6). Free swimming, cruising fish used a tailbeat frequency of <2 Hz, as reported by Altringham and Block (1997). *Thunnus albacares* thus have a substantial power reserve in their large slow muscle mass, which is probably sufficient to power sustained swimming at speeds significantly greater than those used during normal cruising. Sustained, higher speed, aerobic cruising is thus possible using the more efficient slow muscle, without the need to recruit less efficient fast muscle. During bursts of activity when feeding, tailbeat frequency was >8 Hz, but when searching for food between these bursts, frequencies around 3 Hz were used, at a swimming speed of about 2 BL s^{-1}. Altringham and Block (1997) calculated that only about 50% of the slow muscle would be required at this speed and the muscle would still be producing less than maximum

power output. Block *et al.* (1997), tracking small, wild *T. albacares*, noted that speeds of up to 3.5 BL s^{-1} could be maintained for over an hour.

Sarda chiliensis slow muscle also produced maximum power at tailbeat frequencies greater than those observed during steady cruising, and this species also has a large slow muscle mass (Ellerby *et al.*, 2000), suggesting a substantial power reserve in the slow muscle. Data are not yet available to indicate how significant this reserve may be. Most nonscombrid fish have proportionally far less slow muscle, and it is unlikely that slow muscle is able to power swimming at more than the slowest speeds.

VIII. MUSCLE FUNCTION DURING SWIMMING

During swimming myotomal muscle is activated on alternate sides of the body. Anterior muscle is activated first, and a wave of activation travels from head to tail, typically faster than the wave of body bending travels. Slow, sustained swimming in all fish is powered by slow-twitch, aerobic, red muscle. Contraction kinetics of this slow muscle are too slow to generate useful work at high tailbeat frequencies (e.g., Altringham and Johnston, 1990), and most fish possess too little slow muscle to generate sufficient power for rapid swimming. Fast, glycolytic, white muscle is therefore recruited as swimming speed increases (e.g., Bone *et al.*, 1978; Johnston and Moon, 1980). It yields maximum power at appropriate frequencies and there is enough of it to meet the high power demands of fast swimming (e.g., Altringham and Johnston, 1990). During fast starts and bursts of high-speed swimming, it is believed that all of the fast myotomal muscle may be recruited. Early studies on tuna (e.g., Rayner and Keenan, 1967) demonstrated that, as in other fish, slow swimming was powered by slow muscle, while at high speeds the fast fibers were recruited. However, neither these nor any studies since have shed light on how different regions of the large slow muscle mass are recruited with changing speed.

IX. MODELING MUSCLE FUNCTION

To understand how tuna use their muscle to generate thrust, and to understand how they differ from other fish, we first need to describe patterns of muscle activity in a range of fish in some detail. As stated earlier, undulatory swimming is powered by a backward traveling wave of body bending, generated by myotomal muscle contraction. The form this bending wave takes is determined by the arrangement and properties of passive elements in the body, muscle properties and activity patterns, and the interaction between the fish and the reactive forces of the

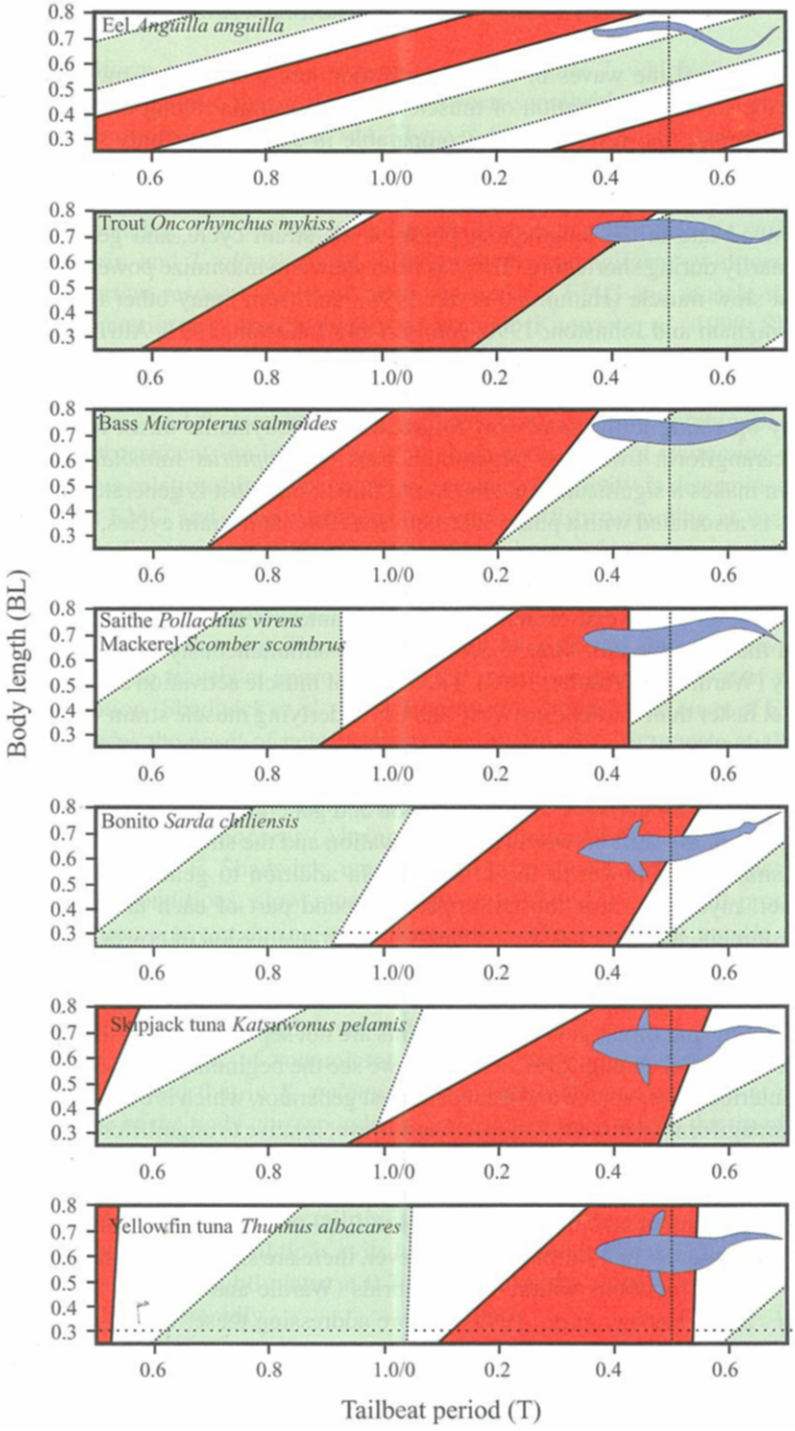
water. More detailed reviews can be found in Videler (1993), Wardle *et al.* (1995), and Altringham and Ellerby (1999).

As data become available for more species, slow muscle activation patterns can be seen to fall into a sequence that can be related to body form and swimming mode (Wardle *et al.*, 1995; Knower *et al.*, 1999; Altringham and Ellerby, 1999). The main features of this sequence, which are independent of swimming speed, are shown in Figure 7. It should be remembered that some fish studied have body forms and swimming modes which vary somewhat from the pattern described, for example, those built for rapid acceleration or extreme maneuverability, and these are not discussed. The colored wedges show when muscle is activated on alternate sides of the body during a tailbeat. The x-axis is time through this tailbeat, and the y-axis position on the body. Let us start with anguilliform swimming, before progressing toward tuna. In anguilliform locomotion thrust is generated against the water along much of the body length, for most of the tailbeat. To achieve this, the body is thrown into almost two complete, large-amplitude waves by the muscle activation pattern shown. At any given instant muscle is active on both sides of the body, and myotomes near the head are activated before those near the tail on the same side have been switched off. During the transition to thunniform swimming (from top to bottom of Figure 7), through subcarangiform and carangiform modes, muscle activity patterns change, leading to:

1. An increase in λ_b, the wavelength of body bending (expressed as a proportion of BL); that is, the number of bending waves on the body at any instant decreases from 1.7 to <1
2. A decrease in the duration of muscle activity on one side of the body, as a proportion of the tailbeat period
3. A decrease in the overlap of activity of muscle at the head and tail of the fish and of muscle activity on opposite sides of the body

This leads to a transition from a more prolonged production of thrust along most of the body length in eels, to short, discrete bursts of thrust at the tail only, in tuna.

Fig. 7. Electromyography (EMG) patterns in the slow muscle of scombrid and nonscombrid fish during steady swimming. Time (x-axis) is expressed in terms of tailbeat period (T). At 0.5 T the tail crosses the swimming track and maximum thrust is generated at the caudal fin (vertical dotted lines). Body position as a fraction of fork length (BL) is given by the y-axis. Virtually all of the slow muscle is found between 0.25 and 0.8 BL. In the bonito and the two tuna species there is little or no slow muscle anterior to 0.3 BL, indicated by the dotted horizontal line. The green and red polygons show when muscle on the two sides of the body is active. These patterns are independent of swimming speed. Data are from deep slow muscle of the two tuna species and from superficial slow muscle of all other species. Data for eel are from Gillis (1998); trout, Hammond *et al.* (1998); bass, Jayne and Lauder (1995); saithe and mackerel, Wardle and Videler (1993); bonito, Ellerby *et al.* (2000); and tuna, Knower *et al.* (1999).


Eel *Anguilla anguilla*
Trout *Oncorhynchus mykiss*
Bass *Micropterus salmoides*
Saithe *Pollachius virens*
Mackerel *Scomber scombrus*
Bonito *Sarda chiliensis*
Skipjack tuna *Katsuwonus pelamis*
Yellowfin tuna *Thunnus albacares*
Body length (BL)
Tailbeat period (T)
0.8
0.7
0.6
0.5
0.4
0.3
0.6
0.8
1.0/0
0.2
0.4
0.6

In the eel the waves of muscle activation and deactivation travel at similar speeds, so that the duration of muscle activity is similar along the body length. Furthermore, the EMG wave is comparable in speed to, or only slightly faster than, the wave of bending. Active muscle shortening therefore occurs during much the same phase of the muscle strain cycle at all points on the body. Muscle is activated late in the lengthening phase of the strain cycle, and generates force primarily during shortening. This has been shown to maximize power output from trout slow muscle (Hammond *et al.*, 1998), and from many other muscles (e.g., Altringham and Johnston, 1990; Johnson and Johnston, 1991; Altringham *et al.*, 1993). It is likely therefore that the slow muscle of the eel is also producing close to maximum power. This is consistent with slow muscle at all points along the body operating in the same way to produce hydrodynamic thrust locally. In the subcarangiform trout and largemouth bass (*Micropterus salmoides*) the body again makes a significant contribution to thrust, but most is generated by the tail. This is associated with a phase shift between EMG and strain cycles, and a change in local muscle function, which is more pronounced in carangiform swimmers.

In the carangiform saithe (*Pollachius virens*) the wave of deactivation travels more rapidly than that of activation so that anterior muscle is active for longer than that near the tail. Muscle activity ceases simultaneously at all points on the body (Wardle and Videler, 1993). The waves of muscle activation and deactivation travel faster than the bending wave and the underlying muscle strain wave. Muscle activation therefore occurs earlier in the muscle strain cycle in more caudal myotomes. To increase swimming efficiency and performance, carangiform fish swim with a longer λ_b of lower amplitude and generate most of their thrust at the tail. The phase shift between muscle activation and the strain cycle may assist the transmission of power to the caudal fin. In addition to generating net positive power, myotomes near the tail appear to spend part of each tailbeat as power transmitters, assisting passive elements in the transmission of power generated by more anterior myotomes (Altringham *et al.*, 1993; van Leeuwen, 1995; Wardle *et al.*, 1995; Altringham and Ellerby, 1999). In anguilliform swimmers, power-generating and thrust-generating elements are not separated, but distributed along the body. In subcarangiform swimmers, we see the beginnings of a separation into an anterior power source and a caudal thrust generator, which is even more evident in carangiform swimmers. As discussed above, relative to anguilliform swimmers, slow muscle is increasingly concentrated around 0.5 BL.

The carangiform pattern is also seen in the slow muscle of *Scomber scombrus*, which has similar swimming kinematics to *P. virens*. EMG/strain patterns suggest it uses its muscle in a similar way. However, there are significant differences in the way muscle functions within the scombrids (Wardle and Videler, 1993; Ellerby *et al.*, 2000; Knower *et al.*, 1999). Before addressing these, we will compare the other scombrids studied with the carangiform swimmers to show the ways in

which thunniform swimming is uniquely different. Figure 7, which shows only EMG patterns, suggests that differences between scombrids and *P. virens* are small; however, one feature stands out. There is a near coincidence between the end of muscle activity and peak thrust at the caudal fin in *Sarda chiliensis*, *Katsuwonus pelamis*, and *Thunnus albacares*. In carangiform and subcarangiform swimmers, including *S. scombrus*, peak force lags muscle activity. *Sarda chiliensis*, *K. pelamis*, and *T. albacares* all differ from the carangiform swimmers in another important respect: the phase shift between the EMG and muscle strain cycles from anterior to posterior myotomes is small (Knower *et al.*, 1999; Shadwick *et al.*, 1999; Ellerby *et al.*, 2000). Recent experiments suggest that this means there is unlikely to be a significant change in muscle function along the body, as seen in *P. virens* and *S. scombrus*. The evidence comes from a combination of mechanical experiments on isolated muscle fibers and studies of swimming fish.

The *in vivo* relationship between strain and muscle activity is determined by simultaneous EMG and sonomicrometry recording in fish swimming at various steady speeds. Sonomicrometry is an ultrasonic technique for measuring instantaneous length changes between implanted pairs of piezoelectric crystals. At the same time video images are collected in order to analyze the midline kinematics in relation to muscle strain. These experiments have shown that the wave of muscle shortening travels at approximately the same speed as the wave of slow muscle activation (Shadwick *et al.*, 1999; Ellerby *et al.*, 2000). The onset of EMG activity precedes the onset of muscle shortening by 30°–50° for muscle at all locations. EMG activity continues well into the period of muscle shortening. This pattern is independent of swimming speed. Work loop studies on isolated muscle from *S. chiliensis*, *T. albacares* (Altringham and Block, 1997), and *K. pelamis* (D. A. Syme and R. E. Shadwick, unpublished) have shown that under these *in vivo* operating conditions, slow muscle between 0.35 and 0.7 BL will produce close to maximum power during steady swimming. The power this muscle produces is probably transmitted directly to the caudal fin via the posterior oblique tendons (POTs; Westneat *et al.*, 1993). This probably explains the absence of a lag between muscle activity and thrust at the caudal fin.

Coupling the results of sonomicrometry with body kinematics, Shadwick *et al.* (1999) showed that in *K. pelamis* the minimum in muscle length at sites along one side of the body corresponds closely to the time at which the tip of the caudal fin reaches it greatest lateral deflection to that side. At 0.4 BL muscle shortening and tail tip displacement are virtually in phase, that is, the muscle shortening on the left side begins when the tail tip is at its rightmost position (point b, Figure 8), and ends when the tail tip is at its leftmost position (point d, Figure 8). The strain peaks are only slightly later at 0.7 BL, because the wave of muscle strain travels caudally very rapidly.

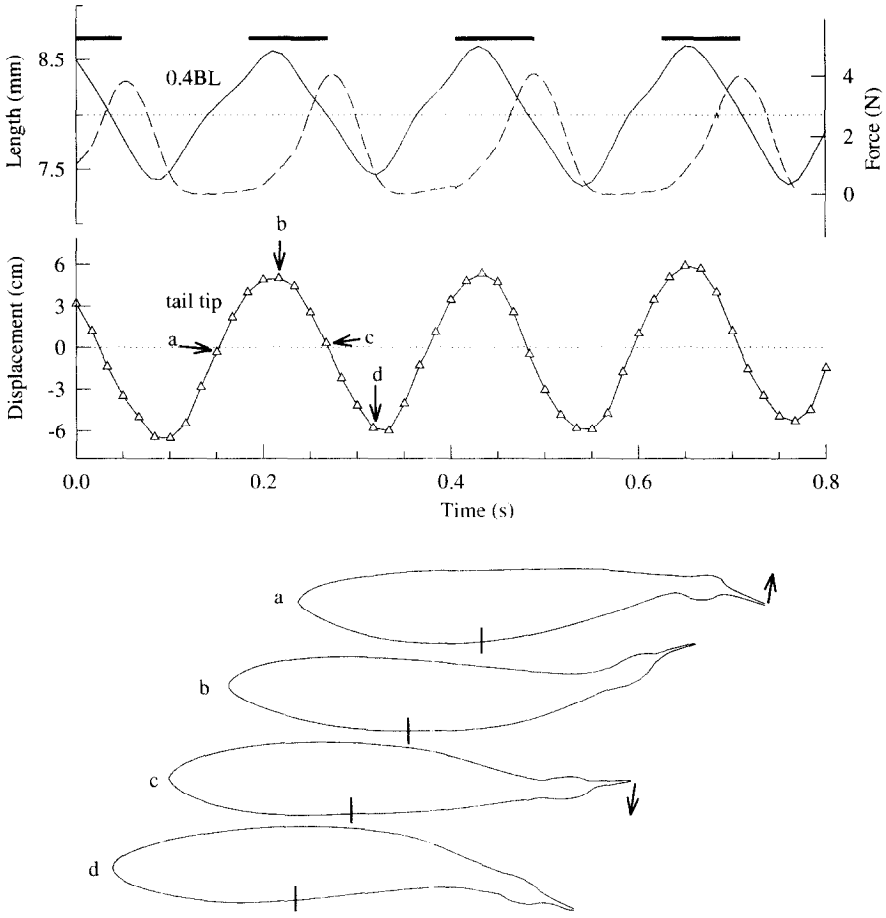


Fig. 8. Slow muscle strain at 0.4 BL (upper trace, solid) and lateral excursion of the tail tip (lower trace) of a skipjack tuna swimming steadily at 2.1 BL s^{-1}. Horizontal bars indicate EMG activity at 0.4 BL. Tail tip displacement to the right of the fish is positive. The four body outlines refer to points a–d on the lower trace. The vertical bars on the outlines indicate 0.4 BL. (From Shadwick *et al.*, 1999.) The time course of caudal tendon force is indicated by the dashed curve, which was recorded in a different experiment and superimposed with its time scale adjusted to match the cycle period and EMG activity of the muscle length trace. (R. E. Shadwick, unpublished.)

X. FORCES GENERATED BY THE MUSCLE

By implanting buckle-type strain gauges on caudal tendons in *Katsuwonus pelamis* and *Thunnus albacares*, Knower *et al.* (1993, 1999) were able to record muscle forces at various steady swimming speeds, as well as in a few bursts. These

records represent the summation of the internal force that is transmitted to the caudal fin via the deep lateral tendons. While this does not account for forces in the superficial tendons, the temporal patterns and relative changes are informative. First, force begins to rise at EMG onset, while the muscle length is still increasing, and peaks approximately as EMG activity ceases (see Figure 8). This coincides with the tail tip crossing the swimming track, at the time when hydrodynamic forces are likely to be maximal (e.g., Lighthill, 1969). Second, the rise of force is slower than its decline after peaking, an indication that the tendon force waveform represents a summation of force from the traveling contraction wave and the more simultaneous deactivation along the body. Third, although the tendons appear to arise from myotomes of the posterior third of the body, the force in the ipsilateral tendon begins to rise well before the activation has occurred that far back. On average the force reached one-third of peak level when only the muscle anterior of 0.65 BL was active (Knower, 1998). This observation demonstrates that anterior muscle force is transmitted directly to the tail, likely via the complex connective tissue framework (Westneat *et al.*, 1993), and illustrates the basis of thunniform swimming—that the anteriorly placed muscle mass drives the caudal propeller directly.

Although there was some variability, tendon force generally showed only a modest increase with speed over the range powered by slow muscle. However, when fast muscle was activated during occasional bursts (TBF up to 16 Hz) tendon forces typically rose 10-fold (Knower, 1998), consistent with a nearly 10:1 ratio of fast to slow muscle.

XI. DO CAUDAL TENDONS FUNCTION AS SPRINGS?

The combination of *in vivo* force data and the mechanical behavior of the tendons makes it possible to assess the potential function of the caudal tendons as energy-saving springs in swimming. These tendons are robust collagenous structures that resemble tendons found in other vertebrates. Shadwick *et al.* (1992) and Knower (1998) subjected excised caudal tendons of *Katsuwonus pelamis* and *Thunnus albacares* to load cycling and determined that the modulus of elasticity and energy dissipation ranged from 0.65 to 1.2 GPa and 7 to 25%, respectively, when loaded to stresses that encompass the *in vivo* range. These compare closely to the properties of mammalian leg tendons that are known to function as effective biological springs in terrestrial locomotion. Knower (1998) performed postmortem tensile tests on tendons from the same fish that furnished *in vivo* force records, and showed that peak tendon forces during steady swimming could impose strains of much less than 1% of tendon length, because the tendons are very thick. Even the maximal burst forces recorded produced strains of only 1.5–2% of tendon

length. Consequently, the strain energy stored in the stretched tendon is insignificant compared to the work done by the muscle in producing thrust. Thus, the caudal tendons in tunas do not function as energy-saving springs, even at maximal swimming effort. This conclusion is based on the following argument (Knower, 1998; Knower and Shadwick, in preparation). The net cost of transport determined for similar size fish (1.6 J BL^{-1}; Dewar and Graham, 1994a,b) was multiplied by speed in BL s^{-1} to yield an estimate, in J s^{-1}, of the metabolic power input required to swim. Assuming a metabolic efficiency of 25%, power input was converted to muscle power output, which is also the power input to the caudal propeller (Webb, 1975). Multiplying by half the duration of the tailbeat cycle gave an estimate, in joules, of the mechanical work performed per tail sweep. A comparison of this quantity with the energy used to stretch the caudal tendons on one side during a tail sweep revealed that tendon strain energy accounted for less than 0.5% of the total mechanical energy used to swim. Even if this proportion rose by an order of magnitude during burst swimming, the tendon strain energy would still not be a significant factor in overall locomotor energetics.

XII. THE UNCOUPLING OF SLOW MUSCLE STRAIN FROM BODY BENDING

Another distinguishing feature of tunas is the uncoupling of slow muscle strain from local body bending. Unlike contraction of the superficial slow muscle in other fish, the shortening of deep slow muscle in tuna significantly lags behind changes in the local midline curvature (Shadwick *et al.*, 1999; S. L. Katz and R. E. Shadwick, unpublished). Analysis of midline curvature in *Katsuwonus pelamis* as a function of time showed that, at axial locations between 0.4 and 0.74 BL (where the majority of the slow muscle mass is located), the wave of midline curvature travels along the body in advance of the wave of muscle shortening (Figure 9).

In *K. pelamis* and probably other tunas such as *Thunnus albacares* (S. L. Katz and R. E. Shadwick, unpublished), the temporal separation of slow muscle strain and local curvature is so pronounced that, in the midbody region, muscle shortening at each location is synchronous with midline curvature at locations that are 9–10 vertebral segments more posterior. Interestingly, this distance closely matches the span of the elongated myotomes (Fierstine and Walters, 1968) and these observations suggest that slow muscle contractions cause deformation of the body at more posterior locations, rather than locally. This arrangement is quite different from the bending beam model of slow muscle strain in other fish (van Leeuwen *et al.*, 1990; Coughlin *et al.*, 1996; Katz *et al.*, 1999), but is consistent with the hypothesis that tunas produce thrust by motion of the caudal fin rather than by body undulations (Fierstine and Walters, 1968; Lighthill, 1970). Can muscle shortening be uncoupled from local bending? It seems likely that forces

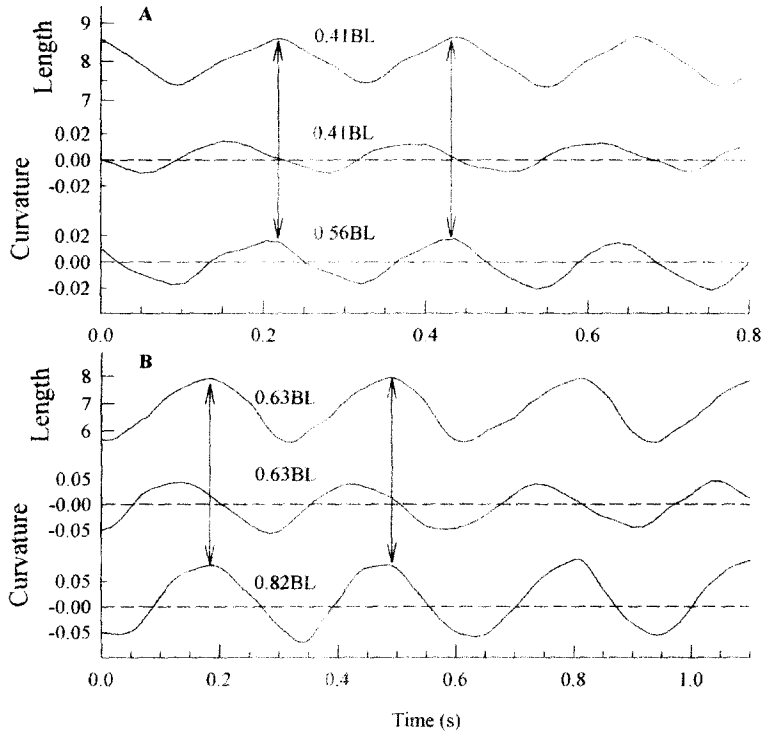


Fig. 9. Uncoupling of muscle strain from local body curvature. (A) Muscle segment length, measured by sonomicrometry (in mm), on the left side of the body at 0.4 BL in a skipjack tuna swimming at 2.1 BL s^{-1} compared with midline curvature (in cm^{-1}) at that same location and at a more posterior location of 0.56 BL. (B) Muscle segment length on the left side of the body at 0.63 BL in a skipjack swimming at 1.75 BL s^{-1} compared with curvature at 0.63 and 0.82 BL. Positive values of curvature indicate the midline is convex on the left. Arrows show the peaks in muscle length coincide with peaks in convex curvature at more posterior locations (from Shadwick *et al.*, 1999) with permission from Company of Biologists, Ltd.

and shortening generated by fibers in fish myotomal cones are transmitted along the backbone through a network of myoseptal and dermal connective tissues (Wainwright, 1983; Westneat *et al.*, 1993; Westneat, this volume). In tunas the contraction of internal slow muscle may project caudally through the posterior oblique tendons that lie within the horizontal septum, the myoseptal connections to the skin, and the robust tendons that link directly onto the caudal fin rays (Fierstine and Walters, 1968). Thus, local shortening could cause bending at more posterior locations, and the slow muscle mass, while primarily located in midbody regions, would function as a forceful actuator to deliver contractile power to the caudal region. If correct, then shearing must occur between the internal slow

muscle and the surrounding mass of fast muscle which, when inactive, must deform in synchrony with the bending midline (Katz *et al.*, 1999). How this may change when the fast muscle actively shortens in fast swimming is not yet known. Studies of fast muscle function in burst swimming remain a challenging goal of tuna biomechanics research.

XIII. VARIATIONS WITHIN SCOMBRIDS

Scomber scombrus is a carangiform swimmer (Wardle and Videler, 1993). *Sarda chiliensis* has swimming kinematics similar to those of *S. scombrus* (Ellerby *et al.*, 2000), but as a close ectothermic relative of the endothermic tuna, has some features in common with them. Overlap between myotomal cones and the lengths of the POTs of *S. chiliensis* are greater than those in *S. scombrus* and more comparable to those of *Katsuwonus pelamis* and *Thunnus albacares. Sarda chiliensis* also has more slow muscle than *S. scombrus,* and a significant component is internalized. Together with the small EMG/strain phase shift along the body, these anatomical similarities suggest that *S. chiliensis* uses its muscle and POTs in a similar way to tuna. However, unlike in tuna, deep muscle strain in *S. chiliensis* appears to be in phase with local bending, further emphasizing its status as a possible transitional stage between carangiform and thunniform swimming. The basic EMG pattern in all scombrids (Figure 7) resembles that of the carangiform saithe. A rapid wave of EMG onset travels down the body, followed by a more rapid wave of EMG offset, such that the proportion of the tailbeat during which the muscle is active (the duty cycle) decreases from anterior to posterior. EMG onset and offset wave speeds are greatest in *T. albacares,* and in combination with the greatest concentration of slow muscle around 0.5 BL and the largest λ_b, make muscle power production a more "pulsatile" event.

XIV. SUMMARY

In summary, in the endothermic tuna, and in *Sarda chiliensis,* muscle is active only on one side of the body at any instant and it has a short duty cycle. This is due to the progression of a rapid wave of muscle activation down the body and the concentration of the slow muscle around 0.5 BL. Internal slow muscle at all locations operates under conditions which generate maximum power: there is no apparent change in muscle function along the body. This power is transmitted rapidly and efficiently to the caudal fin by the POT tendons. Power generation is brief and maximal at the caudal fin just as slow muscle at all locations is switched off. This mechanism yields the features that are the hallmark of "thunniform" locomotion, namely, a low-amplitude body wave and powerful lateral undulations

of the thrust-producing lunate caudal hydrofoil. There is always a price to pay: subcarangiform and carangiform fish are capable of rapid and complex maneuvers. In tuna, maneuverability has been sacrificed for a more efficient thrust generation mechanism.

XV. DIRECTIONS FOR FUTURE RESEARCH

Our current knowledge of anatomical design, muscle function, and swimming mechanics indicates that tunas represent an extreme in undulatory swimming performance. However, there remain many intriguing problems to resolve.

1. Scale effects. Tunas can grow to very large sizes, but most research so far has been on relatively small and immature individuals. Wardle *et al.* (1989) showed that fast muscle twitch time increases with body size in bluefin tuna, indicating that maximal tailbeat frequencies decrease accordingly. Our knowledge of how increasing body size influences swimming kinematics, energetics, muscle mechanics, and preferred and minimum speeds is meager, but is essential for a compete understanding of the swimming performance of the large, mature tunas that constitute the breeding populations.
2. High-speed swimming. We know very little about kinematics of high-speed and burst swimming, and virtually nothing about the mechanics of the fast muscle fibers that power it. Does muscle strain increase to power high-speed sprinting, and is this reflected in an increase in tail tip amplitude? At what speeds are fast fibers recruited, and what contribution, if any, does the slow muscle make to burst swimming? What are the energetic costs associated with maximal swimming performance?
3. Spatial activation of myotomes. It remains unknown whether muscle fibers are activated sequentially according to their axial location or according to the myotome they are part of, and whether activation patterns differ between fast and slow muscle. This issue is potentially very significant in tunas where the highly elongate myotomes can span 13 or more vertebrae, and a cross-section at midbody locations can contain fibers from an equivalent number of myotomes.
4. Regional variation in muscle contractile properties. More experimental evidence is needed to document the variations in muscle contraction speeds which may occur within the slow and fast muscle as a function of axial position, and also with depth at a given position. In addition, the role of superficial slow fibers is unclear. Do they shorten in phase with the underlying slow fibers or in phase with local curvature? At what speeds are they active, and do these fibers have a longitudinal gradient in contractile properties? Wardle *et al.* (1989) predicted that if top sprint speeds are set by the

twitch time of the faster anterior white muscle, then the cycle frequency will be too fast for the slower posterior white muscle to follow and opposing muscles near the tail will overlap in their contractions. This could contribute a stiffening effect and enhance force transmission in the caudal region. Understanding the biomechanical function of these regional variations in muscle properties will be a major challenge.

5. Fluid mechanics and mechanical power. There are no direct measurements of external forces or power output in a swimming fish. Estimates may be made from visualization of fluid flow over the body and in the wake (e.g., Müller *et al.*, 1997; Wolfgang *et al.*, 1999). This type of approach could make possible the calculation of mechanical power production and efficiency in a swimming tuna and, in turn, allow interspecies comparisons, as well as shed light on the importance of the finlets.
6. Internal force production and transmission. We have measurements of tensile forces in caudal tendons and muscle strain along the body, but these do not represent the pattern of force and displacement produced by any single muscle fiber or fascicle. Thus we do not have the equivalent of an *in vivo* muscle work loop as has been obtained in terrestrial vertebrates and birds (Biewener, 1998). This may prove to be an intractable problem, due to the unusual muscle anatomy in fish, but the use of micro force transducers on individual oblique tendons may prove feasible. This could provide information on how the wave of muscle force travels along the body, and how it is focused to the caudal tendons. Finally, the role of the skin in force transmission needs to be addressed experimentally.
7. Interspecies comparisons. Evidence from anatomy, swimming mechanics, and muscle activation suggests there are subtle differences between skipjack and yellowfin tuna slow muscle function (Knower *et al.*, 1999). It would be interesting to determine how these differences are related to differences in their muscle contractile properties. Do differences in fast muscle properties also exist, and what is the functional relevance? In a broader sense, how does the biomechanical design of tunas compare to that of other fast scombrids such as *Acanthocybium*?
8. Convergence with lamnid sharks. Pelagic sharks of the family Lamnidae, such as the mako and great white, share several morphological features with tunas that suggest they are adapted for fast, efficient swimming. They are also able to conserve metabolic heat from their internal slow muscle through the use of a countercurrent heat exchanger (Carey *et al.*, 1971). The evolutionary convergence of these two groups is intriguing because they have evolved independently for over 400 million years. A detailed study of lamnid swimming physiology and biomechanics in the context of convergence with tunas represents a challenging venture for the future.

ACKNOWLEDGMENTS

J.D.A. thanks David Ellerby for many useful discussions and the BBSRC for financial support. R.E.S. thanks Stephen Katz and Douglas Syme for stimulating collaborations, and the National Science Foundation for financial support.

REFERENCES

Alexander, R. McN. (1969). Orientation of muscle fibres in the myomeres of fishes. *J. Mar. Biol. Assoc. U.K.* **49,** 263–290.

Altringham, J. D., and Block, B. A. (1997). Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200,** 2617–2627.

Altringham, J. D., and Ellerby, D. J. (1999). Fish swimming: Patterns in muscle function. *J. Exp. Biol.* **202,** 3397–3403.

Altringham, J. D., and Johnston, I. A. (1990). Modelling muscle power output in a swimming fish. *J. Exp. Biol.* **148,** 395–402.

Altringham, J. D., Wardle, C. S., and Smith, C. I. (1993). Myotomal muscle function at different points on the body of a swimming fish. *J. Exp. Biol.* **182,** 191–206.

Beamish, F. W. H. (1978). Swimming capacity. *In* "Fish Physiology," Vol. 7. "Locomotion" (Hoar, W. S., and Randall, D. J., Eds.), pp. 101–187. Academic Press, New York.

Biewener, A. A. (1998). Muscle function *in vivo:* A comparison of muscles used for elastic energy savings *versus* muscles used to generate mechanical power. *Am. Zool.* **38,** 703–717.

Blake, R. W., Chatters, L. M., and Domenici, P. (1995). Turning radius of yellowfin tuna (*Thunnus albacares*) in unsteady swimming manoeuvres. *J. Fish Biol.* **46,** 536–538.

Blickhan, R., Krick, C., Zehren, D., and Nachtigall, W. (1992). Generation of a vortex chain in the wake of a subundulatory swimmer. *Naturwissenschaften* **79,** 220–221.

Block, B. A., Keen, J. E., Castillo, B., Dewar, H., Freund, E. V., Marcinek, D. J., Brill, R. W., and Farwell, C. (1997). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of their range. *Mar. Biol.* **130,** 119–132.

Boddeke, R., Slijper, E. J., and Stelt, A. van der (1959). Histological characteristics of the body musculature of fishes in connection with their mode of life. *Proc. K. Ned. Akad. Wet. Ser. C Biol. Med. Sci.* **62,** 576–588.

Bone, Q. (1978). Locomotor muscle. *In* "Fish Physiology," Vol. 7. "Locomotion" (Hoar, W. S., and Randall, D. J., Eds.), pp. 361–424. Academic Press, New York.

Bone, Q., and Chubb, A. D. (1983). The retial system of the locomotor muscles in the thresher shark. *J. Mar. Biol. Assoc. U.K.* **63,** 239–241.

Bone, Q., Kiceniuk, J., and Jones, D. R. (1978). On the role of the different fibre types in fish myotomes at intermediate swimming speeds. *Fish. Bull.* **76,** 691–699.

Breder, C. M. (1926). The locomotion of fishes. *Zoologica (N.Y.)* **4,** 159–297.

Brill, R. W. (1987). On the standard metabolic rate of tropical tunas, including the effect of body size and acute temperature change. *Fish. Bull.* **85,** 25–35.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes and dolphin fish. *Comp. Biochem. Physiol.* **113A,** 3–15.

Carey, F. G. (1981). Warm fish. *In* "A Companion to Animal Physiology" (Taylor, C. R., Johansen, J., and Bolis, L., Eds.), pp. 216–233. Cambridge Univ. Press, Cambridge.

Carey, F. G. (1990). Further observations on the biology of the swordfish. *In* "Planning the Future of Billfishes" (Stroud, R. H., Ed.), pp.103–122. Natl. Coal. Mar. Cons., Savannah.

Carey, F. G., and Lawson, K. D. (1973). Temperature regulation in free-swimming bluefin tuna. *Comp. Biochem. Physiol.* **44A,** 375–392.

Carey, F. G., and Scharold, J. V. (1991). Movements of blue sharks in course and depth. *Mar. Biol.* **106,** 329–342.

Carey, F. G., and Teal, J. M. (1966). Heat conservation in tuna fish muscle. *P.N.A.S.* **56,** 1464–1469.

Carey, F. G., Teal, J. M., Kanwisher, J. W., Lawson, K. D., and Beckett, J. S. (1971). Warm-bodied fish. *Am. Zool.* **11,** 135–143.

Coughlin, D. J., Valdes, L., and Rome, L. C. (1996). Muscle length changes during swimming in scup: Sonomicrometry verifies the high-speed cine technique. *J. Exp. Biol.* **199,** 459–463.

D'Août and Aerts, P. (1999). A kinematic comparison of forward and backward swimming in the eel *Anguilla anguilla. J. Exp. Biol.* **202,** 1511–1521.

Davies, M., and Johnston, I. A. (1993). Muscle fibres in rostral and caudal myotomes of the Atlantic cod have different contractile properties. *J. Physiol. Lond.* **459,** 8P.

Davies, M. L. F., Johnston, I. A., and van de Wal, J. (1995). Muscle fibres in rostral and caudal myotomes of the Atlantic cod (*Gadus morhua*) have different contractile properties. *Physiol. Zool.* **68,** 673–679.

Dewar, H. (1993). Studies of tropical tuna swimming performance: Thermoregulation, swimming mechanics and energetics. Ph.D. thesis, University of California, San Diego.

Dewar, H., and Graham, J. B. (1994a). Studies of tropical tuna swimming performance in a large water tunnel. I. Energetics. *J. Exp. Biol.* **192,** 13–31.

Dewar, H., and Graham, J. B. (1994b). Studies of tropical tuna swimming performance in a large water tunnel. III. Kinematics. *J. Exp. Biol.* 192, 45–59.

Dizon, A. E., and Brill, R. W. (1979). Thermoregulation in yellowfin tuna, *Thunnus albacares. Physiol. Zool.* **52,** 581–593.

Ellerby, D. J., Altringham, J. D., Williams, T., and Block, B. A. (2000). Slow muscle function in the bonito, *Sarda chiliensis. J. Exp. Biol.,* **203,** 2001–2013.

Fierstine, H. L., and Walters, V. (1968). Studies in locomotion and anatomy of scombroid fishes. *Mem. S. Calif. Acad. Sci.* **6,** 1–31.

Gillis, G. B. (1998). Neuromuscular control of anguilliform locomotion: Patterns of red and white muscle activity during swimming in the American eel *Anguilla rostrata. J. Exp. Biol.* **201,** 3245–3256.

Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares,* and skipjack tuna, *Katsuwonus pelamis,* and the adaptive significance of elevated body temperatures in scombrid fishes. *Fish. Bull.* **73,** 219–229.

Graham, J. B., and Dickson, K. A. (1981). Physiological thermoregulation in the albacore *Thunnus alalunga. Physiol. Zool.* **54,** 470–486.

Graham, J. B., and Dickson, K. A. (2000). The evolution of thunniform locomotion and heat conservation in scombrid fishes: New insights based on the morphology of *Allothunnus fallai. Zool. J. Linn. Soc.,* **129,** 419–466.

Graham, J. B., Koehrn, F. J., and Dickson, K. A. (1983). Distribution and relative proportions of red muscle in scombrid fishes: Consequences of body size and relationships to locomotion and endothermy. *Can. J. Zool.* **61,** 2087–2096.

Graham, J. B., Lowell, W. R., Lai, N. C., and Laurs, R. M. (1989). O_2 tension, swimming-velocity, and thermal effects on the metabolic rate of the Pacific albacore *Thunnus alalunga. Exp. Biol.* **48,** 89–94.

Hammond, L., Altringham, J. D., and Wardle, C. S. (1998). Myotomal slow muscle function of rainbow trout *Oncorhynchus mykiss* during steady swimming. *J. Exp. Biol.* **201,** 1659–1671.

Hertel, H. (1966). "Structure, Form and Movement." Reinhold, New York.

Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R., and Fournier, D. A. (1992). Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358,** 410–412.

Hunter, J. R., and Zweifel, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus,* and other fishes. *Fish. Bull.* **69,** 253–266.

Jayne, B. C., and Lauder, G. V. (1995). Red muscle motor patterns during steady swimming in largemouth bass: Effects of speed and correlations with axial kinematics. *J. Exp. Biol.* **198,** 1575–1587.

Johnson, T. P., and Johnston, I. A. (1991). Power output of fish muscle fibres performing oscillatory work: Effect of seasonal temperature change. *J. Exp. Biol.* **157,** 409–423.

Johnson, W. E., and Groot, C. (1963). Observations on the migration of young sockeye salmon (*Oncorhynchus nerka*) through a large, complex lake system. *J. Fish Res. Bd. Can.* **20,** 919–938.

Johnston, I. A. (1981). Structure and function of fish muscles. *In* "Vertebrate Locomotion" (Day, M. H., Ed.), pp. 71–113. Academic Press, London.

Johnston, I. A., and Moon, T. W. (1980). Endurance exercise training in the fast and slow muscles of a teleost fish, *Pollachius virens. J. Comp. Physiol.* **135,** 147–156.

Katz, S. L., and Shadwick R. E. (1998). Curvature of fish midlines as an index of muscle strain during swimming suggests lateral muscle produces net positive work *J. Theor. Biol.* **193,** 243–256.

Katz, S. L., Shadwick, R. E., and Rapoport, H. S. (1999). Muscle strain histories in swimming milkfish in steady and sprinting gaits. *J. Exp. Biol.* **202,** 529–541.

Knower, T. (1998). Biomechanics of thunniform swimming. Ph.D. thesis, University of California, San Diego.

Knower, T., Shadwick, R. E., Biewener, A. A., Korsmeyer, K., and Graham, J. B. (1993). Direct measurement of tail tendon forces in swimming tuna. *Am. Zool.* **33,** 30A.

Knower, T., Shadwick, R. E., Katz, S. L., Graham, J. B., and Wardle, C. S. (1999). Red muscle activation patterns in yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas during steady swimming. *J. Exp. Biol.* **202,** 2127–2138.

Lighthill, M. J. (1969). Hydrodynamics of aquatic animal propulsion. *Ann. Rev. Fluid. Mech.* **1,** 413–446.

Lighthill, M. J. (1970). Aquatic animal propulsion of high hydromechanical efficiency. *J. Fluid. Mech.* **44,** 265–301.

Lighthill, M. J. (1975). "Mathematical Biofluid Dynamics." Soc. Ind. Appl. Math., Philadelphia.

Lindsey, C. C. (1978). Form, function and locomotory habits in fish. *In* "Fish Physiology," Vol. 7. "Locomotion" (Hoar, W. S., and Randall, D. J., Eds.), pp. 1–100. Academic Press, New York.

Magnuson, J. J. (1970). Hydrostatic equilibrium of *Euthynnus affinis,* a pelagic teleost without a gas bladder. *Copeia,* 56–85.

Magnuson, J. J. (1978). Locomotion of scombrid fishes. *In* "Fish Physiology," Vol. 7. "Locomotion" (Hoar, W. S., and Randall, D. J., Eds.), pp. 239–313. Academic Press, New York.

Magnuson, J. J., and Prescott, J. H. (1966). Courtship, locomotion, feeding, and miscellaneous behavior of Pacific bonito (*Sarda chiliensis*). *Anim. Behav.* **14,** 54–67.

Müller, U. M., van den Heuvel, B. L. E., Stamhuis, E. J., and Videler, J. J. (1997). Fish foot prints: Morphology and energetics of the wake behind a continuously swimming mullet (*Chelon labrosus* Risso). *J. Exp. Biol.* **200,** 2893–2906.

Nauen, J. C., and Lauder, G. V. (2000). Locomotion in scombrid fishes. Kinematics of finlets in the chub mackerel. *J. Exp. Biol.* **203,** 2247–2259.

Neave, F. (1964). Ocean migrations of Pacific salmon. *J. Fish. Res. Bd. Can.* **21,** 1227–1244.

Pyatetskiy, V. Y. (1970). Kinematic swimming characteristics of some fast marine fish. *In* "Hydrodynamic Problems of Bionics (USSR)," *Bionika* 4, pp. 12–23. 1971, Joint Publications Research Service, 52605, Arlington, VA.

Rayner, M. D., and Keenan, M. J. (1967). Role of red and white muscles in the swimming of skipjack tuna. *Nature* **214,** 392–393.

Rome, L. C., Swank, D., and Corda, D. (1993) How fish power swimming. *Science* **261,** 340–343.

Shadwick, R. E., Knower, T., and Fonseca, M. (1992). The mechanical organisation of muscle and tendon in yellowfin tuna. *Am. Zool.* **32,** 159A.

Shadwick, R. E., Steffensen, J. F., Katz, S. L., and Knower, T. (1998). Muscle dynamics in fish during steady swimming. *Am. Zool.* **38,** 755–770.

Shadwick, R. E., Katz, S. L., Korsmeyer, K. E., Knower, T., and Covell, J. W. (1999). Muscle dynamics in skipjack tuna: Timing of red muscle shortening in relation to activation and body curvature during steady swimming. *J. Exp. Biol.* **202,** 2139–2150.

Triantafyllou, G. S., Triantafyllou, M. S., and Grosenbaugh, M. A. (1993). Optimal thrust development in oscillating foils with an application to fish propulsion. *J. Fluids Struc.* **7,** 205–224.

Van Leeuwen, J. L. (1995). The action of muscles in swimming fish. *Exp. Physiol.* **80,** 177–191.

Van Leeuwen, J. L., Lankheet, M. J. M., Akster H. A., and Osse, J. W. M. (1990). Function of red axial muscle of carp (*Cyprinus carpio*): Recruitment and normalised power output during swimming in different modes. *J. Zool. Lond.* **220,** 123–145.

Videler, J. J. (1993). "Fish Swimming." Chapman and Hall, London.

Videler, J. J., and Hess, F. (1984). Fast continuous swimming of two pelagic predators, saithe (*Pollachius virens*) and mackerel (*Scomber scombrus*): A kinematic analysis. *J. Exp. Biol.* **109,** 209–228.

Walters, V. (1962). Body form and swimming performance in the scombroid fishes. *Am. Zool.* **2,** 143–149.

Wainwright, S. A. (1983). To bend a fish. *In* "Fish Biomechanics" (Webb, P., and Weihs, D., Eds.), pp. 68–91. Praeger Press, New York.

Wardle, C. S., and He, P. (1988). Burst swimming speeds of mackerel, *Scomber scombrus* L. *J. Fish Biol.* **32,** 471–478.

Wardle, C. S., and Videler, J. J. (1980). How do fish break the speed limit? *Nature* **284,** 445–447.

Wardle, C. S., and Videler, J. J. (1993). The timing of electromyograms in the lateral myotomes of mackerel and saithe at different swimming speeds. *J. Fish Biol.* **42,** 347–359.

Wardle, C. S., Videler, J. J., Arimoto, T., Franco, J. M., and He, P. (1989). The muscle twitch and the maximum swimming speed of giant bluefin tuna, Thunnus thynnus L. *J. Fish Biol.* **35,** 129–137.

Wardle, C. S., Videler, J. J., and Altringham, J. D. (1995). Tuning in to fish swimming waves: Body form, swimming mode and muscle function. *J. Exp. Biol.* **198,** 1629–1636.

Webb, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Can.* **190,** 1–159.

Webb, P. W. (1978). Hydrodynamics: Non-scombroid fish. *In* "Fish Physiology," Vol. 7. "Locomotion" (Hoar, W. S., and Randall, D. J., Eds.), pp. 189–237. Academic Press, New York.

Weihs, D. (1989). Design features and mechanics of axial locomotion in fish. *Am. Zool.* **29,** 151–160.

Westneat, M. W., Hoese, W., Pell, C. A., and Wainwright, S. A. (1993). The horizontal septum: Mechanisms of force transfer in locomotion of scombrid fishes (Scombridae: Perciformes). *J. Morph.* **217,** 183–204.

Wolfgang, M. J., Anderson, J. M., Grosenbaugh, M. A., Yue, D. K., and Triantafyllou, M. S. (1999). Near-body flow dynamics in swimming fish. *J. Exp. Biol.* **202,** 2303–2327.

Yuen, H. S. H. (1966). Swimming speeds of yellowfin and skipjack tuna. *Trans. Am. Fish. Soc.* **95,** 203–209.

9

TUNA OCEANOGRAPHY—AN APPLIED SCIENCE

GARY D. SHARP

I. Introduction
II. Historical Tuna Fisheries and Related Oceanography
  A. Longlining—Wide and Deep Studies
  B. Local Weather and Global Climate Change
III. Physics, Fisheries, and Dynamic Perspectives
  A. Physical Structures versus Other Contextual Changes
  B. Continuous Changes in the Big Picture
  C. Changes in Markets and Resource Ownership
IV. A Brief Review of High Seas Tuna Fisheries Development Patterns
  A. Innovations in Technology Play Major Roles in Recent Changes
  B. Pole-and-Line Baitboats
  C. Purse Seines
  D. Longline Fishing Pattern Changes
  E. Ongoing Changes in Longline Fleets and Fisheries Interactions
  F. Ocean Climate Changes and Fishery Responses
  G. Disappearing Traditional Fisheries
V. Habits and Habitats of Tunas
VI. Coordinated Empirical Studies of Tuna Behavior and Abundance within Ocean Gradients
VII. Tuna Schools and Dynamic Interactions
  A. Why Tunas Aggregate
VIII. The Importance of Studying Individual Fish Behavior
IX. The Ecocosmological Question: "Why Are Tunas Where They Are?"
X. Conclusions

I. INTRODUCTION

Empirical science and application are one in the field of tuna oceanography. The observations from fishing vessels and decades of study from various oceanographic platforms have proven of great value to understanding the relationships between ocean variations and fisheries operations (Uda, 1927, 1957; Matsumoto *et al.*, 1960; Hela and Laevastu, 1971; Saito, 1973, 1975; Saito and Sasaki, 1975;

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

Sharp, 1978, 1979; Sund *et al.*, 1981; Marsac and Hallier, 1991; Gauldie and Sharp, 1995; Lehodey *et al.*, 1997, 1998).

There are several major functions that tuna oceanography studies can provide for those working to understand tuna fisheries and related tuna biology. One is to help understand the variations of catch statistics from various fisheries operating within similar or adjacent regions on one or more species of tunas. Another is to help understand the general shifts in apparent population abundances over large and small areas in time. Others include learning more about the responses of tunas to ocean variability and production patterns so that forecasts of behaviors, catch potentials, and status of resource population might be improved. The following is a brief survey of recent and past efforts to improve our understanding and use of fisheries and ocean data.

We have known from fisheries catch data, and recent decades of associated satellite imagery, that tunas tend to aggregate about ocean features and discontinuities (Sharp, 1976, 1978; Laurs and Lynn, 1977; Laurs (1997); Gunn and Block, this volume). The recent ECOTAP research points clearly to the production and feeding regime as the principle attraction to these features in horizontal and vertical dimensions. We also know that much of the offshore, open ocean is more structured vertically than horizontally, providing subsurface features and topography that likely act as both "fueling stations" and "roadways" in this otherwise relatively featureless environment. Major predators such as the tunas have certainly learned to take advantage of these cues and phenomena in order to thrive as well as they do, particularly in the major ocean gyres, often described as being hypertrophic, or "sterile." Lest anyone doubt this, a quick examination of the *Atlas of Tropical Tuna Fisheries* (Fonteneau, 1997) will show that there are few or no oceanic regions between 45°N and 45°S that do not have substantial tuna catches, depending upon the season. This is direct evidence that our abilities to measure primary production, and hence ocean ecosystem productivity, are seriously flawed and lead to underestimation of true ocean production levels through the application of regionally integrated mean seasonal values. Recent studies by Nicholas Welschmeyer of Moss Landing Marine Laboratories have confirmed that conventional (C14) methods for measuring primary production underestimate true production from 1.7 to 2.0 times on a transect from Monterey Bay to Hawaii (Welschmeyer *et al.*, 1999).

The two major reproduction and juvenile growout regions in the Atlantic for several tuna species are the Sargasso Sea, southward toward the equator, and south of the equator into the South Atlantic central gyre (Bard, 1981). The maturing and mature adults appear to congregate seasonally along the western coastal rises, as the short winter and spring blooms and subsequent peak production occurs, following the cascade of sequential higher trophic feeding. Offshore, the production of the North Atlantic Subtropical region (NASTW, per Longhurst, 1995) peaks and phytoplankton accumulates from November, peaks in April, and then declines steadily until June, after which it is low until the cycle begins again. Feed for tunas

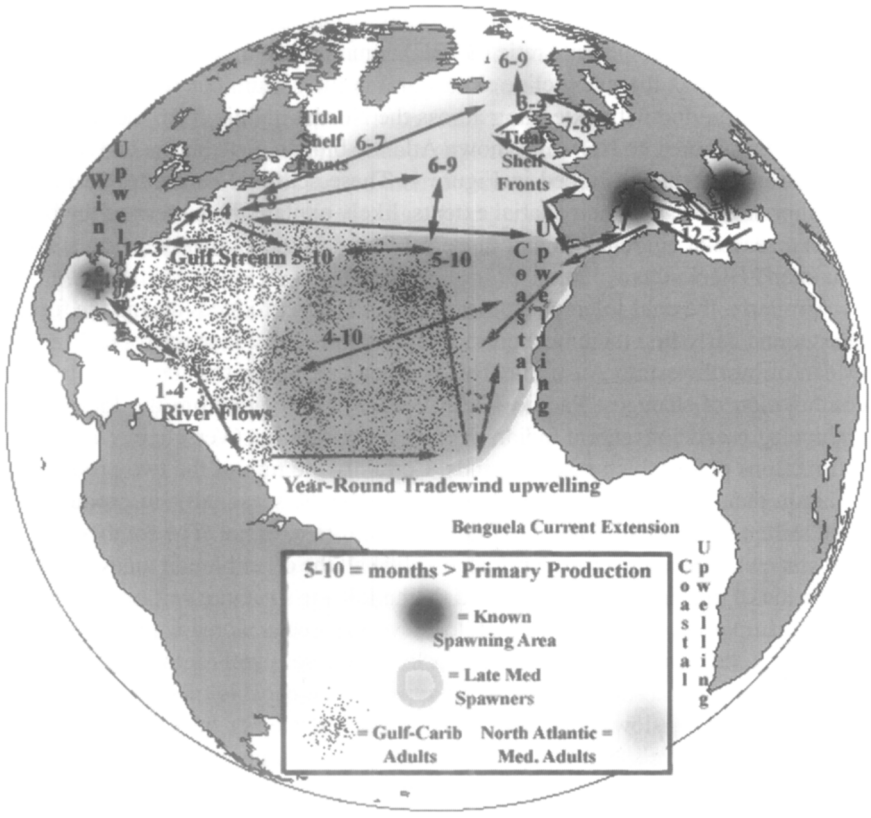


Fig. 1. Historical Atlantic bluefin tuna fisheries data, and the tag and release data from the reviews by Mather *et al.* (1995) and Rivas (1978) along with recent PSAT and archival tag studies provided the information to overlay onto the Longhurst (1995) monthly peak primary production maps for the well-studied North Atlantic Ocean. Three known spawning areas of Atlantic bluefin tuna are identified in the Gulf of Mexico-Caribbean Sea; the northern Mediterranean; and the Black Sea (where spawners have been excluded for more than a decade due to massive ecosystem degradations). I have attempted to outline the pathways from and to these spawning areas for adults, linked by feeding grounds over the annual cycle, with at least one pattern from each of the east–west extremes, bifurcated by the warm Gulf Stream, and the very distinct production patterns north and south of it. An important message is that the distances in the northern sectors are much less than those nearer the equator. This suggests that seasonal east–west mixing of tunas from either the Gulf of Mexico or the Mediterranean would be quite likely in the northern region, although true extents and any distinctive behaviors have been elusive. We are learning quickly from new electronic tagging tools.

will increase with time after the initial blooms. To the north, in the North Atlantic Drift (NADR) and Southern Arctic (SARC) domains, production peaks from June through August as the pycnocline shoals and is fully illuminated, creating large expanses of productivity extending across the North Atlantic from the Bahamas, crossing the Azores, to Norway. Known Atlantic bluefin distribution and seasonal production patterns are linked in Figure 1. These seasonal shifts in oceanic regional production, and their spatial extents, likely explain the pattern of the bluefin tuna seasonal aggregation and dispersal found in the archival tagging studies (Gunn and Block, this volume).

Similarly, the cold-tolerant southern bluefin tuna reproduces during the fourth quarter and early first (summer) quarter in a region of the deepest tropical Indian Ocean off northwestern Australia. This is when and where the surface water is a combination of strongest Pacific Warm Pool flow-through from the Indonesian archipelagos and convergent Indian Ocean gyre circulation (Verschell *et al.*, 1995) as functions of variable seasonal winds. Certainly the mix of the two produces a situation that enhances both chemistry and nutrients, seasonally, to produce the right milieu for the young bluefin tuna larvae to thrive, or not. The southern bluefin's somewhat erratic recruitment success, like all the other bluefin tunas, is likely a function of this production cycle, and their adult age structure variations as well.

The importance and impacts of local versus ocean domain production on bluefin or other tunas with tendencies for localized, seasonal reproduction cannot be overemphasized. Although all tunas appear to be capable of serial spawning, those with longer, slower developing life-history strategies have had opened to them the higher levels of subtropical to subarctic ocean production, with its generally lesser competition and stronger seasonal cycling. Their large adult sizes and lesser ability to cope with tropical upper ocean metabolic demands shorten their residence times in the already crowded upper tropical ocean domains. These wonderful fishes' unique adaptations and yet overlapping pathways point to how the temperate-tolerant tunas and more tropical species have adapted via such different strategies and capabilities. All these interactions are reflected in the rapidly evolving global tuna fisheries. The remainder of this chapter will deal with the successes and types of questions that applications of multidisciplinary research and the power of the new pop-off satellite tags (PSATs) can address and what they cannot yet resolve.

II. HISTORICAL TUNA FISHERIES AND RELATED OCEANOGRAPHY

In order to best understand what has already been learned about tuna oceanography, it helps to understand a bit of the history of fisheries–tuna interactions from localized, historical perspectives. Most modern tuna fisheries started from

coastal hook-and-line fishing centers, and expanded with migrants from these locations. The species of tunas caught were associated with either cool subtropical habitats, for example, albacore and bluefin tunas, or the tropical yellowfin and skipjack tunas. For example, southern California's early 19th century pole-and-line and troll tuna fisheries derived from applications of immigrant Okinawan fishermen's traditional technology and their counterparts from Sicily, the Azores, and Madeira, where harpoons, seines, handlines, and trolled jigs were more traditional. West Africa's industrial tropical tuna fisheries evolved first from Cape Verde's pole-and-line styles, and then those of Japanese joint ventures. These were eventually joined by both Spanish and French high seas seining, that were in turn cloned from southern California's hybrid cultural fisheries developments. Bard and Santiago (1998) review the historical surface albacore fisheries of the Atlantic Ocean. Laurs and Lynn (1977) describe the affinities of subadult albacore for various subtropical habitats, and their submergence as they mature and return to tropical latitudes.

The dynamic features that create major tropical tuna surface fisheries vary. The environmental features that bind the eastern tropical Atlantic and Pacific are the regions' shallow oxygen minima as a result of seasonal winds and upwelling production. More oceanic and island tuna fisheries are created by island wakes and Taylor columns over sea mounts (Bakun, 1996), as well as by convergence and divergence of ocean currents. Each unique fishery situation is caused by local food–fish production. Dynamic local oceanography and the sequential cascades of ecological production favor tropical tunas, particularly skipjack and yellowfin, whose nomadic upper-ocean lifestyles benefit from the minimal competition from other tuna species or other large-sized predator fishes. Why? In the eastern tropical Atlantic and Pacific fisheries, skipjack and yellowfin tunas dominate because the higher productivity typically uses up the available oxygen during the night, and below the photic zone, leaving too little oxygen (as we will explore next) at the other tuna species' preferred habitat depths and temperatures. Thus, the adults of these other species are excluded from all but the very fringes of these vast eastern tropical regions.

Surface-oriented skipjack and yellowfin schools dominate oceanic island surface fisheries. In the upper ocean, where adequate oxygen levels are met, the tropical tunas coexist, but as oxygen levels decline, the smaller tunas' requirements act quickly to exclude them, while the lesser demands of older and larger tunas allow them to swim and explore the lower oxygen levels (Sharp, 1978; Brill, 1994). When oxygen levels reach thresholds between 3.5 and 2.0 ml/liter, most of the tunas are excluded. Despite this limitation, deep thermoclines and scattered production centers draw the larger, cooler-ocean-capable adult albacore and bigeye into the depths, where they tend to scatter, minimizing competition among species and within their own species. Development of oceanic longline fishing technologies was based on these scattered, deep distributions. These adults then find them-

selves orienting to physical-chemical gradients and interfaces and their resulting ecological features, and become vulnerable to handline or longline fishers near islands, sea mounts, and banks, particularly at night. The dynamics of the organisms that form the deep scattering layer are key to this diurnal behavior (Sund *et al.*, 1981; Bertrand *et al.*, 1999a,b).

A. Longlining—Wide and Deep Studies

It is from early studies of longline fisheries by Japanese scientists that we first learned about the relations between ocean properties and the various tuna and billfish species. It was while reading Hanamoto's (1974, 1975) and Saito's descriptions of catches of tunas using vertical longlines that I decided we knew very little or nothing about adult tuna behavior, distributions, or real abundances. The clue came when after several research cruises using and improving vertical longline gear (Saito, 1973; Saito and Sasaki, 1975; Hanamoto, 1975), they reported the species counts by hook position/depth for their many fishing ventures into the tropical central Pacific Ocean where all the Pacific tuna species were known to coexist somewhere within the water column.

Although often caught, skipjack are rarer than other tunas on longlines, and catches usually peak near the surface. Yellowfin were abundant, and peak catches of adults occurred at about 125 m. They were not often caught below 250 m. Albacore were next, caught below the smaller surface-oriented yellowfin, and most often among the first bigeye, peaking at about 200 m or so. Then came the new insight: bigeye catch rates (fish per available hook at each depth) were observed to increase continuously from first depths of encounters to the bottom of the lines, or to wherever available oxygen levels fell below 1 ml/liter, whichever came first. The experimenters could not sink even these "improved" vertical longlines far enough into the ocean to reach the peak abundance of bigeye tuna. It was clear that we had almost no idea where these tuna, and their more cold-tolerant cousins, the bluefin tunas, could live, or actually thrived in greatest abundance. Block and Gunn (this volume) provide recent insights from electronic tagging studies on individual tunas and billfish in three major oceans, and in particular some important insights about the dynamic capabilities of both Atlantic and southern bluefin tunas in comparison to the other species that have been reported.

B. Local Weather and Global Climate Change

The presence of strongly seasonal equatorial convergence/divergence zones and periodic Warm and Cold Events associated with the El Niño-Southern Oscillation (ENSO) impose a series of relatively frequent regional and global cause and effect patterns in ocean fisheries (Glantz, 1992; Le Blanc and Marsac, 1999). These patterns suggest that these and other ocean and atmospheric processes

stimulate or suppress regional production, depending upon where and which species that you are interested in. There are several processes and patterns that can be confusing, even confounding, as they differentially affect catch rates of the several different gear types, as well as species compositions and distributions.

Monitoring both the ocean climate and the fisheries production can provide generally useful information, while ignoring either can lead to quite misleading conclusions about trends in both fishery resources and ocean climate. For example, as part of these large-scale ocean dynamics, local thermocline profiles are either enhanced or not, and the various tuna species involved may actually become more or less vulnerable to the various fishing gears used (Sharp, 1978, 1979; Marsac and Hallier, 1991; Le Blanc and Marsac, 1999). In the case of the post-1982–1983 El Niño Warm Event, there was a dramatic decrease in vulnerability of the yellowfin in the eastern tropical Pacific fisheries. To some analysts the changes in catch rates signaled the long-awaited collapse of those resources, since the catch rates had been generally in decline since the early 1970s. However, the rebound of the thermocline following the reinitiation of the equatorial trade winds at the end of the Warm Event led to a period of extremely high catch rates. Some advocates concluded that this proved that huge resources had always existed, and that there was no reason to manage the resources at all.

Both are, in fact, wrong interpretations. The thinning of the upper ocean habitat due to the ocean's surface heat removal, regional upwelling, and shallow thermoclines associated with upwelling and ocean cooling following the Warm Event made the entire region's tuna more vulnerable to overexploitation than at any time in the history of the high seas seine fishery. Sharp and McLain (1993a,b) described how the misinterpretation of conventional abundance indexes, particularly when interpreted independently of environmental context data, is a prime cause of fisheries management failure.

III. PHYSICS, FISHERIES, AND DYNAMIC PERSPECTIVES

A. Physical Structures versus Other Contextual Changes

In the western Indian Ocean, the Maldives' tuna fisheries are the oldest documented year-round pole-and-line tuna fishery. Maldives' 1200 islands compose 26 atolls that act as a coarse comb, filtering the impinging ocean currents to create production features that attract pelagic fish schools of all types. For more than a thousand years Maldivian culture had its entire economy based on the local production of skipjack tuna, along with the production of coconut palm that provided both food and fishing tools. Tourism is supplanting some of this economic activity, but cannot provide food from day to day. Maldivian tuna fishermen capture reef

fishes each morning, and transfer them into the sea-water-filled hulls of their half-submerged masdohni fishing craft, in order to portage them to the off-island fishing areas. On sighting tuna schools the baitfish are chummed to attract the small skipjack and yellowfin that are then caught using poles, lines, and barbless hooks. For millennia, Maldivian women spent much of their days boiling, salting, and smoking the loined fish for sale in distant markets they would never see. This limited resource base is a rigorous test of any culture, and attests to these and all islanders' durability.

Several joint ventures began in the late 1970s to help modernize Maldivian tuna operations. The traditionally sail-driven fishing fleet was systematically converted to diesel engines that helped improve their ranges and mobility. Unfortunately, the conversion also placed them on a petroleum economy right at a time when tuna values were dropping and oil prices were beginning to increase. Mobile fish collection services were initiated, where the fish were first frozen and then transported to markets. A small cannery operation was built in 1978 with a limited (8 tons per day) capacity. It could not provide the services needed to handle the tuna deliverable from the many islands. A second round of value-added development projects followed, and in 1986 a new modernized cannery was built that now processes up to 50 tons of fish each day. While the older-styled dried and smoked fish products continue as major market items, ongoing construction of freezer storage facilities has increased the production of canning-quality products. These will continue to grow, creating export products for the growing world market.

Seasonal patterns within the adjacent Arabian Sea to the north and west of the Maldives are sufficiently dynamic and restrictive that the coastal nations and Laccadive islanders to the north have only short fishing seasons (Sharp, 1995). Regional fishing occurs as the more nearshore-oriented longtail tuna or skipjack and yellowfin tuna make quick migrations through their coastal fisheries, attracted by the wave of production induced by the onset of the southwest monsoon. Other than the Maldives and Sri Lanka, most other Arabian Sea locations do not support large fishery-dependent cultures because the Monsoon-induced production also generates large areas of anoxia, precluding entry of tunas and other fishes with high metabolic rates for many months every year. The Bay of Bengal has a much larger oxygen-rich area and the coastal regions are only subject to local anoxia during the peak of the southwest monsoon. Tropical tunas abound from Sri Lanka, eastward to the Andaman Islands and Thailand, on through the shallow Straits of Malacca separating Sumatra and Malaysia, and into the Indonesian Archipelago. Subsistence fisheries have dominated these regions until quite recently. The more eastern regions are unlikely to develop major tuna fisheries for export, simply due to the historical patterns of sociopolitical conflicts and the rather disperse nature of the resource. Tuna fisheries are evolving in this region, but there will need to be more cooperation and organized law and order on the sea before they can thrive.

Sharp (1992) described the relatively recent development of the high seas

seine tuna fisheries of the western Indian Ocean. That development took place as a specific result of a collation of monthly oceanographic and climate data sets over the globe. Applying the same criteria that appeared to promote catch success in the eastern Pacific and Atlantic oceans to the monthly mean ocean observations in the Indian Ocean, regions of likely fishing success were described and mapped (Sharp, 1979). The willingness of the Food and Agriculture Organization (FAO), Fisheries Department's Industry Division staff, and the director of the Indian Ocean Fisheries Development Program, Harry Windsor, to invest in the underlying empirical validity of these maps was immediate. The FAO's and Development Program's respective missions to promote experimental fishing resulted in the rapid and uniquely successful collaboration between the two major high seas resource-owning nations and foreign tuna fishing industry interests. The success of this fishery development activity was unique and thrives today.

The Maldives and Seychelles adopted development patterns best suited to their individual cultural legacies. The Maldives devised a locally operated national fishing project. Seychelles, on the other hand, started out by working closely with French and Spanish fishermen—the two European nations with the most developed tuna fishing industries. After a short period of exploration and test-fishing, the Seychelles Fishing Authority now "sells tickets," or access rights, to its broad Exclusive Economic Zone's (EEZ) tuna resource base, and provides support to visiting fleets, but does not own its own fishing vessels or markets. Both island nations have developed into significant providers of tunas to the international marketplace, with minimal perturbations of local cultures, while their economies have grown. To date, this region's tropical fisheries are not in any danger of overfishing. However, to the south and east, the fisheries for southern bluefin tuna have provided nearly 30 years of information about just why all fisheries need to be carefully documented, and managed, prior to the occurrence of debilitating overexploitation.

B. Continuous Changes in the Big Picture

The publication of the *Atlas of Tropical Tuna Fisheries* (Fonteneau, 1997) culminated several years of effort to summarize all of the tuna fisheries catch records within a single resource document, so that the evolution of these fisheries could be traced, and patterns studied. Among the riches of these data sets are several stories of changes in fishing technologies, marketplaces, and products, and access to fishing grounds. Also apparent are the excesses due to the rapid expansion of industrial fleets out onto the world oceans, well before management procedures or adequate information were available. Missing, unfortunately, are the documented historical developments such as those described by Mather *et al.* (1995) in the post-WWII northeast Atlantic, where tens of thousands of tons of giant bluefin were caught each year for several years, and then nothing.

Many of the historical changes in the high seas fisheries behaviors, distri-

butions, and catch compositions reflect epochs of changes in political convention regarding ocean ownership, management, and exploitation regimes. Some changes were due to new fishing technology. Other changes reflect the more inevitable, uncontrollable changes in climate-driven oceanography and subsequent ecological responses. These latter changes occur on all time and space scales, leaving a lot to be measured and monitored over large regions of the world's oceans if truly informed management decisions are to be made, and if the various tuna populations are to be nurtured and fisheries sustained. Life-history strategies define the patterns of environmental variations that each species has adapted to (or not), providing insight into time and space scales over which fisheries management actions should be concerned.

The general expansion of high seas fisheries occurred in response to Cold War politics and Law of the Sea ownership debates, ongoing long before the Second World War. In 1976 the U.S. Congress passed the Magnuson Fisheries Conservation and Management Act (MFCMA). The Act was intended to resolve the ocean fisheries access policies of the USA, independently from the Law of the Sea Accords. These, in turn, were being developed by a host of nations whose interests in the oceans were motivated by recapturing the values of ocean resources from foreign interests. The post-1976 "gold rush" onto the oceans escalated as the MFCMA was cloned by many nations as they sought to obtain their pieces of the action on the high seas. Within the verbiage were definitions that separated the valuable tunas and billfishes as a unique class, the "highly migratory species" (HMS), although many other species of fish, for example, sardine and jack mackerel, exhibit similar or greater migrations along shore and offshore. *Sardinops* even has a similar life history, attaining maturity after 4 or so years, and living 14 or more years.

C. Changes in Markets and Resource Ownership

The special HMS category made management of these species subject to regional nongovernmental management bodies rather than their being managed (i.e., owned) unilaterally by coastal states. Tunas and other "highly migratory species" have thus been exploited in more than one sense in the recent expansions of national interests. Fishery interactions are debated and discussed elsewhere (FAO, 1996), and set the undertones of the aggressive nature of today's resource owners and would-be exploiters. As a result of the development of the Law of the Sea Accords, and the concepts of the Exclusive Economic Zone, there emerged a new generation of international corporations and unusually complex marketing systems. These evolve continuously in efforts to cope with changes in legal ownership, access, and regional and local responsibility for resource management. These same interests manipulate supply and demand, often creating ecological tragedies.

For example, the southern bluefin population was severely affected by early fishing activities, and the consequences have been enlightening, if sad. These long-lived fishes have yet to produce any substantive year classes since the late 1960s, when they were fished intensely on their spawning grounds northwest of Australia. Long life spans, particularly of ocean species, are an adaptation to long sequences of poor opportunities for successful recruitment (Johnson, 1981; Kawasaki, 1983). In their zeal to exploit the bluefin tuna resource, Japan's fisheries interests have evoked every available negotiation tool to continue to exploit the clearly depleted southern bluefin stock. The issue is that this species has such an extreme life history, with literally decades between successful year classes, that they cannot be managed as if they were in any way an "ideal population" with an "annual recruitment" as assumed under typical pelagic fisheries population management models. By continuing to fish down the older, principal reproductive ages, the species is certain to undergo first economical, and then biological, extinction.

Recognition of these limitations has yet to be assimilated into the management of high seas resources. Well-designed ocean and population monitoring are needed to define conditions that are conducive to both good and poor recruitment. Le Blanc and Marsac (1999) have recently reviewed developments in environmental monitoring and prediction at a broad regional scale for the Indian Ocean. They provide a set of examples and objectives that require diverse institutions to collaborate to provide for both more efficient fishing operations and better overall management. The regional collaboration between seiners and tuna management in monitoring Indian Ocean fisheries provides good examples for other regions (Hallier and Marsac, 1991).

Sharp and McLain (1993a,b) also concluded that since the majority of the world ocean is now visited more often by fishing vessels than will be covered any time soon by oceanographic expeditions, it would be wise to encourage the fishing vessels to participate in ocean monitoring and data sharing. This would provide greatly needed information on a lot more than just fisheries behavior, for example, climate change and ocean dynamics. In this light it seems that the nonnegotiable terms of access to any of these living resources should all have built-in requirements that fishing vessel crews measure and report a suite of relevant environmental observations every day they are at sea. The data should be treated and distributed as part of the global weather observation reporting system. This way, ocean measuring and monitoring systems in the ocean can finally be brought into a state of utility such that none of the usual climate, oceanography, and fisheries issues needs to be debated—due to the usual absence of information.

Fish behave from minute to minute, hour to hour, and day to day in response to oceanographic, atmospheric, and solar–lunar processes that operate on similar time and local space scales (ICANE, 1981; Kendall *et al.*, 1996). Also, the daily development of ocean features has been among the recent several decades' lessons

from both *in situ* and high-resolution satellite-mediated studies of ocean climate and weather-related phenomena. However, and despite agency rhetoric, the weaknesses of satellite irradiance sensor data (Clancy and Weller, 1992; Sharp, 2000) are such that most of the world's productive fishery regions cannot be well monitored at operational time and space scales from irradiance sensor-based platforms during the most productive periods, except in a very cursory sense. The problem lies in the interactions between atmosphere, clouds, marine layer moisture, and productive ocean processes that promote fisheries. The best fishing conditions tend to blind satellites to the ocean's processes, and even more limiting, satellite sensors cannot measure subsurface ocean processes.

The seasonal expectation from any location is defined as climate, while what actually happens is defined as weather. Similarly, the ocean weather that matters to individual fishes occurs on time and space scales that defy monthly or longer temporal aggregations for use in more than cursory summaries of cause and effect. Fishing effort, on the other hand, is more often than not monitored through industry, national, or regional fisheries management bodies. However, individual fishing vessel locations and catch statistics are typically unavailable to any but agency staff, as a condition of their being made available to the managers. Another confounding consequence is related to casual use of temporal aggregations. Choice of an appropriate seasonal calendar is more of an issue than one might assume, given that the ocean is dynamic on all time and space scales. In order to understand both short- and long-term responses, research and data analysis need to be based on synoptic measures of fish behavior, environmental status, and trends. These often reflect local to regional scale processes, but are not tied to specific Julian calendar dates. In this sense, the separation of catch and effort data sets into either quarterly or multiyear epochs for the entire globe can be quite misleading.

Oceanographers have come to understand that for each region there are unique symptoms of seasonal processes. Expectations change as a function of changes in climate-driven ocean states. Upper-ocean temperature profiles, salinity, and productivity are all more or less bounded within annual seasonal cycles as functions of insolation, wind speed and direction, and freshwater inflows. For example, each locale has climatological or mean dates for peak surface warming; maximum northern or southern extent of ocean surface warming; or cooling that is a result of upwelling or onset of surface heat-scouring winds. In the Indian Ocean the dominance of the seasonal monsoons has provided the needed navigational security of seafarers for millennia, as the winds reversed on a fairly consistent schedule. They could "ride the wind" from one point to another in one season, and return with the next. The northeast monsoon blows from Asia's plains into the southwest Indian Ocean from December to April. The southwest monsoon blows in the opposite direction from the Indian Ocean into Asia's highlands, starting in about June and continuing until October of most years. Yet there are systematic trends that shift these onset dates in both space and time (Sharp, 1995).

The ENSO Warm/Cold Event fugue is the most frequent perturbation of "ex-

pected" seasonal ocean patterns. Understanding them enough to make credible forecasts has been elusive (Enfield, 1989; Barnston *et al.,* 1999). El Niño Warm Events, or La Niña Cold Events, are the anomalous years. El Niño years can cause severe drought across the Asia–Southeast Asia region, and La Niña episodes can cause flooding, and downstream eutrophication and increased ocean production. There are also longer trends within which the ENSO climate perturbations are superimposed. Fisheries resource bases shift along with them, as measured by changes in catches, distributions, and species composition. This information is all well documented in the recent climate debates, as well as in fisheries literature (Sharp and Csirke, 1983; Glantz and Feingold, 1990; Marsac and Hallier, 1991; Sharp and McLain, 1993b; Beamish, 1995; Gauldie and Sharp, 1995; Glantz, 1996; Lehodey *et al.,* 1997; Klyashtorin, 1998; Le Blanc and Marsac, 1999). There are also long, slow patterns of changes in the onset dates, as well as changes in mean wind speeds, and ocean consequences, over time.

Short-term perturbations such as ENSO events promote long-lasting physical responses and ecological responses. Here is a situation where one can attest to the utility of satellite remote-sensing tools, where high-resolution radar is used to determine sea level height (SLH) changes on the order of meters. In the tropics, in particular where sea surface temperatures (SSTs) may not be dynamic, these SLH changes are direct indicators of thinning (thickening) of the upper mixed layer, and hence enhanced (lessened) vulnerabilities of the tunas to specific fishing methods and gear. As pointed out previously, regional tuna catch characteristics are good indicators of ENSO phases. To put all this in perspective, the 20th century has had the lowest frequency (28) of Warm Events since the 17th century (29), which was the coldest period within the recent five centuries. The 18th and 19th centuries experienced 47 and 49 Warm Events, respectively, suggesting that the baseline of event frequencies (expected recurrence interval) changes significantly on decadal to centennial time scales. Ecological patterns shift with these processes within regional ocean ecosystems.

Only recently have the noncoastal, open ocean phenomena that affect the life histories and behaviors of the large migratory species come into focus. They had not been as well defined previously. Suzuki (1989), for example, posits that most of the world's tuna fisheries' recruitment benefited from the 1982–1983 Warm Event. Marsac and Hallier (1991) showed that the 1990–1991 decreasing trend in catch rate for the western Indian Ocean seine fishery was related to the thermocline deepening associated with the 1990–1991 ENSO Warm Event. They, fortunately, had a rich data time series, including the oceanographic observations, from which to formulate their explanation and test its validity. After introduction of these concepts in the early 1980s, one of the criteria for access set by the Seychelles Fishing Authority was the requirement for an onboard observer program to collect standard oceanographic observations, as well as mandatory logbooks in which fishing operation information was to be kept. In their review of Indian Ocean fisheries and climate processes, Le Blanc and Marsac (1999) identified

many aspects of the seasonal, decadal, and epochal climate-driven ocean properties that affect tuna fishing. They also provide examples of high and low SOI phase-related surface dynamics for the Indo-Pacific regions affected by the ENSO cycle on seasonal, annual, decadal, and centennial time scales.

Fisheries and fish population responses can be easily misinterpreted. Good ocean observations are necessary to go along with several years of age-distribution and recruitment data from which to track and interpret these events in order to corroborate interpretations. It can also be entirely misleading to aggregate fisheries catch data sets without regard for regional and ocean basin climate-related processes, or by using strict Julian calendar quarters. One of the most informative fisheries environmental presentations that I have ever witnessed was a weekly sequenced display (by Francis Marsac) of the tuna seine fleet's catch records mapped over the western Indian Ocean, for the early decade of its operations. The evolution from the seasonal upwelling along the southwest coast of Madagascar, northward and seaward as the monsoon-driven ocean features progressed from year to year, proved that my 1979 insights were correct. The interannual variation was also notable, and important.

IV. A BRIEF REVIEW OF HIGH SEAS TUNA FISHERIES DEVELOPMENT PATTERNS

Fonteneau (1997) collated available catch records, and charted historical patterns, by fishing gear type. Among the most valuable contributions of the Fonteneau *Atlas* is in providing a visual record of the major changes in effort and catch patterns since the mid-1950s. Three distinct fisheries histories were created by separation of the information into pole-and-line, seine, and longline gear types for the decadal epochs 1956–1968, 1969–1978, 1979–1988, and 1989–1993. Many regional fisheries have been in production for several hundreds of years before these *Atlas* summary periods. For example, the previously described Maldivian skipjack fishery was well developed and strong long before these *Atlas* records start, as were the Japanese home island and longline fisheries of the western Pacific Ocean. The eastern Pacific, Bay of Biscay, and Azorean coastal tuna fisheries were also well developed, and the Mediterranean trap and harpoon fisheries were ancient (Mather *et al.*, 1995; Bard and Santiago, 1998).

A. Innovations in Technology Play Major Roles in Recent Changes

Examination of the initial catch levels recorded in the 1956–1968 Atlas maps through to the more recent epoch shows that all these old fisheries underwent changes. Many declined or ceased operation, while others grew. Most of these

older fisheries were transformed from already productive old technologies into more modernized fisheries supported by cold storage and delivering fresh-frozen export products. For example, today most Indian Ocean tropical tuna catches are primarily processed by Thailand's thriving canning industry, started up in the early 1980s. Many traditional fisheries underwent similar transformations.

New fisheries have been initiated over large portions of the world ocean. An important innovation was the general implementation of the fish aggregation device, or FAD technology, that helped many tropical fishermen to become more efficient. Fish aggregating devices (FADs) were studied in the late 1970s and 1980s off Hawaii, as well as in the tropical Pacific surface fisheries, as scientists sought resolution to efficient fish school location—and then bycatch issues that will be discussed later. Some were amazing success stories. For example, the Philippine island coastal tuna fisheries developed and grew, based on their use of piyaos, or tethered bamboo fishing platforms (another form of a FAD). From and around these piyaos immense amounts of small skipjack and yellowfin (and very large adult yellowfin) have been fished, using handlines, hook and line, and longlines. More recently, from the profits of these less technological fishing activities, Southeast Asian corporations have invested in modern high seas purse seines, creating "boomtowns" such as General Santos City in the southern Philippines, a major industrial center built to support these new fisheries. A systematic look at these developments tells several informative stories.

B. Pole-and-Line Baitboats

Skipjack tuna dominates the pole-and-line fisheries of the world, although each of the other species is caught, in some seasons, within their normal annual migrations or for particular local markets. Most of these fisheries, as plied in the tropical oceans, were initially set up as day-fisheries, leaving the dock after obtaining baitfish and fishing nearshore for various seasonally productive locations. These include the small coastal fisheries operating from Baja California south to Northern Peru, and the Atlantic fisheries based in the Azores, Madeira, the Bay of Biscay, and Cape Verde, and along the coasts of west and equatorial Africa, as far south as Ghana. Sri Lanka, Thailand, Malaysia, the Andaman Islands, and Indonesia have poorly documented day-fisheries for tunas. Papua New Guinea's joint-venture pole-and-line fishery came, and went. All these fisheries experience distinct seasonality, a symptom of migratory behavior by these fishes in response to regional climate-driven oceanography.

In the Pacific, the Hawaiian Islands tuna fisheries were created by late 19th and early 20th century immigrants from Okinawa and other Asian fishing centers to service the local island community's fresh fish needs. In the 1950s Honolulu became the location of a Bumble Bee tuna cannery that processed the local fresh (unfrozen) skipjack into one of the best canned tuna products ever produced. Their

operations were subject to seasonal production limits and longer-term trends in fishery production. The cannery was operated at the whim of the seasonal ocean currents.

On the other hand, some pole-and-line fisheries were more versatile, and developed long-range tactics early on. For example, the California-based baitboat fishery operating along the Baja California coast from the 1930s to the 1970s fished on small (40–65 cm) so-called school fish, using chipped ice at first, and then ammonia refrigeration and circulated brine, to conserve them. In some years these would be mostly skipjack. In others, as much as half the catch would be yellowfin. After WWII Asian fresh fish markets in Los Angeles began offering premium prices for larger, fatter tunas. These included the summer run Pacific bluefin that routinely migrated up from the local banks off the southern Baja California peninsula, along shore northward to Isla Guadalupe, and onward into the Southern California Bight.

Throughout the 1950s and into the mid-1960s it was also common for the baitboat skippers to make a circuit from the coastal "local" banks offshore to San Benedicto for an afternoon of two- and three-pole fishing for large yellowfin and occasional heavy bigeye for these markets. They would often continue their offshore run by sailing westward overnight to the Revilla Gigedo Islands, to Roca Partida, and onward to "Cadillac" or "Brito" bank, and then head northward back to Isla Guadalupe to top off with some fresh bluefin, or back to the bait grounds along the coast. The larger specimens would reach weights of several hundred pounds, and careful handling brought good prices.

There was a post-WWII development in southern California of long-range baitboats. The larger "tuna clipper" fishery from San Diego would sail due south from Cabo San Lucas, if they had a load of good bait, to Clipperton Island. Once they had tried their luck, or run out of bait, they would then either head due east for Costa Rica, or sail east-southeast onward to the Galapagos Islands and associated banks. There they would be able to find abundant baitfish, and also large yellowfin and bigeye tuna with which they could more quickly fill their holds. These vessels and crews were true explorers from old European stock. A good bit of offshore exploration, using sounders and sharp-eyed lookouts, led to an ever-broader distribution of fishing activity.

Baitfish was this fishery's limiting resource. The typical cyclic pulsing of sardine and anchovy populations caused these more exploratory fishermen no end of grief, as each region's baitfish would flourish, and then disappear for a season or longer. Expansion southward eventually induced several joint ventures with Central and South American industries, where today several landing sites and canneries serve local baitboat fleets and foreign-flagged superseiners buying and processing their catches nearer the fishing grounds.

Meanwhile, in the mid-1960s, the California fleet moved southward, and offshore, as the Okinawa-styled Japanese home island fisheries that were operated all

around Japan for several centuries also began expanding southward. They moved offshore and well into the southwest Pacific Island fishing grounds, creating new fishing communities. Local competition grew as fisheries development programs were promoted by either the UN or the Japanese Aid agency (JICA). Hawaii's only cannery closed in the late 1970s. The local skipjack fishery was reduced to focus on only local fresh fish markets. By the early 1980s, many of the Pacific Island communities either formed their own fishing fleets or made contracts with Japanese and U.S. firms to expand their local fishing activities. Soon thereafter, their pole-and-line catches were diluted by the expanding tuna seine fleets that had quickly evolved from the sturdy southern California tuna clippers.

Similarly, west equatorial Africa's baitboat fisheries evolved, as described before, from Portuguese traditional fishing styles and through Japanese fisheries development projects. Fishermen from Cape Verde also emigrated to Brazil in the late 1970s and early 1980s. Brazil's pole-and-line fishery developed in the late 1970s and operated by taking advantage of the local *Sardinella* for bait and numerous oil platforms (that act as FADs) near Cabo Frio, where strong upwelling attracts tropical tunas. These were all short-range fisheries, and many were day-fisheries.

C. Purse Seines

One of the great innovations in tuna fishing took place in the late 1950s—Marco Puretic's hydraulic "power block," designed to handle the new seine nets that had been scaled up from sardine seines to meet the demands of high seas tuna fishing, particularly for large-volume skipjack and yellowfin schools. There were numerous styles of fishing and different approaches to each type of tuna, depending upon the boat owner/operator's objectives. Some of the older low-deck wooden California sardine and salmon vessels were readily converted to heavier tuna seine gear. Individual skippers specialized in seasonal runs to the bluefin grounds, where they would fish only at night for the coveted large-sized bluefin, rather than scramble for skipjack schools among the throngs of baitboats.

Night fishing is an art, and requires a lot of coordination. The tuna vessels were operated without any visible light, except for a single powerful flashlight in the crow's nest that was swept about periodically to mark each vessel's location in areas where more than one boat was working. The nets were set around "glowing" surface schools, as the fish school's passage caused the plankton to fluoresce. Some of these vessels and crews got very proficient, and were able to fill their holds, unload, and be back on the grounds, often several times, before similar-sized baitboats working the "school fish" from dawn to dusk made a full load. One early lesson was that bluefin tunas passed their nights near the ocean surface.

As the California fleet began to age, or shift from wood to steel hulls, the new vessels were outfitted with seine winches and power blocks, and sailed offshore

and away from the coastal baitboat action. Many families made their fortunes just after the Second World War by investing in these new wider-ranging boats. The tuna purse seine fishermen had already made the switch from coastal day-sailors and nearshore fishermen to the high seas. They designed and built larger new vessels that were self-contained, seaworthy, and livable, as the time that they spent on the ocean was extended in order to fill these big, expensive-to-operate vessels. They delivered premium fish in large loads to ever more capacious canneries.

The tuna clipper and seiner skippers soon discovered that skipjack and small yellowfin would aggregate about floating objects, for example, logs, dead whales, and even their own fishing boats while they were shut down and adrift at night. They began marking logs (or various portable FADs) with radar reflectors or lights, in order to track them all night. By early morning's first light these fishermen could be ready to set their nets around these natural (or artificial) FADs, and haul in a good size catch before setting off to find surface schools for the rest of the day. There were often several other nontuna species (e.g., dolphinfish, turtles, sharks, rainbow runners, and assorted small fishes) associated with the FADs that were captured in the nets, sorted, and returned to the sea, or eaten by the crew. Beyond this general shift in efficiency, the fishermen discovered that larger yellowfin tuna—more valuable than the smaller schooling skipjack, yellowfin, or bigeye—were attracted to and also schooled beneath "porpoise" or dolphin herds. In 1967, the Inter-American Tropical Tuna Commission (IATTC) began officially "managing" the eastern tropical Pacific yellowfin fishery within a well-defined Commission Yellowfin Regulatory Area (CYRA). The vessels could fish outside the CYRA once catch quotas were attained. Another kind of race was on.

Starting with yellowfin fishery regulation in 1970, the California seine fleet would spread westward after the closure of the CYRA to fish on dolphin–tuna aggregations. By this time, new larger, faster steel seiners were emergent, stimulated by loopholes and mandates in the IATTC regulations. Marco Industries thrived as they scaled their power block and net handling gear to ever larger vessels. The high seas seine fleet was now focused on dolphin herds rather than schoolfish aggregations. Also, the idea that yellowfin reproduced mostly around coastal islands was soon dispelled. Full age structures were located out on the high seas. Unique cohorts were found at some locations, appearing only in seasonal situations as they followed seasonal oceanographic features. Yellowfin fisheries from Baja California south to Central America had two 6-month cohorts; in the southern coast region, one slightly off-cycle cohort dominated (Sharp, 1978). These were often "joined" by unique cohorts from offshore sources.

The vessels were able to increase their production from yellowfin as a "by-catch" in their dolphin fishing ventures in the offshore regime. The fishermen discovered that the dolphin herds quickly learned to avoid their vessels, so they created a new type of fishing crew member, the "speed boat" or chase boat drivers, whose job it was to herd the dolphins into position so that the ever-faster seiners could set their ever-larger seine nets around them so as to catch the asso-

ciated yellowfin tuna. Some of the smarter, or perhaps only more desperate, dolphin herds responded by learning to break up into smaller herds, in a "starburst" behavior, as they heard the seiners coming over the horizon. Now the skippers bought faster speed boats, and more of them. Some skippers with their newer bigger boats hired helicopters, pilots, and "chopper mechanics" in order to locate ever more elusive dolphin herds. This became one of the most costly fishing methods ever devised.

These earlier efforts resulted in longer, faster, more stressing chases that sometimes caused situations where many hundreds of dolphins might be killed during a set of the net, affecting the time needed to remove the tunas from the net, and causing no end of handling problems. This was not an easy situation for the fishermen, either, as they were now also forced to deal with the dead weight of these large mammals, as well as the usual fish handling routine. They, too, responded quickly by working on methods to minimize the numbers of dolphins retained in the net before the net haul was finalized. Installation of "Medina panels" in the seine nets and perfection of the "backdown" procedure were well deployed within the U.S. fleet by the mid-1970s.

The Bumble Bee cannery in Honolulu began processing some amounts of the offshore catches delivered by the high seas seine fishery. However, they were not set up to handle large production and vessels would be tied up for extended periods waiting to unload. Eventually, the public outcry regarding dolphin deaths that forced the fishermen into a legal compliance situation collided with the economics of the oil crisis of the early 1970s and the increasing economic competition due to a general overcapitalization. As a result, many of the U.S. vessels were sold, and others went even further offshore, into the west and south Pacific, where dolphins and competition were not an issue. As the situation evolved, many of the U.S. vessels moved even farther south and west, making Hawaii a less attractive delivery point.

However, access to the numerous Pacific Island economic zones needed to be negotiated. As well, the issues of delivering catches from distant sources needed to be addressed. The capacity of the small cannery in American Samoa was increased to handle the larger loads delivered by these giant superseiners, a system of trans-shipping ports was created to handle these larger vessels' catches, and other canneries were planned around the Pacific Island community and Indonesia. The effects of these developments are important to understanding the patterns of the expansion of the seine catch and effort statistics, and eventual concentration of particular seine and baitboat operations near the regional processing plants.

Meanwhile, in the mid to late 1970s, the Spanish and French were undergoing similar growing pains. Their tropical Atlantic seine fleets expanded well offshore, away from the traditional baitboat fishing grounds. Catch rates quickly rose, and then began to decline. Competition due to overcapitalization was cutting into their economic viability. This was resolved in an unusual, but reasonably positive way.

In the early 1980s, the FAO efforts to develop the Indian Ocean tuna fisheries

had been initiated. Both Spanish and French tuna industries were working toward gathering information about the availability of tunas around and about the western Indian Ocean. Several Spanish baitboats were sent to test-fish in and about the Seychelles Islands and over the Plateau—they understood that superseiners were unable to work there due to the working depth of their large nets. Although they could catch reasonable amounts of fish, there was no place for these small baitboats to unload their catches. It also cost nearly half their market value to transship them to the nearest processing ports in the Atlantic or western Pacific oceans. The larger seiners, however, could catch larger quantities, from a larger resource, and ferry their catches to distant ports for unloading and remain profitable. While the seine operations proved economically feasible, the baitboat operations were abandoned. Meanwhile, the Seychellois developed their strategy for pricing access to their EEZ and its tuna resources. The catch processing problem was soon resolved by Thailand when they decided to open a tuna processing facility for Indian Ocean and western Pacific tuna. They now dominate world canned tuna exports.

So, with a little historical perspective, we can explain much of the evolution of the surface fishing effort as outlined in the Fonteneau *Atlas*. However, the most interesting patterns over this period are those of the longline catch and effort. They display a combination of operational decisions, investments, changing market strategies, and fishery-induced and oceanographically driven population shifts over the period from 1956 to present.

D. Longline Fishing Pattern Changes

The early (1956–1968) records of catch and effort distributions from the longline fleets show widely distributed, primarily Japanese owned and operated high seas operations that were focused on Pacific and Atlantic ocean albacore, yellowfin, and bigeye; eastern Indian Ocean southern bluefin; and northwestern Pacific swordfish. The significant shifts during the 1970s were signaled by more broadly distributed and higher catches of bigeye and less albacore in the North Pacific, indicating that the gear had been extended to fish deeper to target the more valued bigeye. This, of course, was the result of direct industrial applications of Japanese vertical longline research referenced above and behavioral studies done in the mid-1970s by Hanamoto (1974, 1975). During the 1979–1988 period catches increased and the broadening fishing effort was, again, tightened up and focused on large bigeye, albacore, and large yellowfin in their respective habitats (Hanamoto, 1987; Uosaki and Bayliff, 1999).

The newly emerged shallow longline fishery for yellowfin in the northern Arabian Sea was unique. It was focused on tunas that are most likely trapped within this warm region. They are constrained from entering the deep water habitat by the high-salinity, low-oxygen water from the Gulf environment as it spills over the

sill at the Strait of Hormuz, into the Oman Gulf. Once into the Arabian Sea, this low-O_2 watermass sinks and spreads out at middepths across the seasonally oxygen-deplete Arabian Sea, and southward into the subequatorial Indian Ocean. This low-oxygen water in the Arabian Sea locks those predators with high metabolisms into a constrained surface habitat along the coasts of northern Oman, eastern Iran, and western Pakistan.

After the early (1956–1968) decade there was also a significant shift from the highly exploited eastern Indian Ocean southern bluefin spawning ground fishery in the third and fourth quarters to the more southerly focus of the south of Australia, New Zealand, and South Africa. Although this effort pattern persisted, catches declined in the 1980s and early 1990 records, suggesting that the resource was heavily overfished, and has yet to recover. The continuing escalation of international conflicts over Japanese demands on this resource will continue to cause conservation-minded citizens no end of anguish until the situation is resolved. From the records, the Southern Ocean longline effort that was once aimed at southern bluefin seems to have been retargeted slightly to the north, into more transitional waters, for albacore.

The Atlantic bluefin longline catches in the North Atlantic and Mediterranean appear to have evolved from two early minor fisheries, one that remains intact and progresses from fourth quarter activities on the Grand Banks to the warmer upwelling area south of Cape Hatteras in the following (first) quarter, and another that occurred off northeastern Brazil before 1968. As was explained to me by the late Luis Rivas (Rivas, 1978), this latter bluefin catch was primarily made by a Cuban fishery operating on mature bluefin that aggregated during the second quarter on a massive seasonal squid resource. When the squid no longer appeared, the target bluefin disappeared from the region, long before any management was imposed. No one has any clue why the squid disappeared, as they were not heavily exploited by anyone. Whether the bluefin tuna no longer aggregated off northeastern Brazil due to their food supply disappearing or due to being fished is unresolved.

The patterns of longline swordfish catches also changed dramatically from the early period into the present decade. The catches that were once limited to a nearbycatch fishery in the Pacific Ocean albacore and bigeye fishery east of Japan shifted over two decades to the seasonally dynamic tropical Atlantic activity dominated by Japanese and Cuban vessels. Additional new swordfish longline fisheries grew over the period, one off Argentina and others off the eastern USA and Canada into the Gulf of Mexico and the Caribbean. This latter longline swordfish fleet grew rapidly, and was clearly overexploiting the resource in the early 1980s. The fleet dissipated as many of the southeastern fishermen moved their vessels to Hawaii to begin development of a new Hawaii-based longline fishery for swordfish and bigeye tuna. The remaining longline effort comprises smaller, seasonal longlining activities that target yellowfin in the growing fresh tuna (ahi)

markets along the eastern seaboard and Gulf of Mexico. Although not a true by-catch, the swordfishery has shown constant signs of decline and debility since the late 1970s despite the vessel departures. This may have as much or more to do with longline effort outside the EEZ than with coastal fisheries.

E. Ongoing Changes in Longline Fleets and Fisheries Interactions

Significantly, the recent trend in tuna fisheries research is in studies of fisheries interactions, as reviewed by Shomura *et al.* (1994, 1996). Boggs' (1996) discussion of "Unresolved Problems and Questions from the [1994] FAO Consultation on Interactions of Pacific Tuna Fisheries" centered on the major contributions from tag and recapture studies in the history of tuna research in support of management. While no one would disagree that basic operational fisheries information and biological sampling from the catches provide the most important information, the interpretation of these data needs to be carefully moderated from synoptic contextual information (Sharp, 1987). The common fallacy has been to treat the variations in catch as due to population responses within environmentally induced "noise." The facts are that fisheries are first and foremost direct consequences of their changing environmental contexts, and as such, cannot be treated as if they were (1) somehow subject to either "inherent stochasticities," or (2) stable, unless otherwise determined.

Bertignac and Ardill (1996) provide useful insights into the recent developments in the Indian Ocean tuna fisheries—from the rise of the western Indian Ocean high seas seine fishery, to the short-lived rise and fall of industrial drift gillnetting for albacore. The most significant recent development has been that of the entry into the eastern Indian Ocean and Arabian Sea of "hundreds of longliners (mainly under Taiwanese and, more recently, under Chinese registry)." Except for a few joint ventures and charters, Indonesia has the only other substantial domestic longline fleet operating in the Indian Ocean. Although these fleets target mostly yellowfin tuna, south of Java southern bluefin are also targeted. Catch reports and biological sampling are rare.

Bertignac and Fonteneau (1996) describe similar interactions for the western Pacific fisheries. These new fleets are spreading out along the coasts, and then offshore, to fish on the same, or mixtures of, adjacent resource bases that supply the cultural nearshore fisheries. Conflicts are inevitable, and both sociological and ecological consequences of the spreading of fishing effort will vary, depending upon location and historical patterns. The management problems are associated with invoking responsible vessel ownership, monitoring multinational corporate management, and the tractability of obtaining useful data from such fleets. None of these are trivial issues.

A similar transition that needs to be watched is the refitting of Gulf of Mexico

shrimp trawlers with longline gear, and their movement into the Pacific swordfish and bigeye fishery offshore of northern South America. In the eastern Pacific region just south of the equator, longline fisheries regularly land more prime sashimi-quality (high fat content) bigeye than are found anywhere else in the Pacific Ocean. The issue there is that the Japanese, in their long-term plans, made large investments in newly designed high-tech vessels with onboard blast-freezing equipment that were focused on the bigeye fishery south and west of the Galapagos Islands, extending offshore and southward into the Marquesas Islands. In the recent decade there has been a convergence or superimposing of several developing purse seine fleets in the Pacific region. The seiner fleets depend upon fish aggregating devices to attract the region's abundant skipjack schools. Unfortunately, these schools are often observed to have mixed-in undersized (<40 cm) yellowfin and bigeye that are discarded since they have low market value. This bycatch, although not great in weight, turns out to be huge in terms of numbers of individuals. The result has been severe declines in the recruitment of bigeye into the longline fishery, which depends upon fish of greater size and age for its economic success.

Hall (1996, 1998) has described the evolution of the tuna–dolphin problem and the likely ecological impacts of this regional situation that was caused by a shift in fishing technology to accommodate the need to minimize exploitation of dolphins in tuna fishing operations. These enlightened perspectives have begun to swing the pendulum of public, international, and agency opinion back toward support for careful, more rational fishing on dolphin-associated yellowfin schools, using simple, valid ecosystem arguments, and recognizing that dolphin death rates can be controlled.

F. Ocean Climate Changes and Fishery Responses

ENSO Warm Events cause a general spreading of the Warm Pool east and west (Forsberg, 1980; Lehodey *et al.*, 1997, 1998). Thus, more of the smaller, Warm-Pool-associated skipjack spill over into the eastern half of the Pacific Ocean to compete with their larger, cool-ocean-adapted cousins, as well as westward into the Indian Ocean. In contrast, the release of the ENSO Kelvin Wave from the Warm Pool allows the habitat of the three large tuna species living at depth in the western Pacific Warm Pool to emerge. This phenomenon, in turn, makes these larger tunas more accessible to both surface fishing gear and longline fisheries. Not unexpectedly, the availability of surface schools of skipjack in the described region has been observed to be greatest since the onset of the recent decade or so of increased ENSO Warm Events. A general warming trend occurred along this equatorial eastern Pacific region that is usually described as being dominated by influences of the Humboldt Current's colder upwelled water and trade winds. The westward trades tend to scour away surface heat, and cause the thermal profiles to

be steeper, and surface temperatures to be cooler, in general. With an enhanced warmer surface layer, skipjack and yellowfin from adjacent north, south, and west habitats have converged, creating a concentration that, in turn, has attracted seiners.

One might wonder whether the patterns of ENSO observations that indicate a several-decade-long upward trend in frequency of Warm Events might continue, and reinforce the growth of the affected region's surface fisheries, causing further declines in longline catch rates for bigeye tuna. This could cause further economic erosion of the longline fishery. If, on the other hand, the trend were to slow, reverse, and return the region to cooler SSTs and shallower thermoclines, the growth of the surface fishery might be suppressed, or reversed, and allow a few more recruits to the longline fishery for older, larger bigeye. Of course, an alternative scenario is that a cooler period might simply spread the surface fishery north and south, and along with the shallow thermocline, make these regional fish even more vulnerable, resulting in an increase in this fishery's debilitating effects over an even larger area. The point here is that dynamics in these fisheries reflect climate variations.

These are important questions and suggest one of the purposes of gathering and using time series of climate and ocean observations, along with closely associated fisheries data. Even rich fishery data sets are not really very useful without good empirical environmental information. The oceanographic and climate data provide context or bases for believing that certain conditions or changes in conditions will affect the resource's availability and vulnerability to the various fishing methods and gear types. Along the way we have learned that there are obvious generalities evident from comparisons of the patterns of surface and subsurface fisheries within a well-measured ocean regime. What is good for one is rarely good for the other. Increased catches of larger tuna are an early biological signature of ENSO Warm Events in the western Pacific Ocean, while, as we have discussed, schools of smaller Warm Pool skipjack spread westward. The physical dynamics and ecological responses promote the success of tuna reproduction, too. Enhanced post-Warm Event recruitment in tunas is well recognized, although difficult to discern from simple changes in availability.

In recent modeling exercises, Lehodey *et al.* (1998) explore forecasting ocean production centers and tuna forage as a means for predicting local availabilities and abundances of these widely dispersed and highly mobile species. Referencing the basic studies by Okubo (1980) of the behavior of small planktonic organisms within a dynamic physical and biological oceanographic milieu that dominates their short-term distributions and evolved behaviors, Lehodey *et al.* (1998) show that over the ocean basin scale, their estimations of concentrations of food species follow a generic pattern that includes the highest densities of high catches in the Warm-Pool-related fishery. That is a reasonable expectation. This is a very useful

example of the integration and application of many subdisciplines throughout the ocean sciences and ocean modeling communities.

On the other hand, Bertignac *et al.* (1998), in a companion paper, suggest that there is an analogy between the random and directed skipjack tuna movements and the diffusion–advection paradigm (Okubo, 1980; Sibert and Fournier, 1994) in the creation of a simulation—a so-called spatial population dynamics model. The objectives were to examine the distributions of fish concentration centers and then, using satellite color sensor data and seasonal SST climatologies, to forecast the most productive fishing areas, using an underlying population dynamics model. What seems obvious from a historical perspective is that the results for the more antitropical and eastern Pacific regions fit the early Barkley *et al.* (1978) paradigm for the ecophysiological type of skipjack tuna for which they had estimates, but their population model is based on a Warm Pool physiological type. Such modeling activities only marginally reflect the distinguishing factors between the two recognized patterns of growth and maturity patterns (Sharp, 1978). While I would not argue that their simulation with an L-infinity in the mid-60 cm does not represent Warm Pool skipjack, it would be inappropriate as a simulation of either eastern tropical Pacific or Polynesian skipjack, where immature fish are found at much larger sizes, and adults can attain 90 cm or more.

Sibert *et al.*'s (1999) application of the advection–diffusion models for tuna movements, using minimal tag and release data, continues to be mired in assumptions. Using the entire available SPC tagging data set, there is no explanation of the tag return function relating time-at-large and distance traveled. These functions have a general shape in most tuna tagging studies. For example, in the eastern Pacific Ocean, yellowfin tuna tagging has been active for over 40 years. Most (>99%) of the several tens of thousands of returns were recaptured within 1200 nautical miles of their release, with up to 50% or so of those returns being within a month or so and within a hundred or so miles from the release sites. The distribution of the return distances have depended entirely on tagging locations and local properties (islands, banks, seasonal ocean convergences, etc.) relative to adjacent aggregation areas. A similar relationship is obvious in a figure (Figure 5, p. 392, Sibert *et al.*, 1999) where 20 of the 40 or so well-matched or best predictions among the several hundred made are found within the three primary regions of maximum tagging activity and intense local fishing effort.

By employing the short-term tag returns, Sibert *et al.*'s analyses of the models' efficacies are seriously biased, as discussed by Gauldie and Sharp (1995). Gauldie and Sharp matched the monthly ocean climatology of the 30- and 90-m temperature distributions to the patterns of the observed skipjack tuna movements to the same data sets that Sibert *et al.* (1995) employed. We showed that there were strong seasonal north–south movement patterns, and predicted similar east–west patterns, associated with ENSO dynamics. Lehodey *et al.* (1997, 1998) confirmed

that prediction. We also found less than 100 of the several thousand SPC tag returns to be useful in long-term, distance-traveled estimations. The point to make is that there is little predictive value for those tags not caught beyond their immediate release areas, or within a relatively small distance from one fisheries activity center and adjacent aggregation locations. This was known from previous studies, and recent efforts continue to confirm this. The remaining small numbers of tags captured long distances from their tag and release locations provide only hints at outer bounds of the ranges of these fishes. Due to the limited development of high seas fisheries for skipjack during the intense tagging period, the returns mostly represent the localized distribution of regional fisheries more than generalizable tuna movements. Typically, the few extreme tagged fish movements are usually plotted up as arrows in managements' annual reports, in order to assume ever-larger regional resources. Why more fish do not join the ranks of these wide-ranging individuals is likely explained best by the "leakage" from homing populations that characterizes the anadromous salmonids. In the long-term, this population expansion is a guarantee against failure of a locale to provide for future needs. In the case of tropical tunas, it explains their ubiquity in all the oceans.

The general messages delivered throughout previous volumes (Sharp and Dizon, 1978; Clark and Mangell, 1979; Sharp *et al.*, 1983; Bard *et al.*, 1998), and this volume, are the described size-specific behaviors, aggregation phenomena, and seasonal responses of tunas to oceanographic and biological production dynamics. Previous and present studies pinpoint the dynamic variabilities of the very parameters in the fundamental biological simulation equations that Sibert *et al.* (1999) have decided to hold constant. These include the highly variable and environmentally dependent catchability coefficient, aggregation size effects, and an array of poorly estimated parameters regarding regional–seasonal movements. Meanwhile natural mortality is allowed to float, as the main subject of study. But mortality is not the quest in modern fisheries science—defining the basic characteristics of the ecosystem that nurture survival and minimizing human interference are the important issues (Sharp, 2000).

The value of large-scale tag-and-recapture experiments has been debilitated by the well-known issues of reporting error. Over time, fishermen have learned that various locations and environmental conditions induce more productive fishing, depending upon the gear employed. The different gear types, deployed during different times or seasons, create another suite of poorly accounted for issues in the interpretation of tag returns, and inferences regarding fish behavior. This is where archival pop-off (i.e., PSAT) tags are indispensable tools. With a lot fewer assumptions, and a lot more ocean and location data available from both individual fishes and aggregations of individuals, these dynamic resources will reveal their true characters. Assuming that none of these dynamics exist to fulfill a wish for convenient mathematical analysis is folly. Perhaps someday we will learn enough to be able to credibly forecast these complex dynamics at realistic resolu-

tions. That, of course, depends upon there being good systematic observations of the ocean, the fish, and fisheries. Tag dispersion experiments are only a small fraction of the necessary information.

G. Disappearing Traditional Fisheries

It would be improper to leave out descriptions of gear types from some of the old-world fisheries, as their disappearances are key to unraveling the continuous changes in baselines used to manage modern high seas fisheries. Mather *et al.* (1995) review the Atlantic bluefin fishery and biological information available prior to 1977, with a few newer insights provided by more recent literature that help dispel certain opinions about these fishes' growth and development patterns. One of the more informative summaries is their graphical depiction of several regional fisheries, as sampled over periods ranging from one year to over two decades. The most telling message of these regional graphs is the fact that there were substantial size class modes of fish over 250 cm along the western Atlantic from the Bahamas to Cape Cod and Ipswich Bay, Nova Scotia. These "giant" tunas dominated the catch at Prince Edward Island, a famous sport-trophy fishing ground. In recent years, these giants have declined dramatically in number, and many new-generation tuna researchers have simply never seen a true convergence of giant bluefin tuna (over 250 cm).

In the northeast Atlantic, off Norway, these giant fish contributed in some years, but not in others. They were significant in the North Sea handline fisheries, and appear in the rather typical adult fish distribution from the Spanish coastal fishery. In the Mediterranean, the giant tuna occur in the Sicilian tonnara (traps), and in the harpoon or "antenna" boat fisheries, two of the oldest recorded European fisheries. The giants' most significant contribution was in the eastern Atlantic/Mediterranean milieu in the Turkish Aegean and Black Sea fisheries. This latter fishery ceased to exist in the mid-1970s, and most of the Spanish, Sicilian, and Libyan trap fisheries have also declined to very low levels or have been abandoned. There has been a small recent resurgence in the Sardegnan trap fishery, but there have been very few fish of true giant size classes.

The North Sea handline fishery was abandoned in the early 1960s due to its complete failure. This and most of the older traditional fisheries declines can be attributed to the combined effects of the emergence of the seine fishery off Norway along with the North Sea handline fishery in the early 1950s, the advance of Japanese longline fisheries in the Atlantic and Mediterranean; and the increased French and Spanish seining activities along the eastern Atlantic and western Mediterranean. In the recent decades there has been untold damage done to this already stressed population by the clandestine roller-gillnet fisheries operated from Sicilian or Tunisian ports.

With this somewhat longer perspective, it is clear that use of catch statistics

from the period from 1960 or so to the present yields a very pithy assessment of what might be expected from less manipulated or debilitated populations. This is a classic example of the continuously shifting baseline problem in the world's fisheries.

V. HABITS AND HABITATS OF TUNAS

Bard *et al.* (1998), in their excellent review of what has been learned in the two recent decades, point out that laboratory and experimental research on skipjack tuna (*Katsuwonus pelamis*) was the benchmark or measurement basis from which most of the original energetics-based conceptualizations about tuna ecophysiology were derived (Sharp and Dizon, 1978). At the end of this earlier synthesis (Sharp and Dizon, 1978), I was convinced that up until about age one, or about 40 cm, a tuna was a tuna. All were alike in most ways. As laboratory studies have grown to include other tuna species (see chapters by Graham and Dickson, Brill and Bushnell, and Farwell in this volume), differences between the species are still emerging, and help us to better understand their adaptations and behaviors.

Field observations provide the most applicable insights to help us dispel dogma and tuna myths. These species have, indeed, carved up their environment and thrive, often in the face of incredible odds. Josse *et al.* (1998) and Bertrand *et al.* (1999a,b,c) bring the more holistic picture together by coordinating their simultaneous observations of different tuna species movements, within a fully defined acoustic survey environment. Yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) seem to exhibit nearly opposite approaches to their shared environment. Yellowfin tuna spend their days making excursions from around the top of the thermocline, both up and downward. Their nights are spent nearer the surface, diving down into the emergent scattering layer to feed. Bigeye swim upward from the cooler depths to stay with their food resources. These behaviors seem to be keyed to the movements of the deep scattering layer (DSL). The daytime deep-diving behaviors of tuna species are conveniently explained as a similar response to food availability, and as a means of minimizing competition from other upper ocean species.

One fundamental point is that skipjack (*Katsuwonus* and *Euthynnus*) species, as well as the longtail (*Thunnus tonggol*) and blackfin tuna (*Thunnus atlanticus*), do not get "large," as do other tunas. The longtail and blackfin tuna are tropical neritic species with life histories otherwise more like that of skipjack, and they are similarly limited in the adult size they can attain. This is not simply because they cannot obtain sufficient food energy to maintain themselves and then pay their unique metabolic costs of swimming, growth, and maturation—that is a truly circular argument. The concept emerged from an "Occam's razor" interpretation of the observation that maximum sizes increase and there are both greater ages and

larger sizes at onset of maturity observed, for example, in skipjack, arrayed from the warmest to the cooler extremes of their upper ocean habitat. This is a generic property that has been observed in many species from bacteria to hothouse plants, as well as in coastal pelagic fishes where adequate data on growth, fat content, maturation, and environmental time series are available (Mallicoate and Parrish, 1981; Parrish *et al.*, 1985, 1986; Schulein *et al.*, 1995). Thus the observed growth differences could easily be a general result of available habitat temperatures as a determinant of metabolic rates where somatic growth is traded off against higher respiration rates. As well, there are the added complexities of food availability and subsequent stress-related reproductive imperatives.

Another empirical corroboration is that it is not uncommon to find skipjack of 90 cm (over 20 kg) in the eastern tropical Pacific south of the equator. Skipjack of such large sizes are virtually unheard of west of the international date line in the Warm Pool. Yet, swimming in abundance in the great depths of the Warm Pool region, where the 23°C isotherm may lie as deep as 450 m, large (>100 kg) yellowfin and bigeye are common. Albacore (*Thunnus alalunga*) also occur, but are less abundant than in the adjacent regions to the north and south of the Warm Pool, or east of the date line (Parrish *et al.*, 1989). Here, again, we see another dichotomy. Skipjack, yellowfin, bigeye, longtail, blackfin, and albacore are capable of extensive overlap throughout their adult lives within the environments that support their egg and larval stages. Yet the adults of these species have parsed out the broad ocean environment, using temperature extremes, habitat, and vertical and latitudinal partitioning of food resources as major habitat-defining properties.

Relatively puzzling, the above information considered, is the odd ecological position and resulting behavior and physiology of albacore when compared with the other *Thunnus* species. Beyond the relatively small amounts of red muscle and long pectoral fins, these fishes have unusually numerous hemoglobin forms, and many "unique" proteins, unshared with other Thunnids (Sharp and Pirages, 1978; Collette, Reeb, and Block, this volume). Albacore start life in much the same way as do bluefin tunas, with extensive juvenile migrations from their natal habitats in the equatorial ocean into subtropical ocean waters (16–20°C). Then as they grow and mature, they submerge into the well-oxygenated middepths of the tropical latitudes. Few, if any, adult (>95 cm) albacore occur in surface fisheries. Longline-caught adult albacore from the Atlantic, Pacific, and Indian oceans can obtain relatively large sizes (to over 130 cm), but never the extremes attained by the yellowfin, bigeye, or three bluefin tuna species [i.e., Pacific bluefin (*Thunnus thynnus orientalis*) and Southern bluefin tuna (*Thunnus maccoyii*) to 150 cm and Atlantic bluefin tuna (*Thunnus thynnus thynnus*) to 250 cm or more]. The explanation for why albacore do not also get larger remains open. They differ in several other ways.

For example, tagging studies of tunas are numerous, and although many al-

bacore have been tagged, very few have been recaptured (less than 1%), in contrast to other tunas where recaptures can run as high as 10%. Explanations are many. Tagging mortality may be very high. Anecdotally, albacore fishermen nearly always remark about the fact that they must slow down their boats while trolling jigs, or the hooks tear out of the mouths of the juvenile albacore that take their lures. The greater impacts due to higher trolling speeds ordinarily cause other juvenile tunas to pop up to the surface and plane long before the hooks would cut through their jaws. Also, when fished with pole and line, albacore seem to have "soft mouths." and many are lost off the hooks, compared with other tunas. Similar-sized skipjack, bonitos, mackerels, and all the other tunas seem to be more durable and tougher. Aquarists have had problems keeping live albacore, too, while most other scombrids have proven to be hardy in aquaria (C. J. Farwell, personal communication).

Bach *et al.* (1996) made a study of albacore using experimental longlining research techniques similar to those developed by Boggs (1992), and described in full by Abbes *et al.* (1999). They found that the albacore catch-depth positions were not different from those of large yellowfin (warm water) but significantly different from bigeye typically found at cooler depths. Catch rates from longline sets made at different times of day also varied in response to the unique patterns of night and daytime swimming depths exhibited by each species, with albacore acting more like yellowfin. Bard and Josse (1996) have documented another of the unusual distinctions that may contribute to the albacore's general fragility relative to other tunas. They noted that when the albacore were brought on deck, they were usually bleeding from the gills or throat, and were dead or died quickly, rather than flapping about like other tunas in the catch. In further examinations they discovered that this was due to ruptured gas bladders. This phenomenon was not observed in other tunas from the same catch. This relatively fragile organ in albacore might help explain their intermediate location within the water column and ecological milieu.

Although the adult albacore's niche seems to lie within the range of adult yellowfin, and overlap with young bigeye, as juveniles they appear to thrive best on the transitional fringes of the subtropical ocean (from about 16 to 20°C), where bluefin are the only potentially abundant thunnid competition. Juvenile migrations of both species can be notoriously long, but the habitat preferences of adult albacore seem to be more tuned to the middepths of near-tropical ocean than those of the bluefin. The southern bluefin may be the only exception. The two species appear to overlap at the warmer end of the juvenile bluefin habitat, with the albacore being slightly more abundant in the adjacent subtropics until the older adult southern bluefin begin their spawning migrations into specific warmer ocean regions with tropical SSTs.

The three bluefin species seem to spread themselves out across the subtropical to temperate oceans, aggregating seasonally at the productive subtropical to tem-

perate ocean convergences as juveniles. The adults are hardy and cold tolerant. Although they can foray into deeper tropical to temperate environments, they spend most of their nighttime at the surface in warmer waters where temperatures range from 9 to 23°C or so. From the surface layer they forage to depths of over 1000 m. This is a generality (Gunn and Block, this volume), and southern bluefin (Farley and Davis, 1998) seem to key into warm, productive surface waters to spawn. It also appears that the southern and Atlantic bluefin, like the tropical tunas, are serial spawners (Hunter and Goldberg, 1980; Hunter *et al.*, 1986; Schaefer, 1998; Farley and Davis, 1998), provided that they enter the spawning areas in good energetic states, and then find accessible forage. Without local forage, they likely leave local, particularly warmer environments to recharge depleted body fat, as Sharp and Dotson (1977) reported for juvenile albacore.

Adult bluefin tunas are obliged to enter tropical environments, as do all tunas, that are not apparently best suited for their growth and maintenance in order to situate their eggs and larvae in amicable locations. Larval tuna survival environments need adequate food resources and minimal predators. This basic obligation is likely the key to their relatively smaller numbers and erratic spawning successes compared to the more ubiquitous skipjack, yellowfin, and bigeye, and even the "fragile" albacore. The bluefins' late maturation and immense adult sizes provide several advantages over the tropical tunas. They can tolerate and operate in a greater range of ocean conditions; they can store more energy to be used in reproduction; and they can carry huge numbers of propagules to invest in short-term, local spawning events. The burden is that they must survive longer, within a broader, if perhaps less competitive, subtropical milieu while growing into their adult form and full reproductive capabilities.

The Mediterranean provides a full suite of seasonal options for the Atlantic bluefin, with seasonal warm surface water spawning areas distributed across the northern and eastern extents, overlaying cooler habitat. The year-to-year environmental variability in the Mediterranean Sea creates another source of variability for these fishes' early life stages to cope with. While their well-dispersed life-history phases are clearly "Darwinian" survival tactics, the adults appear to converge and congregate in small size-similar groups for localized spawning. What is obvious from the catch by size graphs in the Mather *et al.* (1995) historical review is that the variously located bluefin tuna fisheries each interact with a unique fraction of the total population. It also appears that there is a form of "homing" or repeat performances as these size cohorts wander about the Atlantic and enter various gamuts of fishermen.

Also apparent from these data sets is that eastern Atlantic coastal and Mediterranean fishery catch numbers tended to peak every 5 to 7 years. From the Mediterranean and Atlantic trap fishery data, the bluefin cohorts converged from both north and south, each with unique catch and fish size patterns (Mather *et al.*, 1995). Once inside the Mediterranean, intermediate recruitment peaks could be

seen as arising from these different cohorts, suggesting that there were some physical reasons, as well as some age-specific behaviors, that tended to create apparent cycles. Today, due to the reduction of breeding populations and "cropping" of age classes, fisheries that focus on either their seasonal feeding or spawning migrations pose the single greatest threat to their survival.

In capsulated form, bluefin tunas become more capable opportunists as they grow, being able to explore and exploit more voluminous and heterogeneous habitats as they search for nutrition. As adults, they can process and store massive amounts of energy that is then used to travel in search of the right places to deposit their stored energy as investments in a next generation. The dichotomy is that the tropical tunas invest more frequently, within a less varied and broadly dispersed milieu, supporting generally larger populations, while the bluefin tuna populations undergo extreme oscillations, based on smaller populations, exploring an even more vast environment. Both strategies work. The latter is adaptive to long-term climate variations, but is more susceptible to human intervention when populations are small.

Clearly, the broad and nearly continuous distributions of the several *Thunnus* species is an odd situation that is difficult to explain in usual zoogeographical contexts, often defined by specific temperature and food preferences. Specific developmental characteristics of each species delimit the various life-history stages, by species, in the ocean continuum. It is also clear that the tunas' general tendencies to aggregate about mammals and large sharks, topographic features, or other "objects" (FADs)—as well as within the convergence-mediated patches of plankton—create the concentrations that fisheries are dependent upon. Developing insights into these aggregation associations has been slow, beyond their acting as "feeding stations" (see Boggs, 1996, for a review of prior behavioral research). As Sharp (1978) pointed out, prediction of precisely where and how many tunas there will be is not feasible, but projections of where and when tunas will be vulnerable is important, and can be learned by carefully planned and executed research programs.

VI. COORDINATED EMPIRICAL STUDIES OF TUNA BEHAVIOR AND ABUNDANCE WITHIN OCEAN GRADIENTS

The importance of systematic and coordinated research methods emerges as the next requirement for the integration of basic research projects with fisheries and environmental time series information before our task is completed. Recent research from the ECOTAP (Etude du Comportment des Thonides par l'Acoustique et la Peche; Abbes and Bard, 1999) study based in Tahiti provides good examples

of careful project planning, execution, and analysis needed to document the behaviors of several tunas within a complex environment of both narrow and broad gradients. Having reviewed the recent ECOTAP literature, including several posters that they have produced for various recent meetings, I applaud the scope of their efforts. They set out to learn about the potential for a new longline fishery in the region of French Polynesia. A rigorous, vigorous, and yet practical research program was planned and executed. Through multivariate statistical approaches, and carefully stratified simultaneous observations, they have generated a useful understanding of how these species respond to and share the resources across a large region of the world's ocean. From the coordinated measurements of physical, chemical, and planktonic production, they have developed insights about the tunas' relative distributions based on their different physiological limitations.

Yellowfin tuna are caught on longlines throughout the region, from 50 to 350m, except in the very northern extent where low oxygen levels at depths of about 200 m preclude their presence below that level. A few degrees to the south, they fully occupy this depth range. Overlying all of this is a "layer" of skipjack tuna and other small- to medium-sized surface-oriented predator species coexisting and competing for resources in the upper ocean. As the skipjack grow, they reach deeper into the habitats shared by these larger tunas. Because of the shallow strata of plankton-induced oxygen depletion in the north of their study region, and warm surface temperatures above 100 m, albacore are excluded from the surface and less oxygenated depths. Albacore are present wherever the low oxygen and $<26°C$ SST phenomena do not intersect, and their relative abundance increases toward the south to at least the 450-m depth limitation of the researcher's observing systems. Bigeye occupy the full range, but are situated between 250 and 550 m at 20°S, and their habitat's vertical dimension decreases systematically toward the north, such that between 4° and 6°S, they occupy the water column between 100 and 250 m, overlapping the bottom portions of the skipjack, yellowfin, and albacore habitats.

Available temperatures, per se, in this region do not pose critical limitations for any of these species. The combined effects of oxygen, food abundance, and seasonal changes create this dynamic interaction. When the ECOTAP observations of micronekton abundance were plotted along a southwest-oriented transect from 11° to 14°S, Bertrand and Josse (1999) found that the micronekton were concentrated in a weak convergence zone. As expected, to the north they found that remineralization caused oxygen depletion below the shallow mixed layer. To the south, oligotrophy limited micronekton growth and distributions. Thus, they described the food production distribution within their study area. Their study took place from 1995 to 1997, a period of extended low Southern Oscillation Index and frequent ENSO Warm Events, creating an alternative scenario to that expected from earlier observations made by previous researchers.

The participants in the ECOTAP program focused on several specific subjects that are brought together in the end to define their integrated research strategy. Their first objectives were to test the efficacies of hydroacoustic tools in identifying the behaviors of micronekton, the food organisms that attract tunas to all the documented ocean fishing regions (Blackburn, 1968; Carey and Olson, 1982; Olson and Boggs, 1986; Marchal *et al.*, 1993; Roger, 1994; Roger and Marchal, 1994; Bertrand *et al.*, 1999). Next came the problem of *in situ* location and identification of individual tunas, in order to explore their interactions and unique behavior within the larger system.

The next subjects needing exploration were methods to approach and resolve the fine-scale behaviors of the region's tunas, within their constantly changing milieu, and all within the larger context of regional oceanic gradients and their dynamics. Recognizing that longline catch rates poorly reflect abundance or distribution when the hooks do not cover the entire habitat (Hanamoto, 1987), ECOTAP scientists carried out acoustic studies to locate and identify the three important tuna species in the region. Bertrand *et al.* (1999) caught, measured, and attached ultrasonic tags to several yellowfin and bigeye tunas in order to track well-identified individuals while using a split-beam echosounder to measure their individual target strengths and behaviors. They could not, however, discriminate between species using these tools, posing a challenge regarding species-specific behavioral or abundance information. They verified the utility of the split-beam echosounder in tracking individuals, despite variations in target strengths as each fish changed orientation and swimming behavior. The above dilemma and related problems need to be resolved, especially if seeking answers to questions about the distributions and behaviors related to developmental state, size, and sexual status of the several species.

The ECOTAP team produced a reasonable and clear picture of the oceanic habitats of the three tunas of greatest importance to the region's longline fisheries, as they set out to do, and then delivered their results into the real world as Tahiti and French Polynesia endeavor to develop and enhance their longline fisheries. I should make it clear that these are not the first acoustic tracking studies of this type, but they do represent uniquely full-featured simultaneous oceanic tracking of more than one species, without the interference of local island or topographically forced dynamics. The ocean fisheries helped define their research plans. This is "system science," long the focus of my personal objectives.

The first stage in development of all rigorous tuna behavior studies has been to refine the local-scale observations such that they give you fine detail on the behaviors of the fish with respect to identified features or structure(s) in the water column (Boggs, 1992; Holland and Sibert, 1994). Bach *et al.* (1998) have summarized previous and ongoing FAD-related tuna behavior studies. They concluded that their acoustic survey tools would also need to be improved so that they could be used to cover greater depths and wider horizontal areas, a problem com-

mon to most tuna FAD research to date. As previously discussed, small bigeye often mix in with FAD-associated skipjack and yellowfin schools in the seine fishery in the equatorial eastern Pacific. Without the influence of the FADs, bigeye are usually found at great depths during daylight hours, with occasional forays into the warmer surface layers. Dagorn *et al.* (1999) followed four medium-sized (25–50 kg) bigeye for periods ranging from 6 to over 30 h each. The fish traveled very different distances during the tracking periods, covering 25.5 km in a 6-h track and over 106 km in a 33.5-h track, and ranged from 10 to 60 km from the point of origin (demonstrating the point that tunas are not "advection" analogs, but actively search their habitats at speeds that far outrun internal ocean dynamics). These fishes and all active swimming species must be treated as volitional and motivated predators.

Bach *et al.* (1998) tagged several small (48–60 cm) yellowfin—some near and some away from FADs. In tracks of over 48 h, they describe results similar to Josse *et al.* where the small yellowfin made forays to 250-m or greater depths from the surface layer. The FAD-associated fish ranged to depths from 175 to over 250 m during the day, with short forays to over 400 m. At night the fish rose nearer the surface, wandering about between 50 and 250 m. Brill *et al.* (1998, 1999) described similar sonic tagging experiences off Hawaii, for both small and large (45 to 90 cm) yellowfin, and found that they tended to stay in the uniform surface layer. Comparing these results with those from the more open ocean tracks, and those with simultaneous acoustic plankton survey data, there is clearly more to studying tuna behavior than only focusing on their specific temperature and oxygen needs. The greatest frustration with these labor-intensive sonic tagging studies is that they tend to be relatively short-term, that is, most less than 24 h. Fortunately, the newer archival tagging technology has provided means for obtaining verification over extended periods of these fishes' behaviors. There is also the more realistic perspective of changes in diel behaviors in response to environmental conditions as the fish exploit features and move from region to region (Holland *et al.*, 1990, 1992; Dagorn *et al.*, 1999; Gunn and Block, this volume).

There are certain advantages that studies within the larger ECOTAP region (Abbes and Bard, 1999) and basinwide archival tagging studies (Gunn and Block, this volume) offer over more localized island or FAD-based studies. These include the movements within long-scale linear gradients and large-scale ocean processes within which these fishes operate as individuals, species, and competitors—in contrast to the local feature basis of island or sea mount attractions within either seasonal migrations or seasonal shifts in latitudinal current patterns. Both local and open ocean studies have their place, but the fine-tuning of our understanding depends heavily upon learning how these species operate within a common milieu, and how they partition themselves as they grow and develop the many special adaptive strategies that each has evolved.

VII. TUNA SCHOOLS AND DYNAMIC INTERACTIONS

To fisheries managers, abundance is the question. To fishermen, efficiency is the question. To physiological ecologists (and the fish)—given the continuous changing habitat conditions—the spectrum of behavioral responses and species specific developmental stage-wise adaptations hold the answers. One such question that has significance to population abundance assessments and fisheries production is that of the dynamics of tuna school sizes, as measured by fish landed within a single set of a seine net, or independently, from acoustic information. The main reason that FADs are used is to concentrate fish from relatively sparse abundances, as described above for the large tunas. The dynamics and interactions of the aggregations require special consideration, for several reasons. The need for careful analysis including environmental information is to alleviate the dichotomies that result of simplistic conceptual models where only one parameter is used to define changes in relative abundance, vulnerability, and all the non-fisheries density related interactions.

Sharp (1978) and Sharp *et al.* (1983) described why it is nearly impossible to distinguish between changes in availability and changes in abundance without good records of both measures of habitat situation and catches by size/age groups. Superschools are observed to form and break up in time around most of the objects that have been observed to aggregate tunas. The reason for these associations is still poorly understood (Dagorn and Freon, 1999). My early studies (Sharp, 1978) showed that school sizes tended to be larger where the available habitat's vertical dimensions were narrowest, suggesting that there is a relation between local fish school densities, encounter rates, and school or aggregation size. The modal small school was about 7 tons, although smaller schools would not be set upon in most circumstances in today's ravenous seine fishing environment.

Bertrand and Josse (1999) continued the study by surveying bigeye abundance in the study region, finding about 1.33 fish per km^2, or 33.8 kg bigeye per km^2. They also measured tuna densities around FADs, and found 3.65 fish per km^2. In a comparison with IATTC stock assessments, within a well-fished region, they found that IATTC estimates showed an average density of 0.83 fish per km^2. Thus, they confirmed my original statement (Sharp, 1978) that "if tunas were truly uniformly dispersed in their habitat they would be so rare as to be virtually nonexistent." They were also able to confirm that their acoustic techniques "allow observation of such 'virtually nonexistent' tuna."

A. Why Tunas Aggregate

The largest recorded single seine set capture in the early (pre-1976) IATTC logbook records was a 200-ton skipjack school, aggregated on a piece of discarded

hawser. Typically, the catch from individual fish schools taken in the early seine fisheries followed a negative binomial size distribution. Years of observations aboard fishing vessels show that smaller free swimming tuna schools tend to be more size homogeneous. As the school size increases, there is a clear increase in size range, multiple size–age modes, and often mixed species. In yellowfin genetic studies (Sharp, 1978), larger schools with mixed size/age classes have tended to comprise more than one genetic unit. Clumps of similar-sized individuals with rare alleles were observed in schools that were sampled for either size-related differences (broad size ranges) or very narrow size ranges, suggesting lifelong cohesion as a result of fish size similarity (Sharp, 1978). There is apparently an inherent need for same size fish to maintain coherence.

Bonabeau and Dagorn (1995) began by looking for universal principles for fish school size distributions. Because of the sampling problems, tuna school size dynamics remain a mystery (Bonabeau *et al.,* 1999). Clark and Mangel (1979) and Clark and Mangell (1984) showed that if there were a habitat-mediated concentration effect, it could severely bias abundance estimates based on catch per unit effort statistics. In fact, as discussed above, the entire aggregation phenomenon needs to be better understood, including some intense efforts to study the coherence of various schooling structures, from small size-similar schools to multispecies aggregations. The studies need to be done in the open ocean rather than only in areas where FADs or island phenomena dominate the situations.

VIII. THE IMPORTANCE OF STUDYING INDIVIDUAL FISH BEHAVIOR

Electronic archival tags are among the many new tools that allow us to study individual fish behaviors over extended time and space domains. The pop-off archival satellite tag (Block *et al.,* 1998; Gunn and Block, this volume) offers the greatest variety of synoptic behavioral and environmental data collection. There are relatively large amounts of life-history and migration data derived from decades of tuna tagging (Bayliff, 1996) and returns from fisheries catches. There is only a modicum of behavioral data from sonic tracking of tunas. Most of these data were collected within the coastal and fisheries environment for a few hours to a few days. However, longer records of the movements and migrations of large numbers of fisheries-independent tunas, and the study of their daily behaviors in different environments under different modes of behavior (traveling, feeding, spawning, etc.), have yet to be collected in sufficient quantity, but vast amounts of new information are now being acquired.

It is tempting to make the leap from the fisheries catch information to their more complex behaviors from a few small examples, but the complexities of schooling, population structure, and breeding units remain to be understood

(Sharp, 1978). Without exaggerating, it is simply imperative that more systematic research into these topics be undertaken. The history of the development of the archival tag and the transition from implants to the pop-off satellite generation have been slow until just the recent few years, when the various researchers involved began to home in on the differences between anecdotal data sets and replicate-rich, but expensive, tagging efforts. All of the recommendations from the recent reviews of tuna fisheries interactions include enhanced tagging efforts. But I would suggest that there is no more valuable information than that derived from archival pop-off satellite tags, given the problems with reporting, tag shedding, and our ignorance of age-specific behaviors of most all of the tuna species. Whatever moneys are being spent on distribution and mixing studies is being short-circuited by individuals or corporations with opposing agendas.

Again, the differences between FAD- and island-associated research have begun to emerge, telling us that "local" feeding behaviors and growing phases of tuna migrations are distinct from their behaviors during the traveling and dispersive phases (Block *et al.*, 1998; Lutcavage *et al.*, 1999). The differences associated with traveling and dispersion behaviors are likely associated with seasonal and interannual oceanographic processes, as well as experience gained as each cohort-unit explores the larger habitat available to them, if so motivated. One can quickly surmise that a fish or group of like-experienced and similar-size individuals that find themselves located within a food-rich, amicable environment will not be as likely to move on into a less productive environment as those fishes in regions of limited food.

IX. THE ECOCOSMOLOGICAL QUESTION: "WHY ARE TUNAS WHERE THEY ARE?"

The answer is simply, "because they can be there." At evolutionary extremes, bigeye and albacore tunas offer good examples of life-history patterns that have succeeded to varying but lesser degrees in accomplishing the niche expansion that has been more completely attained by the bluefin tuna group. They have adapted similar strategies, but accomplished different capabilities. The trade-offs in ultimate adult size, longevity, and propagule delivery capability are complex, difficult to evaluate measures of survival tactics, and should be carefully considered when theorizing about relative productive potentials and likely recruitment successes.

As forecasts are the ultimate objectives of science, credible fisheries recruitment forecasts are the Holy Grail of fisheries oceanography. The designing of research into conditions promoting, or not, the survival of various life-history stages of tunas has only just begun to deal with local environments. The seasonal cycles within the oceans are of greatest impact on these processes. We also now know that interannual variability and decadal scale regime shifts tend to create the

more large-scale dynamics that make it imperative that we not get trapped into the idea that every year produces the same recruitment expectations. This fuzzy assumption has been a major failing of recent fisheries management as a product of model-dominated parameterized science over observation-driven science. These are not new issues (for reviews see Sharp, 1981a,b, 1995), but they do get in the way of progress and precautionary management of poorly understood resource species. There is a lot more systematic science needed to done. The combination of archival tagging, ocean observations, and ecological monitoring is the only available solution to the remaining dilemmas, presuming that they are embedded within the matrix of continued collection catch and effort statistics, and better pinpointed catch locations, within a more realistic temporal and spatial framework of synoptic measurements.

Recruitment successes are "events" resulting from the intersections of many rare and unlikely phenomena, and many normal biophysical interactions and processes. Mostly, these are not subject to mean and variance or equilibrium system-based statistical procedures (Lasker, 1975; Hunter and Goldberg, 1980; Sharp, 1981a,b). Credible predictions of future recruitment survival patterns can only be usefully accomplished from individual (species and size) based modeling perspectives and thorough understanding of survival requirements for each subsequent life-history phase. This does not preclude forecasts for larger regions and major phenomena such as ENSO variations of simple species-specific recruitment responses such as above, below, or about some longer-term mean responses, particularly for most tropical tunas, and even some of the cold-water tunas.

Our principal ecological problems still lie with understanding species distributions and aggregation-size behaviors and relationships. Recognizing that the temperate tunas live in a poorly understood, dynamic and inhomogeneous domain, their behaviors are apparently more opportunistic (exploratory). Where they might be located at any time likely depends upon their individual or group experiences within these more dispersed features, structures, and processes, enabling them to locate food resources and grow to adulthood. Even more complex issues must be resolved for their reproduction to be successful. Combined, the where and when solutions are subject to physically driven ecological responses, life-history stages, experience, and additional constraints posed by fishing pressures.

Attempts at environment-free statistical population forecast models will certainly continue to fail, as they have done for most long-lived fishes, for the same reasons. The tunas are not alone in creating this dilemma, as many species with fine-scale requirements within limited, environmentally "noisy" habitats need to contend with similar problems. The common denominators of these species include longevity, migratory dispersion, large adult size, and immense investments in propagule deliveries and distribution (sometimes even live-bearing), and their combinations, as means of resolving the temporal and spatial inhomogeneities for their young. Most adult fishes are mobile and responsive to most ocean situations.

With this perspective, the increased study of individuals is certainly appropriate if we are ever to truly come to comprehend how these many species have succeeded in carving up the world's oceans into such overlapped habitats. Through species-specific physiological adaptations, morphological accessories such as their individualized circulatory plans, and their sometimes shared, sometimes unique biochemical capabilities, tuna species have adopted adaptive behaviors that operate across most of the upper ocean, to at least 800 m, between the bounds of the polar oceans. They are not alone, as they are feeding alongside marine mammals and other large, widely dispersed denizens whose life histories are also cryptic and only available for study using the new digital archival tools.

X. CONCLUSIONS

These many anecdotes make the point that tuna oceanography is both an important applied science and an essential economically relevant activity. The direct applications of knowledge about species distributions, interactions, and behavioral responses to environmental processes and patterns are useful from the earliest stages of fisheries development into the expansion phases that have characterized most ocean fisheries. As well, the insights that well-measured ocean patterns and changes provide are crucial to the longer-term responsibility of managing and nurturing these highly mobile, renewable resources. Where I have advocated that fishing vessels be incorporated into the tasks of environmental monitoring, it is clear that the fish themselves now offer even more opportunities, as they become integrated into the observation systems, to provide synoptic information about their own forays within their vast array of options. The emergent archival tag technology, particularly the PSAT archival tags, provides new ways for all oceanography to become better applied, and ever-larger perspectives on fishes and oceans to emerge. There are few or no better uses of ocean science funds than to attend to these issues.

Ultimately, the likelihood of success in managing exploitation rates of fish populations with the primary objective of maintaining them in perpetuity depends upon the integration of information about individual self-sustaining population units and their interactions with competitors within the constantly changing ecological milieu. This is the realm of "applied physiological ecology," and includes careful study of physical ocean and atmosphere variability as a basis for interpretations. This necessary understanding can only arise from carefully thought out, systematic studies of the oceanographic and ecological milieu, that is, the target fish species, their ecological interactions, and the various aspects of each fishing gear type that promote their success, or not. This is "fisheries oceanography." These two applied science topics are how and where empirical scientific knowledge is applied to the management and optimization of all the fisheries interac-

tions, with the objectives of sustaining all living resources and the humans who are dependent upon them. These objectives are clear. The politics are often more obscure. The challenge is to continue to gather observations in order to continue to learn and then better apply what is known toward these objectives. It is an exciting time now that we have the tools, and a critical mass of concerned tuna scientists.

ACKNOWLEDGMENTS

I am first and foremost dedicated to the best interests of the fish and fishermen. If applied wisely, the science that I perceive as being most noteworthy is an important means of ensuring the survival of both. Everyone who has been involved in this difficult research deserves credit for their diligence and foresight in their efforts to resolve important problems in basic ecology, applied science, and fisheries conservation. First Davy and then Kishinouye, followed by John Magnuson, Frank Carey, and Bruce Collette—from their works came the insights that sequentially got many of us interested. Meanwhile, Luis Rivas, Rodriguez-Roda, and Frank Mather III kept our sights on why, and for whom, we do our science. Recent progress has been remarkable. In my experience, there are many who forget that we are allowed to do our work for reasons other than filling library shelves, or resumes. The world's fisherfolk need our answers now, if not yesterday. It is all about the future. I thank Andre Boustany for reading an early draft and helping me to sift and order the original draft so that those who are learning about tuna biology, ecology, and oceanography for the first time might keep a common thread as they read what I have written. To Don Stevens and Barbara Block, whose patience and efforts over the recent decades have been remarkable, I thank you. I can only hope that as a recognized poser of tough questions, and a general skeptic, those whose efforts I have not highlighted will forgive me. All sincere efforts are appreciated, and all information shared is cherished.

REFERENCES

Abbes, R., Asine, A. S., Bach, P., Josse, E., Lebourges, A., and Wendling, B. (1995). Etude du comportement des thonidés par l'acoustique et la pêche à la palangre en Polynésie Française. Rapport de la campagne ECOTAPP, Doc. Int. ORSTOM/IFREMER/EVAAM, p. 157.

Abbes, R., and Bard, F.-X., Eds. (1999). ECOTAP, Etude du comportement des Thonidés par l'Acoustique et la peche en Polynésie Française, Rapport Final. Convention Territoire, EVAAM-IFREMER-ORSTOM, no. 951070.

Abbes, R., Misselis, C., and Bach, P. (1998). Temporal efficiency of different baits in longline fishing. Poster at Tuna Conference 1998, Lake Arrowhead, CA.

Bach, P., Wendling, B., Abbes, R., and Josse, E. (1996). Characteristics of albacore catches achieved by experimental fishing using instrumented longline in the French Polynesian Exclusive Economic Zone (EEZ). Presented at the Sixth South Pacific Albacore Research Workshop, Raratonga, Cook Islands, 5–7 March 1996.

Bach, P., Dagorn, L., Josse, E., Bard, F.-X., Abbes, R., Bertrand, A., and Misselis, C. (1998). *SPC FAD Info. Bull.* **3,** 3–19.

Bakun, A. (1996). *Patterns in the Ocean.* California Sea Grant/CIB pp. 323.

Bard, F.-X. (1981). Le thon germon (*Thunnus alalunga*) de l'Océan Atlantique. De la dynamique de population à la stratégie démographique. Thèse Doctorat ès Sciences Naturelles, Université de Paris VI.

Bard, F.-X., and Josse, E. (1996). Peculiarity of swimming bladder of large albacore (*Thunnus alalunga*) caught by longline. Doc. SPAR 6th meeting. (Available on request.)

Bard, F. X., and Santiago, J. (1998). Review of albacore (*T. alalunga*) historical surface fisheries data (1920–1975) for possible relationships with the North Atlantic Oscillation. ICCAT SCRS/98/, no. 106. ICCAT, Madrid, Spain.

Bard, F.-X., Bach, P., and Josse, E. (1998). *In* "Symposium ICCAT on Tuna, June 1996" (Beckett, J., Ed.), pp. 126–139. ICCAT, Madrid, Spain.

Barkley, R. A., Neill, W. H., and Gooding, R. M. (1978). *Fish. Bull., U.S.* **76,** 653–662.

Barnston, A., Glantz, M. H., and He, Y. (1999). *Bull. Am. Meteorol. Soc.*, Feb.

Bayliff, W. H. (1996). *FAO Fish. Tech. Rep.* **365,** 592–612.

Beamish, R. J., Ed. (1995). *Can. Spec. Pub. Fish. Aquat. Sci.* **121.**

Bertignac, M., and Ardill, D. (1996). *In* "Status of Interactions of Pacific Tuna Fisheries in 1995. Proceedings" (Shomura, R. S., Majkowski, J., and Harman, R. F., Eds.), FAO Fish. Tech. Paper 365, pp. 67–83. FAO, Rome.

Bertignac, M., and Fonteneau, A. (1996). *In* "Status and Interactions of Pacific Tuna Fisheries in 1995" (Shomura, R. S., Majkowski, J., and Hartman, R. F., Eds.), FAO Fish. Tech. Paper 365, pp. 84–123. FAO, Rome.

Bertignac, M., Lehodey, P., and Hampton, J. (1998). *Fish. Oceanogr.* **7,**(3), 311–316.

Bertrand, A., and Josse, E. (1999). *Prog. Mar. Ecol. Ser.,* **191,** 127–140.

Bertrand, A., Josse, E. and Massé, J. (1999a). *In* "Proceedings of the 5th Indo-Pacifique Fish Conference, Nouméa, 1997." Séret B. and Sire J.-Y. Eds. Paris: Soc. Fr. Ichtyol., pp. 443–450.

Bertrand, A., Josse, E., and Masse, J. (1999b). *In situ* acoustic target strength measurement of bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) by coupling split-beam echo-sounder and sonic tracking. *ICES J. Mar. Sci.* **56,** 51–60.

Bertrand, A., LeBorgne, R., and Joss, E. (1999c). Acoustic characterization of micronekton distribution in French Polynesia. *Mar. Ecol. Prog. Ser.* 191:127–140.

Bertrand, A., Misselis, C., Josse, E., and Bach, P. (1999c). Caracterisation hydrologique et acoustique de l'habitat pelagique en Polynesie Francaise: consequences sue la distribution horizontale et vertical des Thonides. Presented at Les Espaces de L'Hallieutique—4th Forum Hallieumetric, Rennes. 29/6–01/07/99. (meeting document available on request)

Blackburn, M. (1968). *Fish. Bull., U.S.* **67,** 71–115.

Block, B. A., Dewar, H., Williams, T., Prince, E., Farwell, C., and Fudge, D. (1998). *Mar. Technol. J.* **32,** 37–46.

Boggs, C. (1992). *Fish. Bull., U.S.* **90,** 642–658.

Boggs, C. (1996). *In* "Status of Interactions of Pacific Tuna Fisheries in 1995. Proceedings" (Shomura, R. S., Majkowski, J., and Harman, R. F., Eds.), FAO Fish. Tech. Paper 365, pp. 38–47. FAO, Rome.

Bonabeau, E., and Dagorn, L. (1995). *Phys. Rev. E* **51**(6), R5220–5223.

Bonabeau, E., Dagorn, L., and Freon, P. (1999). *PNAS.* **96**(8), 4472–4477.

Brill, R. W. (1994). *Fish. Oceanogr.* **3**(3), 204–216.

Brill, R. W., Lowe, T. E., and Cousins, K. L. (1998). How water temperature really limits the vertical movements of tunas and billfishes—It's the heart stupid. Abstract from the American Fisheries Society, International Congress on Biology of Fish, July 26–20, 1998, Towson University, Baltimore, MD.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J. (1999). *Mar. Biol.* **133,** 395–408.

Carey, F., and Olson, R. (1982). *Collect. Vol. Sci. Pap. ICCAT* **17,** 458–466.

Clancy, R. M., and Weller, R. A., (1992). "Sea Surface Temperature: Ad Hoc Working Group Report." Joint Oceanographic Institutions, Washington, DC.

Clark, C. W., and Mangel, M. (1979). *Fish. Bull., U.S.* **77**(2), 317–337.

Clark, C. W., and Mangel, M. (1984). *Amer. Nat.* **123,** 626–647.

Dagorn, L., and Freon, P. (1999). *Can. J. Fish. Aquat. Sci.* 56(6), 984–993.

Dagorn, L., Bach, P., and Josse, E. (1999). *Mar. Biol.*

Enfield, D. B. (1989). *Rev. Geophys.* **27**(2), 159–187.

FAO (1996). "Proceedings of the second FAO Expert Consultation on Interactions of Pacific Tuna Fisheries." Shomura, R. S.,; Majkowski, J.; Harman, R. F. (eds.) Shimizu, Japan, 23–31 January 1995. FAO Tech. Rep 365. Rome, pp. 612.

Farley, J. H., and Davis, T. L. O. (1998). *Fish. Bull., U.S.* **96**(2), 223–236.

Fonteneau, A. (1997). *Atlas of Tropical Tuna Fisheries: World Catches and the Environment.* L'Institut Français de Recherche Scientifique pour le Développement en Coopération, Paris.

Forsberg, E. D. (1980). *Spec. Rep. IATTC* **7.**

Freon, P. (1999) *Dynamics of pelagic fish distribution and behaviour: Effects on fisheries.* Fishing News Books, Oxford.

Gauldie, R. W., and Sharp G. D. (1995). *Fish. Oceanogr.* **5**(2), 100–113.

Glantz, M. H. Ed. (1992) *Climate Variability, Climate Change and Fisheries.* Cambridge University Press. pp. 450.

Glantz, M. H. (1996). "Currents of Change: El Niño's Impact on Climate and Society." Cambridge Univ. Press, Cambridge.

Glantz, M. H., and Feingold, L. E., Eds. (1990). "Climate Variability, Climate Change and Fisheries." Environmental and Societal Impacts Group, NCAR, Boulder, CO.

Hall, M. (1996). *Res. Fish. Biol. Fish.* **6,** 319–352.

Hall, M. (1998). *Res. Fish. Biol. Fish.* **8,** 1–34.

Hanamoto, E. (1974). *La Mer* **12**(3), 128–136.

Hanamoto, E. (1975). *La Mer* **13**(2), 58–71.

Hanamoto, E. (1987). *Bull. Jpn. Soc. Fish. Oceanogr.* **51,** 203–216.

Hela, I., and Laevastu, T. (1971). "Fisheries Oceanography." Blackwell, Fishing News, London.

Holland, K. N., Brill, R. W., and Chang, R. K. C. (1990). *Fish. Bull., US,* **88,** 493–507.

Holland, K., Brill, R., Chang, R., Sibert, J., and Fournier, D. (1992). *Nature.* **358,** 410–412.

Holland, K., and Sibert, J. R. (1994). *Environ. Biol. Fishes* **40,** 319–327.

Hunter, J. R., and Goldberg, S. R. (1980). *U.S. Natl. Mar. Fish. Serv., Fish. Bull., U.S.* **77**(3), 641–652.

Hunter, J. R., Macewicz, B. J., and Sibert, J. R. (1986). *U.S. Natl. Mar. Fish. Serv. Fish. Bull.* **84**(4), 255–292.

ICANE, (1981). Investigación Cooperativa de la Anchoveta y su Ecosistema ICANE entre Perú y Canadá. Callao, Bol. Inst. Mar Perú-Callao. Vol. Extraordinario, IMARPE, Callao. pp. 288.

Johnson, L. (1981). *Can. J. Fish. Aquat. Sci.* **38**(5), 571–590.

Josse, E., Bach, P., and Dagorn, L. (1998). *Hydrobiologia* **371/372,** 61–69.

Kawasaki, T. (1983). *In* "Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources" (Sharp, G. D., and Csirke, J., Eds.), FAO Fish. Rep. 291(3), pp. 1065–1080. FAO, Rome.

Kendall, A. W., Jr., Perry, R. I., and Kimeds, S., Eds. (1996). *Fish. Oceanogr.* **5**(Suppl.1).

Klyashtorin, L. B. (1998). *Fisheries. Res.* **37,** 115–125.

Lasker, R. (1975). *Fish. Bull. U.S.,* **73,** 453–462.

Laurs, R. M. (1997). *In* "Changing Oceans and Changing Fisheries: Environmental Data for Fisheries Research and Management" (Boehlert, G. W., and Schumacher, J. D., Eds.), pp. 9–16. NOAA Tech. Memorandum NMFS. NOAA. La Jolla.

Laurs, R. M., and Lynn, R. J., (1977). *Fish. Bull. U.S.* **75**(4), 795–822.

Laurs, R. M., Fiedler, P. C., and Montgomery, D. R. (1984). *Deep Sea Res.* **31,** 1085–1099.

Le Blanc, J-L., and Marsac, F. (1999). Climate information and prediction services for fisheries: The case of tuna fisheries. CLIMAR 99—WMO Workshop on Advances in Marine Climatology, Vancouver, 8–15 September 1999. (Available on request.)

Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., and Picaut, J. (1997). *Nature* **389,** 715–718.

Lehodey, P., André, J-M., Bertignac, M., Hampton, J., Stoens, A., Menkès, C., Memery, L., and Grima, N. (1998). *Fish. Oceanogr.* **7**(3).

Longhurst, A. (1995). *Prog. Oceanogr.* **36,** 77–137.

Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., and Howey, P. W. (1999). *Can. J. Fish. Aquat. Sci.* **56,** 173–177.

Mallicoate, D. L., and Parrish, R. H. (1981). *CalCOFI Rep.* **22,** 69–81.

Marchal, E., Gerlotto, F., and Stequert, B. (1993). *Oceanol. Acta* **16,** 261–172.

Marsac, F., and Hallier, J. P. (1991). *In* "Proceedings of the Expert Consultation on the Stock Assessment of Tunas in the Indian Ocean," Bangkok, Thailand, 2–6 July 1990. Indian Ocean Commission, Colombo, Sri Lanka.

Mather, F. J., III, Mason, J. M., Jr., and Jones, A. C. (1995). "Historical Document: Life History and Fisheries of Atlantic Bluefin Tuna." NOAA Technical Memorandum NMFS-SEFSC-370. NOAA.

Matsumoto, W. M., Kazama, T. K., Aasted, D. C. (1981). *Mar. Fish. Rev.* **45**(9), 1–13.

Okubo, A. (1980). *Diffusion and Ecological Problems: Mathematical Models.* Springer-Verlag, New York.

Olson, R. J., and Boggs, C. H. (1986). *Can. J. Fish. Aquat. Sci.* **43,** 1759–1775.

Parrish, R. H., Mallicoate, D. L., and Mais, K. F. (1985). *Fish. Bull., U.S.* **83**(4), 483–496.

Parrish, R. H., Mallicoate, D. L., and Klingbiel, R. A. (1986). *Fish. Bull. U.S.* **84**(3), 503–517.

Parrish, R. H., Bartoo, N. W., Herrick, S. F., Jr., Kleiber, P. M., Laurs, R. M., and Wetherall, J. A. (1989). "Albacore Management Information Document." NOAA Tech. Mem. NMFS-SWFC-126. NOAA. La Jolla.

Porch, C., Kleiber, P., Sibert, J., and Bailey, R. (1995). ICCAT, SCRS/95/91.

Rivas, L. R. (1978). In: *The Physiological Ecology of Tunas.* (G. D. Sharp and A. E. Dizon, Eds.), pp. 369–393. Academic Press. San Francisco/New York.

Roger, C. (1994). *Environ. Biol. Fish* **39,** 161–172.

Roger, C., and Marchal, E. (1994). *IATTC Rec. Doc. Sci.* **32,** 237–248.

Saito, S. (1973). *Mem. Fac. Jpn. Soc. Sci. Fish.* **21**(2), 107–182.

Saito, S. (1975). *Bull. Jpn. Soc. Sci. Fish.* **41**(8), 831–841.

Saito, S., and Sasaki, S. (1975). *Bull. Jpn. Soc. Sci. Fish.* **40,** 643–649.

Schaefer, K. M. (1998). *IATTC Bull.* **21**(5), 201–272.

Schulein, F. H., Boyd, A. J., and Underhill, L. G. (1995). *S. African J. Mar. Sci.* **15,** 61–82.

Sharp, G. D. (1976). *In* "Maguro Gyokyo Kyogikay Gijiroku, Suisano-Enyo Suisan Kenkyusho" (Proceedings of the Tuna Fishery Research Conference). Fisheries Agency–Far Seas Fisheries Research Laboratory, Shimizu, Japan.

Sharp, G. D. (1978). *In* "The Physiological Ecology of Tunas" (Sharp, G. D., and Dizon, A. E., Eds.), pp. 397–449. Academic Press, San Francisco/New York.

Sharp, G. D. (1979). Areas of potentially successful exploitation of tunas in the Indian Ocean with emphasis on surface methods. Tech. Rep. IOFC/DEV/79/47. Indian Ocean Programme, FAO, Rome.

Sharp, G. D. (1981a). *In* "Report and Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes" (Sharp, G. D., Conv., Ed.), IOC Workshop Rep. Ser. no. 28, pp. 6–62. UNESCO, Paris.

Sharp, G. D. (1981b). *In* "Report and Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes" (Sharp, G. D., Conv., Ed.), IOC Workshop Rep. Ser. no. 28, pp. 125–148. UNESCO, Paris.

Sharp, G. D. (1987). *In:* The Benguela and Comparable Ecosystems." A. I. L. Payne, J. A. Gulland and K. H. Brink, Eds.) *So. Afr. J. Mar. Sci.* **5,** 811–838.

Sharp, G. D. (1992). *In* "Climate Variability, Climate Change and Fisheries" (Glantz, M. H., Ed.), pp. 377–416. Cambridge Univ. Press, Cambridge.

Sharp, G. D. (1995). *In* "Arabian Sea Oceanography and Fisheries" (Thompson and Tirmizi, Eds.), pp. 239–264. Vanguard Books (PVT) LTD, Lahore, Pakistan.

Sharp, G. D. (2000). *In* "The Future of Fisheries Oceanography" (Harrison, P. J., and Parsons, T., Eds.). Blackwell Books, London.

Sharp, G. D., and Csirke, J., Eds. (1983). "Proceedings of the Expert Consultation to Examine the Changes in Abundance and Species Composition of Neritic Fish Resources," San Jose, Costa Rica, 18–29 April 1983. FAO Fish. Rep. Ser. 291(2, 3). FAO, Rome.

Sharp, G. D., and Dizon, A. E., Eds. (1978). *The Physiological Ecology of Tunas,* pp. 485. Academic Press. San Francisco/New York.

Sharp, G. D., and Dotson, R. (1977). *Fish. Bull., U.S.* **75**(2), 447–450.

Sharp, G. D., and McLain, D. R. (1993a). *Oceanography* **5**(3), 163–168.

Sharp, G. D., and McLain, D. R. (1993b). *Oceanography* **6**(1), 13–22.

Sharp, G. D., and Pirages, S. W. (1978). (G. D. Sharp and A. E. Dizon, Eds.), pp. 41–78. *In* "The Physiological Ecology of Tunas." Academic Press. San Francisco/New York.

Sharp, G. D., Csirke, J., and Garcia, S. (1983). *In* "Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources," San Jose, Costa Rica, 18–29 April 1983 (Sharp, G. D., and Csirke, J., Eds.), FAO Fish. Rep. Ser. 291(3), pp. 1177–1224. FAO, Rome.

Sharp, G. D. (1987). *In* "The Benguela and Comparable Ecosystems." (A. I. L. Payne, J. A. Gulland, and K. H. Brink, Eds.) *So. Afr. J. Mar. Sci.* **5,** 811–838.

Shomura, R. S., Majkowski, J., and Langi, S. (1994). "Interaction of Pacific Tuna Fisheries," Vols. 1 and 2. FAO Fish. Tech. Pap. 336(1) and 336(2). FAO, Rome.

Shomura, R. S., Majkowski, J., and Hartman, R. F., Eds. (1996). "Status and Interactions of Pacific Tuna Fisheries in 1995." FAO Fish. Tech. Pap. 365. FAO, Rome.

Sibert, J. R., and Fournier, D. A. (1994). *In* "Proceedings of the First FAO Expert Consultation on Interactions of Pacific Ocean tuna Fisheries," Volume 1—Summary report and papers on interaction. R. S. Shomura, J. Majkowski, and S. Langi (Eds.). FAO Fisheries Technical paper 336/1. pp. 108–121.

Sibert, J. R., Hampton, J., Fournier, D. A., and Bills, P. J. (1999). *Can. J. Aquat. Fish. Sci.* **56,** 925–938.

Sund, P. N., Blackburn, M., and Williams, F. (1981). *Ocean. Mar. Biol. Annu. Rev.* **19,** 443–512.

Suzuki, Z. (1989). *In* "Planning the future of billfishes. Research and management in the 90's and beyond." (R. H. Stroud, Ed.) Proc. Second International Billfish Symposium, Kailua-Kona, Hawaii, August 1–5, 1988. Part 1: Fishery and stock synopsis, data needs and management. National Coalition for Marine Conservation, Inc., Savannah, Georgia. pp. 165–177.

Uda, M. (1927). *J. Imper. Fish. Inst.* **23**(3), 80–88.

Uda, M. (1957). *J. Tokyo Univ. Fish.* **38**(3), 363–369.

Uosaki, K., and Bayliff, W. H. (1999). *IATTC Bull.* **21**(6).

Verschell, M. A., Kindle, J. C., and O'Brien, J. J. (1995). *JGR-Oceans,* AGU, Washington, D.C. **18,** 409–418.

Welschmeyer, N. A., *et al.* (1999). *EOS* **80,** 248.

10

TUNAS IN CAPTIVITY

CHARLES J. FARWELL

I. Early History
II. Tunas in Captivity
  A. Commercial Tuna Farms
  B. Captive Tuna Research Facilities
III. Aquarium Displays of Tunas and Related Species
IV. Methods of Collection and Care
  A. Collection
  B. Captive Care of Tuna
  C. Handling Techniques
  D. Growth
V. Research Opportunities with Captive Tunas
VI. Future Efforts

I. EARLY HISTORY

Members of the Family Scombridae have captured the attention of humankind for millennia. In this chapter I examine how captive populations of bluefin tuna have been maintained. Included in the *History of Animals* (Aristotle, 2350 B.P.) are detailed descriptions of the Atlantic bluefin tuna, *Thunnus thynnus,* and their annual spring migrations to spawn in the Mediterranean Sea. Pliny (1950 B.P.) chronicles a description of vast schools of tuna impeding the forward navigation of Alexander the Great's fleet (Butler, 1982). Bluefin tuna were highly valued for food throughout their history with man and elaborate undersea traps were built and maintained for the purpose of catching tuna. The earliest traps were set by the Phoenicians over 3000 years ago and evolved into the specialized traps called "tonnara" used today (Butler, 1982; Maggio, 2000). These traps have been used throughout the Mediterranean from Spain to Turkey and into the Bosporus. To aid in catching tuna, the Romans and the Greeks built watchtowers specifically for the purpose of sighting or locating the migrating tunas. Early Roman cities, such as Baelo Claudia, 200 B.C. (Bologna, Spain), were built in coastal areas for the com-

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

mercial trade of catching and salting tuna. The practice of using tonnara to catch bluefin continues today, primarily in Spain, Portugal, and Italy, although only a few of the tonnara remain in use. Mediterranean Sea traps were set to catch giant bluefin in a short period of time. The flesh would be canned, salted, or preserved in olive oil for future use. Once empty the traps would be hauled out of the water, mended, and reset for a new catch, repeating the process until the migration had run its course.

The importance of tuna to early civilizations living in this area is captured by the drawings of tunas appearing in Italian cave paintings dating back 4000 years B.P.; images of tuna on Phoenician coins date back to 2500 years B.P. (Butler, 1982) and on pottery vases depicting the bartering over tuna from 2400 years B.P. (Maggio, 2000). In other areas of the world, shell mounds containing skeletal remains of *Thunnus* species have been found, indicating they were a part of the early diet of humans. *Thunnus* bones date from the early to middle Jomon period of Japan, 6000–4000 years B.P. (Komiya, 2000), and in coastal areas of British Columbia from 3000 years B.P. (Crockford, 1997). This leads to the conclusion that the value of tuna, revered both as food and for its beauty, was appreciated in early times and universally sought by many cultures.

II. TUNAS IN CAPTIVITY

A. Commercial Tuna Farms

1. Canada

The first use of anchored, floating net pens for commercial use to hold bluefin tunas for extended periods of time occurred in 1975 at St. Margaret's Bay, Nova Scotia, Canada. The original idea was to hold the tuna for an extended period of time, allowing the tuna to be sold at a time when market forces would bring a higher price for the fish. Giant bluefin tuna were captured during the summer season when they migrated into Canadian waters. Feeding the impounded tunas over the holding period had the added value of increasing the size, weight, and oil content of each tuna, thus generating a greater monetary return. The first pens were engineered and built by Japanese technicians; they were attached to mackerel traps by means of a tunnel made of netting which could be opened and closed so the tuna could be moved from the traps into the holding pens (Buchanan, 1977). The original impoundment consisted of eight pens that could accommodate a total of 600 tunas with an average mass of 500 kg each. The nets used in the impoundment were oval in shape and measured 100 by 50 m and were 15 m deep (Buchanan, 1977). The early success of the Nova Scotia bluefin tuna impoundments started a worldwide effort at duplicating their efforts.

Today there are tuna ranches or farms throughout the Mediterranean Sea, Ja-

pan, Australia, and Mexico. All three bluefin tuna species are currently involved in farming operations. Collection of tuna for the farming operations in the Mediterranean area, Mexico, and Australia rely primarily on tuna caught by purse seine. The seined tuna are transferred to a tow-pen, which is approximately 45 m in diameter and 15 m deep. Once the tunas are captured the tow-pen is slowly brought back to the central holding pen area at a speed through the water not exceeding 1 knot. Transfer of the tuna is accomplished by mating the tow-pen to the holding pen and driving the tuna through the common opening.

2. MEDITERRANEAN

In recent years in the Mediterranean, Atlantic bluefin tuna penning has increased and operations vary depending upon the target size of the bluefin. Pens are found currently in Spain, Italy, and into the Adriatic Sea, as well as other Mediterranean countries. Penning operations, focused on juvenile fish start in late winter to early spring and run through to fall; the sizes are mixed, ranging from 15 to 40 kg, and 2 to 4 years of age. Penning of giants accounts for a significant amount of the quota being taken in Europe. For example, in Spain 7 farms or pen operations with a combined total of 45 pens hold a capacity of 6000 mt (metric tons). Italy has 1 pen operation. Croatia has 5 farms with a total of 17 pens of unknown holding capacity. Traditional traps are found in Spain, Sicily, Portugal, Morocco, and Tunisia. Fishing effort for bluefin to be held in traps and for stocking the pens is timed to coincide with the spring migration of the giant tunas that come into the Mediterranean Sea for the purpose of spawning during the summer months. Harvesting from the pens frequently extends throughout the year and into spring of the following year, and the tuna are sold either as fresh or quick-frozen. The traps are harvested as they fill with fish; the fish are removed, slaughtered, and prepared for shipping to market.

3. AUSTRALIA

Australian tuna farming focuses on the southern bluefin tuna, *Thunnus maccoyii*. The primary location for the operations are in the Port Lincoln area of southern Australia. It is the largest of all tuna farm operations with as many as 100 pens with a starting mass of approximately 5000 mt and a harvest mass of 7000 mt in 2000. The dimensions of the pens in Australia are the standard used by the other farms and have their roots in the original impoundments of Nova Scotia. The southern bluefin tuna are collected seasonally during the Austral summer months in the Great Australian Bight. The average age and size at the time of collection is 3 years old and 20 kg mass (Glencross *et al.*, 2000). After being transferred to the farm pens they are maintained for up to 8 months and fed a diet of sardines and a commercially available product called "wet pellets" (Glencross *et al.*, 1999). Maximum growth occurs during the summer period of warmer water, 17–

21°C; approximately 30% of the initial body mass is added during this time (Glencross *et al.*, 2000).

4. Japan

In Japan, young of the year Pacific bluefin tuna, *Thunnus orientalis,* are collected off of Shikoku and Kyushu islands by commercial fisherman trolling small-feathered lures along the edge of the Kuroshio Current. The live tuna are held in onboard tanks with running seawater and are then transported back to the tuna farms where they are transferred to large rectangular pens, measuring 24 by 50 m and 15 m deep. Each pen can hold up to 5000 individual small tunas and over time these tuna are divided among other pens to accommodate for growth. They are fed 10% of their body weight per day over the course of three meals consisting of locally caught baitfish. The mass of the newly collected tunas ranges from 220 to 300 g; at 1 year of age they have grown to 4–6 kg. The population of tunas in each pen is reduced by splitting the number of tuna into other pens at intervals timed to the growth of the tuna, thus reducing the stocking density of the original pen. At this stage the food ration is lowered to approximately 5% of the estimated total mass of tuna in the pen. They are harvested at age 3 with a mass of approximately 40 kg (Suwa, 1989).

5. Mexico

The size of the Pacific bluefin tuna collected for farming in the eastern Pacific ranges from 20 to 50 kg, and they are 2–4 years of age. They are caught from June through September in the waters off of Mexico and California. Fish are maintained in pens until late January or February in a coastal area of Baja California, Mexico. The pen nets are 45 m in diameter and 15 m deep, and are stocked with up to 45 mt of bluefin per pen. Bluefin are fed once per day with sardines and anchovy, with food totals estimated to equal 5% of the biomass of tuna in each pen.

B. Captive Tuna Research Facilities

The open ocean, pelagic environment of most scombrid species has made it challenging to conduct field research. Their high metabolic rates and specialized swimming result in significant space requirements if held in captivity. The major challenge is that tunas must swim continuously, which makes collecting and captive care difficult.

1. Kewalo Research Facility

In 1958 the National Marine Fisheries Service built the first permanent tuna research facility specifically designed for maintaining tunas in captivity at Kewalo Basin, Honolulu, Hawaii. The researchers at Kewalo Basin in collaboration with

the local tuna fishers pioneered the techniques for collecting, transporting, and keeping yellowfin tuna, *Thunnus albacares,* in captivity. The holding facility consists of three 76,000-liter circular tanks, a larger 757,060-liter tank designed specifically for tunas, and a number of smaller research tanks of various sizes. A high-capacity flow-through water system provides 3000 liters of oceanic-quality water per minute for this facility (Brill, 1999). The Kewalo Research Facility has operated continuously since its inception, and has supported physiological and behavioral studies of visual acuity, sound sensitivity, olfaction, energetics, thermoregulation, geomagnetic sensitivity, and spawning and rearing of tuna eggs. The species investigated include yellowfin tuna, skipjack tuna (*Katsuwonus pelamis*) and kawakawa (*Euthynnus affinis*). The Kewalo Research Facility has earned a highly regarded reputation for the wide spectrum of scientific investigation conducted over the last 40 years by an international group of scientists. A partial list of scientific publications is included in the NOAA Technical Memorandum, "The Kewalo Research Facility—Leading the Way for More Than 40 Years" (Brill, 1999).

2. Achotines Laboratory

In 1984, the Inter-American Tropical Tuna Commission (IATTC) opened Achotines Laboratory in Panama. Early work focused on the techniques of collection, transfer, and maintenance of late larval and early juvenile scombrid species. Continued research included early life history studies of local scombrid species, including the black skipjack (*Euthynnus lineatus*). In 1993 a mutual agreement between the IATTC, the Republic of Panama, and the Overseas Fisheries Cooperation Foundation of Japan led to the building of an enlarged rearing facility for yellowfin tuna. The new facilities, completed in 1997, include four holding tanks, the largest of which is 1,361,900 liters. Successful collection of brood stock and subsequent captive spawning events for the yellowfin tuna have provided larval tuna for studies on age, growth, and food selectivity (Anonymous, 1994, 1996). Additional investigations include nutritional requirements and growth rates of the captive brood stock maintained in seawater ranging from 21 to 29°C (Anonymous, 1997).

3. Japan

The earliest attempts to keep tunas in captivity for studying culture and rearing techniques occurred in Japan at the Fisheries Institute, Kinki University (Harada *et al.,* 1971, 1973a,b, 1980), and at the Marine Science Museum of Tokai University (Suzuki *et al.,* 1972). Subsequent to these efforts, both Pacific bluefin tuna (*Thunnus orientalis*) and yellowfin tuna have been collected and kept in floating ocean pens for both research and commercial farming in various locations throughout the southern islands of Japan.

Two major facilities of the Japan Sea-Farming Association (JASFA) are dedicated to research on breeding and rearing of tunas; they are located in the southern

islands of Japan. Yaeyama Station on Ishigaki Island, Okinawa Prefecture, established in 1985, primarily works with yellowfin tuna. Holding facilities at Yaeyama Station for brood stock consist of a series of anchored floating pens differing in size, with the largest being 20 m in diameter and 8 m deep. Potential brood stock is collected as young of the year (375 g) and raised to sexual maturity. Longevity up to 7 years of age (80–130 kg) has been obtained with successful spawning. Observations on hatching rates, larval growth rates, and diet effects on survivorship are the focus of research (Masuma, 1992, 1993).

The second research station is located in Amami O'Shima, Kagoshima Prefecture, and is the newest facility within the association, having opened in 1995. It is dedicated to research on the breeding of Pacific bluefin tuna. This facility is unique and the only one of its kind in the world. Mature and adolescent bluefin tuna are held in a 14-ha cove, which is closed off from the outer harbor with double barrier nets. The average depth of the cove is 20 m. Outside of this embayment there are two floating pens, 40 m diameter and 23 m deep, used for holding brood stock tunas. Tunas ranging from 5 to 20 kg have been transported to both facilities by boat, and larger 80-kg bluefin tuna were successfully transferred from a commercial farm to the JASFA Station at Amami O'Shima by towpen. Breeding behavior was first observed in 1997, and fertilized eggs were collected at that time. Rearing of eggs started in 1997 and has continued each summer for the last 3 years. The size of the juveniles at the end of 3 months is 3 cm. Estimated size of the current brood stock is 250–350 kg; feeding is done once a day with a diet consisting of squid and mackerel with added vitamins (Masuma and Oka, 1996).

4. Tuna Research and Conservation Center, Monterey, California

The Tuna Research and Conservation Center (TRCC) opened in the fall of 1994 and is jointly operated by Stanford University's Hopkins Marine Station (HMS) and the Monterey Bay Aquarium (MBA). The TRCC maintains a research population of tunas and is vital link to the successful display of tunas at the MBA in the outer bay exhibit. The two facilities together (research and display) are currently among the largest facilities maintaining captive tunas in land-based tanks. Currently over 130 tunas (three species) are being maintained for both research and exhibit purposes. Early research on the techniques of maintaining tunas in captivity was conducted in the TRCC facility and it serves as the exploratory research center for investigating how to keep new species for display. The TRCC facility maintains yellowfin, *T. albacares,* skipjack, *K. pelamis,* and Pacific bluefin tuna, *T. orientalis,* as well as ectothermic scombrids such as bonito, *Sarda chiliensis,* and Pacific mackerel, *Scomber japonicus.* This provides a phylogenetically broad range of scombrid fish for comparative physiological study (Altringham and Block, 1997; Ellerby *et al.,* 2000; Marcinek *et al.,* 2001a). Populations are

maintained at both facilities (TRCC and MBA) with little mortality (<10%) for long durations (up to 7 years for yellowfin and 3 for Pacific bluefin tuna). Research is focused on the physiology and husbandry of scombrids and the development of electronic tagging technologies for wild pelagic species. Captive populations of tuna have been instrumental to the development of a successful electronic tagging program. Methodology for archival tag implantation surgery and pop-up satellite (PSAT) tag attachment to living tuna was perfected under laboratory conditions (Block *et al.,* 1998a,b). Testing of the tags in a controlled environment allowed observation of survivorship, tag placement, suture healing, and, for the PSAT tags, release and transmission function.

The facility contains four holding tanks, each with its own life support system. The volumes of the four holding tanks are one 327,000, two of 109,000, and one of 20,000 liters. The life support systems provide seawater at rates of 4536, 1512, and 378 liter/min. These flow rates are equivalent to a turnover rate (the time required for one holding tank volume to pass through the water treatment system) of one tank volume of water every 75 min for the three larger tanks and one every 60 min for the smallest tank. Tunas' high oxygen demand and excretion rates coupled with a semiclosed recirculation system necessitates a high turnover rate of seawater. The system is semiclosed, with a minimum of 400 liter min^{-1} of new seawater added to make up for water losses associated with routine tank cleaning and nitrite dilution. Each system is independent of the others, but can be cross-connected in case of equipment failure. The system supplies seawater 100% saturated with oxygen to each tank at a set temperature, and at pH values between 7.7 and 8.0. Return water to the system does not fall below 85% oxygen saturation.

Biological and mechanical filtration is accomplished through the use of horizontal rapid sand filters. The filters were selected to meet specified surface area criteria (Spotte, 1970; Wheaton, 1993), that is, flow not exceeding 6 liter min^{-1} cm^{-2} of filter bed surface area. At this flow rate, mechanical removal of particulate matter is thought to be most efficient. The high oxygen demand of tuna was the first consideration in the engineering design for the life support systems and is met by passing all filtered return water through packed aeration towers (Hackney and Colt, 1982). Seawater returning from the biological filters is sprayed into the top of the aeration tower onto a bed of high-surface-area bio-rings. The flow of water is spread over the medium and a thin film of water is created as it passes down through the packed column. Diffusion of gasses at the water–air interface results in water saturated with atmospheric gases including oxygen. The return water to the holding tanks for tuna is brought back to 100% oxygen saturation levels in this manner. Make-up water is supplied to the TRCC from Monterey Bay Aquarium at a maximum flow rate of 454 liter min^{-1} and is added to the top of each aeration tower at flow rates proportional to tank volume and stocking density. This volume of water allows for dilution and flushing of residual waste products from the individual holding tanks.

Aeration towers perform multiple functions beyond bringing the returning water back to 100% oxygen saturation. Off-gassing of excess atmospheric nitrogen gas (N_2) can help prevent introduction of gas bubble disease to the captive fish populations (Anonymous, 1974a; Colt, 1986). Also, when modified with a countercurrent airflow source, towers can aid in stripping off excess carbon dioxide, which is essential in semiclosed recirculation systems (Colt and Bouck, 1984). The current engineering solution is to incorporate a means of off-gassing CO_2 from the water in the aeration tower by injecting air into the lower portion of the tower with a blower. The air flows up through the media countercurrent to the water flow and strips off dissolved carbon dioxide, returning the pH to normal values. Air blowers with outputs of 23.7 and 67.8 $m^3\ min^{-1}$ provide high-volume, low-pressure air to the 2- and 2.5-m diameter aeration towers. The airflow/water flow rate ratio through the aeration towers is 4.75 cubic meters of air per liter of water per minute per square meter of surface area—these flow rates have proved to be sufficient to maintain the desired pH levels of 7.7–8.0.

Foam fractionator towers remove dissolved organic compounds from the return seawater through the attraction that occurs between the electric charge on the surface of small air bubbles and the bivalent charges associated with most nitrogenous waste products. A mixture of water and air is induced through a venturi into the bottom of the fractionator tower. The air–water mixture contacts the incoming water as it passes from the top of the tower to the bottom drain. This countercurrent system allows maximum mixing and contact between the air bubble solution and the filtered incoming water. The resultant foam mixture of water and organic molecules is carried to the top of the tower where it is accumulated in an isolated section of the tower and subsequently washed into a waste discharge line. Approximately 20% of the return water is passed through this treatment process before being added to the aeration towers. This water treatment system physically removes organic compounds and consequently lowers the filtrate load on the biological filters. A schematic diagram of the TRCC life support system is shown in Figure 1.

Each of the three large holding tanks is fitted with a pliable vinyl curtain that extends around the inner circumference of the tank. The function of the curtain is to soften any potential collisions of the tuna with the tank wall. The curtain extends from just below the water surface to a distance of 10 in. (25 cm) from the tank bottom. This permits surface skimming of the water into the overflow boxes and cleaning the bottom along the tank edge. Each curtain is marked with vertical black lines running from top to bottom. The lines are spaced 25 cm apart and are 2.5 cm wide. The purpose of the striping is to give a visual reference to the tuna, marking the perimeter of the tank. An additional feature on each of the tanks at TRCC is a 0.5-cm square, knotless nylon netting jump screen designed to prevent fish from jumping out the tanks. The knotless netting is less abrasive than knotted netting, thus preventing skin and fin abrasions from jumping fish. The netting has significantly reduced mortalities associated with fish exiting the tank.

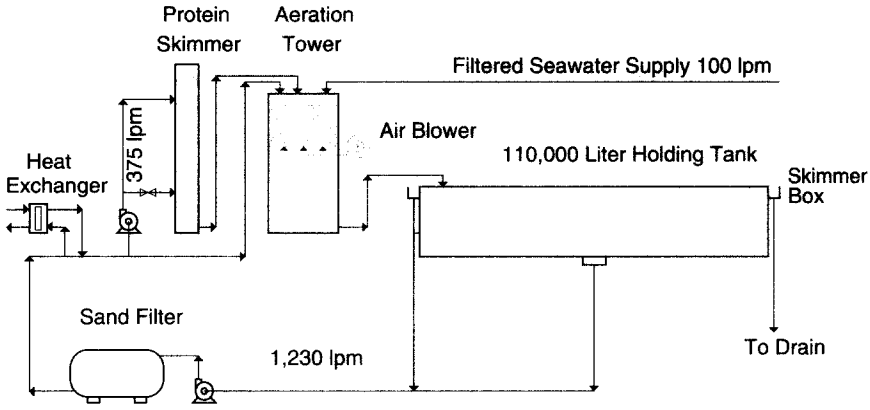


Fig. 1. Diagram of the operational facility designed specifically to keep captive tunas at the Tuna Research and Conservation Center in Pacific Grove, California.

Lighting of the tanks is accomplished with fluorescent lights fitted with high-frequency ballasts that eliminate the 60 Hz flicker associated with fluorescent lighting. The lights are controlled with timers that turn the lights on and off sequentially. This allows for subtle changes at dawn and dusk in light intensity, preventing startling the fish with a sudden change in light, which may cause wall collisions and injury or mortality to the specimens. A low-wattage night-light is fitted above each tank, allowing the tuna to navigate without colliding with the tank walls. A battery-powered night-light is placed over each tank and automatically turns on in the case of a power outage.

III. AQUARIUM DISPLAYS OF TUNAS AND RELATED SPECIES

One of the earliest attempts at maintaining a species of the family Scombridae in captivity occurred at Marineland of the Pacific where a display of eastern Pacific bonito was established in 1966. Courtship displays and related behaviors on these bonitos were reported by Magnuson and Prescott (1966). Currently seven aquariums in the world are displaying tuna, six in Japan and one in the United States. Most of these displays were designed specifically for keeping tuna on permanent display. Aquariums in Japan maintaining exhibits include Tokyo Sea Life Park, Nagoya Port Aquarium, Kaiyukan Aquarium in Osaka, Aburatsubo Marine Park, Kagoshima, and Aqua-Marine Fukushima.

Tokyo Sea Life Park Aquarium in Japan was the first aquarium to design and build a permanent display for tunas with a water volume of 2,200,000 liters. Collecting and research on captive care of tunas started in 1987 and included five

species: bluefin, yellowfin, little tuna (*Euthynnus affinis*), skipjack, and Oriental bonito (*Sarda orientalis;* Abe, 1993). The opening ceremonies were held in October 1989 and it has been a popular attraction. Nagoya Port Aquarium, opened in October 1992, includes a special exhibit featuring the Kuroshio Current. This is a 670,000-liter display of bluefin, yellowfin, little tunny, and skipjack. These two facilities maintain exhibits of scombrids only; the other facilities keep tunas in mixed-species community displays. Kaiyukan (July 1990) displays tunas in a 5,400,000-liter exhibit with a large collection of sharks, rays, and other fish from the surrounding seas of Japan. Kagoshima City Aquarium (May 1997) features a 1,500,000-liter exhibit of tunas along with other teleosts and elasmobranches.

In 1998 Aburatsubo Marine Park (1986) added Pacific bluefin tuna to their ring tank, which is also a community of mixed species. The newest aquarium to open is the Aqua-Marine Fukushima (July 2000), a public aquarium that features a 2,050,000-liter tank that is divided into two sections, the Kuroshio Current (warm water) and the Oyashio Current (cold water). The Kuroshio section displays yellowfin, bluefin, and skipjack tunas.

Monterey Bay Aquarium's Outer Bay Waters exhibit opened in March 1996. The exhibit's central focus is a 3,780,000-liter open ocean tank. The species of scombrids displayed currently include Pacific bluefin, yellowfin, two species of skipjack tuna, and bonito. Other species of fish, sunfish (*Mola mola*), barracuda (*Sphyraena argentea*), pilot fish (*Naucrates ductor*), soupfin shark (*Galeorhinus galeus*), and pelagic rays (*Dasyatis violacea*) make up the community population of this exhibit display. The life support system is designed to specifically meet the rigorous demands of keeping large numbers of tunas in captivity. High water turnover through biological filtration, ozone treatment of the water, and carbon dioxide off-gassing for pH control provide oceanic water quality.

IV. METHODS OF COLLECTION AND CARE

A. Collection

Specimens for the TRCC and MBA are collected using various methods. For yellowfin tuna, the commercial liftpole or jackpole is the method of choice if school fish can be chummed to the boat. Live bait, either anchovies or sardines, are chummed to attract the tuna to the stern of the boat. The jackpole, which is 3.0–3.5 m in length, is fitted with a 2.5- to 3.0-m length of heavy test monofilament line terminating in a barbless lure called a squid. The squid can be with or without feathers and is moved across the water to attract the fish. At the instant the tuna bites the squid, the fish is lifted out of the water and guided onto a smooth vinyl tarp that is suspended over one of the holding tanks. The barbless hook

comes out of the fish's mouth as soon as the tension on the line is reduced. Each fish is inspected for injuries before sliding the tuna off the tarp into one of the holding wells (5.3–7.5 m^3). For skipjack a similar technique is used with lighter-weight fishing gear.

Bluefin tuna are more challenging to collect and require the use of standard rod and reel sportfishing techniques using baited barbless hooks. Bluefin behavior differs from yellowfin in that they rarely will bite on the liftpole lure, which necessitates using standard rod and reel sportfishing tackle. The heaviest tackle that the tuna will bite on is used. Bluefin are caught on 20-kg line with 2/0 to 5/0 circle hooks. The hooked fish is brought to a swim step at the stern of the boat as rapidly as possible and is led by the fishing line into a seawater-filled vinyl sling (Figure 2). The sling with the fish is lifted up onto the deck of the boat and the tuna is guided into one of the holding wells. The use of the water-filled sling is a critical part of the collection. It is fabricated from a smooth-surface, pliable vinyl material, with the length, width, and depth matching the size of tuna being collected. The construction allows for water to be held in the sling; overflow holes adjust the water level to just cover the fish. Velcro straps and drawstrings at either end of the sling are used to pull the ends together, reducing the risk of the fish slipping out of the stretcher. The tuna tend to remain calm as long as there is water covering them inside the sling. Removal of the tuna from the sling is accomplished by pushing the head end of the sling down into the water and at the same time pulling the sling back and away from the fish (Figure 3).

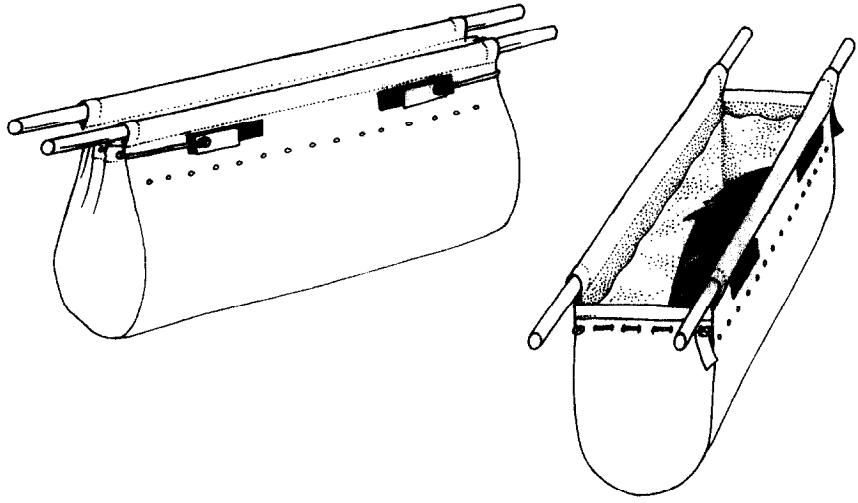


Fig. 2. The use of vinyl slings to transport tunas in an envelope of water has proven extremely successful.

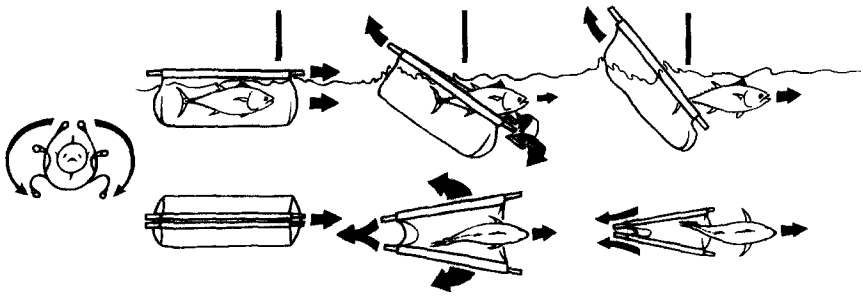


Fig. 3. Top sequence shows release of tuna into the wells during capture and collection. Bottom sequence shows release of tunas in a tank and the ease of movement of the fish without human interaction with the surface of the animal. The use of the sling prevents having to touch the tunas.

An increase in oxygen consumption occurs in newly caught specimens (Gooding *et al.*, 1981). This is compensated for by adding oxygen to the water pump discharge lines that supply seawater to the holding wells. The oxygen saturation levels are maintained at a range of 130–150% saturation for 1 to 2 h after collection and then reduced to 110% saturation. Oxygen levels are monitored continuously during the collection period and are controlled as necessary. The collected tunas for the TRCC are brought to land and are off-loaded from the boat using the vinyl slings. The water level in the wells is lowered, permitting individual capture of fish by a person in the well using the vinyl stretcher. Each tuna is then lifted out of the holding well and is either placed into a temporary holding tank located on shore or transferred directly into a specially designed transport tank for truck transfer to Monterey, California. The transport tank volume is 11,400 liters. The maximum internal dimensions are 3.7 × 2.3 m and 1.7 m deep; the inside corners and bottom edges are curved, creating a more suitable environment for the tunas. The tank is equipped with a recirculating water system, 400 liter m^{-1}, and includes a venturi injection system for adding oxygen. Internal spray bars add water to the top of baffle boxes that aid in aeration and removal of carbon dioxide, one of the most important aspects of transport. Temperature control is very important. The initial starting temperature of the transport water is adjusted to accommodate an elevation in temperature over time and to provide best water temperature for each species. For bluefin tuna, a low transport temperature of 15°C, has proven to be best. The lower temperature allows high levels of dissolved oxygen and also theoretically lowers the metabolic rate. Yellowfin tuna have been transported at higher temperatures, 17–18°C starting temperatures, to more closely match the collecting location temperature and also the temperature of their final holding tank at the TRCC. The fish density ranges from 5.0 to 10.0 kg m^{-3} and transportation time to Monterey is approximately 10 h. Once at the TRCC, the fish are individu-

ally removed from the transport tank, tagged with a passive induced transponder tag (PIT), and measured.

The use of PIT tags allows researchers to monitor and track individual fish within the collection. Fork length measurements are used to accurately estimate the total biomass of fish held in each tank (important for calculating feeding rations) based on established length and weight relationships. Subsequent measurements of these fish over time allow captive growth rate determinations to be made. These data are used to calculate a regression function for change in mass over time. The resulting regression formula can then used to determine the average growth of fish held in each tank and changes in biomass within each tank over time.

B. Captive Care of Tuna

The feeding regime of tunas is calculated according to the biomass of fishes. The dietary goal is to have each fish consume a specified amount of kilocalories per kilogram body weight per day (kcal kg^{-1} day^{-1}). When maintaining a fish population at a specified caloric allotment, proximate analysis of total calories and percent content for both fat and protein of food items is necessary as food items' caloric content changes with time and size (Table I). If the food items are not analyzed regularly, the caloric allotment given to the tank may be incorrect. From these data, the amount of food to be fed to the collection can be calculated, and the calories derived from fat can be monitored to achieve a diet low in fat. Food items used for captive tuna consist of squids (*Loligo opalescens* and *Illex* sp.), anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*), smelt (*Spirinchus starksi*), and a commercially available, high-vitamin-content gelatin mix. Feeding observations of bluefin tuna have shown that they have a preference for sardines and that initial feeding time of newly caught specimens can be shortened by offering a diet mostly of sardines. For all species, having older specimens in the tank that are eating helps start the feeding process.

The practice of reporting diet as a percentage of body weight can be mislead-

Table 1.
Proximate Analysis of Commonly Used Food Items for Tuna

	Squid		Sardines		Herring		Anchovy	
	Small (28 g)	Large (47 g)	Small (35 g)	Large (75 g)	Small (11 g)	Large (50 g)	Small (11 g)	Large (34 g)
Percent protein	16.6	16.5	19.0	17.2	14.4	16.5	16.2	16.3
Percent fat	0.6	0.6	2.1	15.3	4.2	9.6	0.9	12.9
Kcal/100 g	63	66	97	208	96	153	73	182

ing as the caloric content of the food items can vary significantly between species, size, and season. To avoid this problem, reporting diet as kcal kg^{-1} day^{-1} takes into account variations due to differences in caloric composition of the food and facilitates applying a consistent feeding regime to the collection. These data allow the recalculation of food rations to maintain a set diet of approximately 20 kcal kg^{-1} day^{-1} for the yellowfin tuna. The bluefin tuna are fed a diet of approximately 30 kcal kg^{-1} day^{-1}, based on the assumption that they have a higher metabolic rate. Tuna are susceptible to the stress of overcrowding and poor water quality. The effects of overcrowding may be expressed in various physiological signs and in external physical appearance. Comparison of hematocrit values and blood serum enzyme activity between wild caught and captive Pacific bluefin tuna has shown a measurable decrease within 5 weeks of captivity; increases in fat content in both the muscle and the liver were also noted (Murai *et al.*, 1982).

C. Handling Techniques

It is often necessary to handle individual fish within the collection, which can add stress to captivity. To reduce the chance of injury the following techniques have proven successful. The water level is lowered to 85–90 cm and a small group of people enter the tank and, with a vinyl barrier net (crowder), isolate a section of the tank. One end of the crowder is attached to the tank curtain and the crowder is stretched across the tank floor, creating a section that can be closed off by taking the free end of the crowder back to the tank wall. With the crowder in the open position an individual fish is identified and guided into the closable section; once the fish swims into this area the section is closed (Figure 4). The tuna can then be guided into a stretcher for the purpose of moving to a new tank, physiological monitoring such as blood sampling, or growth measurements.

D. Growth

Data on growth measurements of captive tunas reported in the scientific literature include larval culture work (Harada *et al.*, 1973b, 1980; Harada, 1973; Olson and Scholey, 1990), rearing of juvenile or young of the year tunas (Harada *et al.*, 1971; Suzuki *et al.*, 1972), and some reports of captive adults held for either brood stock or commercial interests (Masuma and Oka, 1996; Carter *et al.*, 1998). To minimize compromising the health of the fish due to overhandling while recording growth accurately in a captive population of fish, fork length measurements are recorded at the time of capture and death. If possible, additional fork length measurements are made when moving fish among tanks and during physiological research activities (e.g., blood sampling) occurring in the tanks. This is a relatively noninvasive technique for measuring growth as water can be kept in the sling,

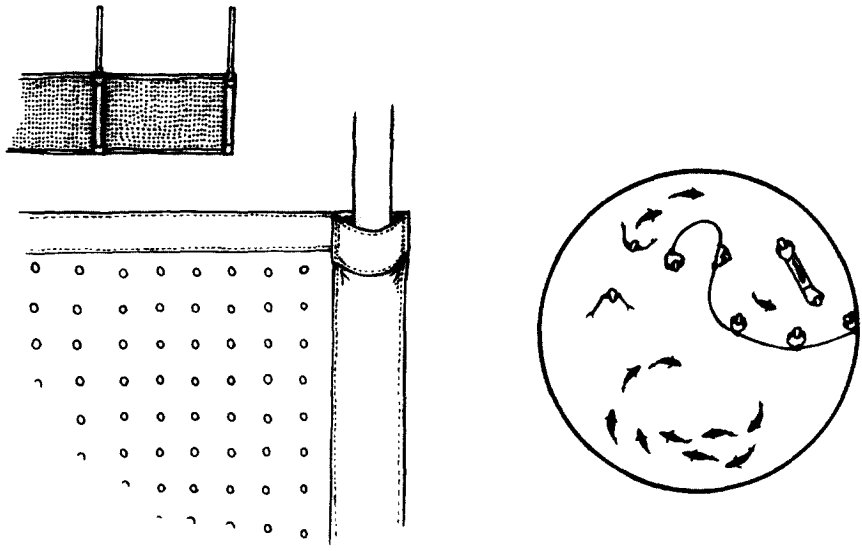


Fig. 4. To capture live tuna in the tanks, a crowder made of vinyl is used. The vinyl has numerous small holes that permit the crowder to be moved through the water without much resistance. The fish are cordoned off into one side of the tank prior to being captured with slings. The tunas are never handled manually in any aspect of capture.

which greatly reduces struggling. Captive bluefin and yellowfin tunas have both grown more slowly than their wild counterparts (Table II). Several factors may affect growth in captivity, which may explain the differences between the wild and captive populations of tuna. Wild tuna probably consume more food than captive fish on a restricted diet, which is a likely explanation of the reduced captive growth rates. Glencross *et al.* (2000) found that growth of farmed southern bluefin in sea pens in south Australia virtually ceased when the water temperature dropped below 15°C. Captive yellowfin tuna are held at 20°C at TRCC, which is at the lower end or below their thermal preference in the wild, 19 to 26°C (Carey and Olson, 1982; Block *et al.*, 1997; Holland *et al.*, 1990). Temperature effects probably play less of a role with captive bluefin as their growth rates are more similar to the wild growth rate than the captive and wild yellowfin growth rates. This is probably because the water temperature for the captive bluefin (18°C) is their preferred temperature in the wild (Marcinek *et al.*, 2001b). Thus, the growth of captive bluefin is probably more diet limited than temperature limited. Since our captive yellowfin are at the lower end of their thermal tolerance, they are probably both diet limited and temperature limited.

Table 2.
Growth Rate of Bluefin and Yellowfin Tuna

Bluefin tuna	Growth rate (mm day^{-1})	Yellowfin tuna	Growth rate (mm day^{-1})
Wild (Bayliff *et al.*, 1991)	0.71	Wild (Anonymous, 1974b)	1.20
Wild (Bayliff, 1993)	0.68	Wild (Hennemuth, 1961)	1.18
Wild (Koski, 1967)	0.58	Wild (Davidoff, 1963)	1.11
Wild (Yukinawa and Yabata, 1967)	0.55	Wild (Wild, 1986)	1.07
Wild (Foreman, 1996)	0.52	Wild (Anonymous, 1983)	0.75
TRCC Tank 1	0.63	MBA Outer Bay Waters Tank	0.51
TRCC Tank 2	0.49	TRCC Tank 1	0.37

V. RESEARCH OPPORTUNITIES WITH CAPTIVE TUNAS

Captive populations of tuna have been instrumental for physiological studies as outlined above. Perhaps less appreciated is that they are also important for the current rate of development and success of electronic tagging programs on tunas in the wild (see Gunn and Block, this volume). The captive populations have proven extremely important for validating hypotheses from wild tagging data such as the nature of the specific dynamic action or the warming of the tuna visceral region after feeding (Figure 5). Controlled experiments with ambient temperature or caloric intake values that are regulated can be accomplished in a tank environment. This allows for examination of tag data in relationship to known variables. Methodology for archival tag implantation surgery and pop-up satellite tag attachment to living tuna was perfected under laboratory conditions prior to moving to the wild (Block *et al.*, 1998a,b). Testing of the tags in a controlled environment allowed observation of survivorship, tag placement, suture healing, and, for the PSAT tags, release and transmission function. Observations of archival tags in yellowfin tuna in captivity have demonstrated that very small fish can handle the surgery quite well and show minimal effect. In some cases fish are feeding the next day after archival tag implantation (Block *et al.*, 1998b). The ability to recover the tags from captive animals has demonstrated that in all cases, internally placed tags are encased in a mesentery and are almost always invested with tissues and blood vessels upon recovery, indicative of no rejection when placed in the peritoneal cavity.

External PSAT tag observations led to selecting a tag shape and a place of attachment to the tuna that would minimize contact between the tag and the fish's body. Use of a controlled setting to examine dart head materials such as the performance of nylon versus titanium has led the TRCC team to select the latter as the optimal material for tagging. PSAT float development for both types of pop-up sat-

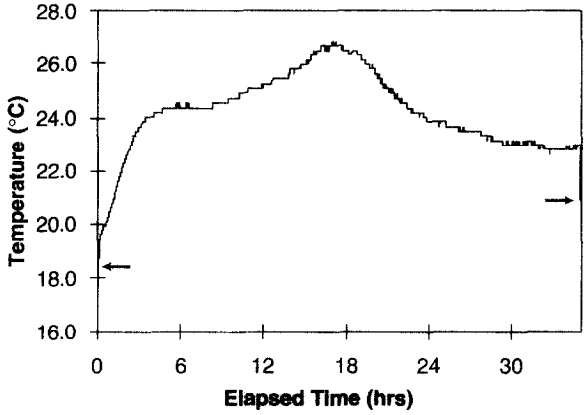


Fig. 5. The warming of the stomach due to the specific dynamic action associated with digestion in a captive Pacific bluefin tuna. This experiment documents the rise of body temperature (left arrow) after ingestion of 1200 cal from an all-squid feeding. Right arrow indicates the bluefin regurgitating the tag. The tank temperature remained constant at 20°C during this experiment. The electronic tag is fed to the bluefin by insertion into the mantle of the squid offered as food.

ellite tags (Microwave Telemetry, Inc., and Wildlife Computers) was performed by experimenting with the shape of the syntactic foam and examining the fish carrying the tags in holding tanks. This empirical effort led to a float design that would provide maximum buoyancy with minimal drag, further ensuring the success of field applications. Long-term monitoring of the test fish and post-tag placement for adverse effects on the tuna has led to a high return rate of the deployed tags.

The access to tunas reliably provided by penned wild fish also has benefited the tagging programs as PSAT tags attached to Pacific bluefin tuna in pens located in Baja California, Mexico, have provided further testing of the technology incorporated into these tags. These pens, 45 m in diameter and 15 m deep, presented a more challenging physical environment for the testing. Greater space and deeper water depths in the pens allowed for more active swimming behavior, further testing tag attachment techniques and placement. Sea surface conditions at time of tag release tested the transmission and flotation of the tags under natural conditions. The characteristic dawn and dusk diving behavior associated with wild bluefin tunas wearing archival tags was observed in the tagged pen fish, indicative of the isolume and not prey as the key motivation behind this behavior.

To further examine the use of the electronic tag technology on small Pacific bluefin tuna prior to large-scale releases in the wild, a controlled set of releases of captive bluefin from the TRCC facility have proven extremely useful for discerning the efficacy of external tags on small bluefin. This provides a way to test software as well as hardware on PSAT tags throughout the year. In November 1999 two small Pacific bluefin tuna were released from the TRCC into Monterey

Bay 0.4 km in front of Monterey Bay Aquarium (Figures 6 and 7). One fish's tag successfully popped up in this experiment and provided a test of new software prior to a large-scale use of PSAT tags on wild bluefin tuna in the Atlantic. In 2000, several Pacific bluefin and yellowfin that had been in captivity from 1 to 3 years were released. Each bluefin was tagged with a PSAT tag programmed to pop up in 5 to 60 days. The tags provided an opportunity to test a new leader and dart system for small fish. These tunas were initially put into a tow-pen used for transporting tunas to a commercial tuna farm. The release site was 10 km out of Monterey Bay. The fish were released as a school, inclusive of individuals without tags

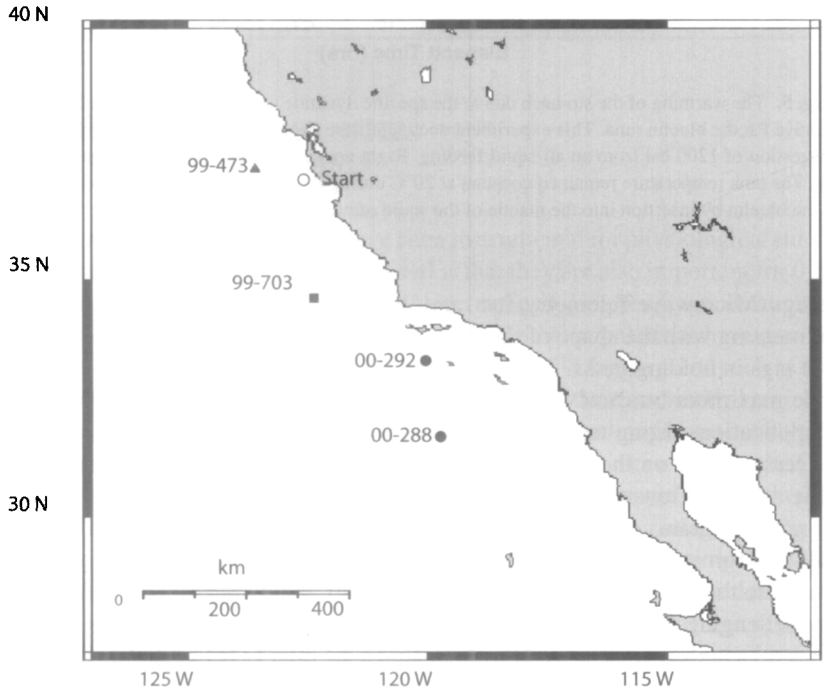


Fig. 6. Release of a captive bluefin tuna with electronic tags allows testing of specific hardware, software, tag applicator tips, and/or placement. In this experiment small Pacific bluefin tuna and a single yellowfin tuna were released from the TRCC into Monterey Bay. Tag 99-473 (solid triangle) was a 103-cm Pacific bluefin tuna that was tagged in November 1999 and carried a pop-up satellite archival tag for a 5-day duration. All other fish (solid circles and solid square) were released from a tow-pen simultaneously from Monterey Bay after over a year or more in captivity. These latter fish were released on September 28, 2000, and included tag 00-292 (solid circle), a 121-cm Pacific bluefin tuna tagged for 45 days, and 00-288 (solid circle), a 117-cm Pacific bluefin tuna that carried a PSAT tag for 60 days. Also released with a pop-up duration of 7 days was a 132-cm yellowfin (99-703, solid square). The success of captive release experiments back into the wild helped to initiate studies on wild populations of Pacific bluefin tuna.

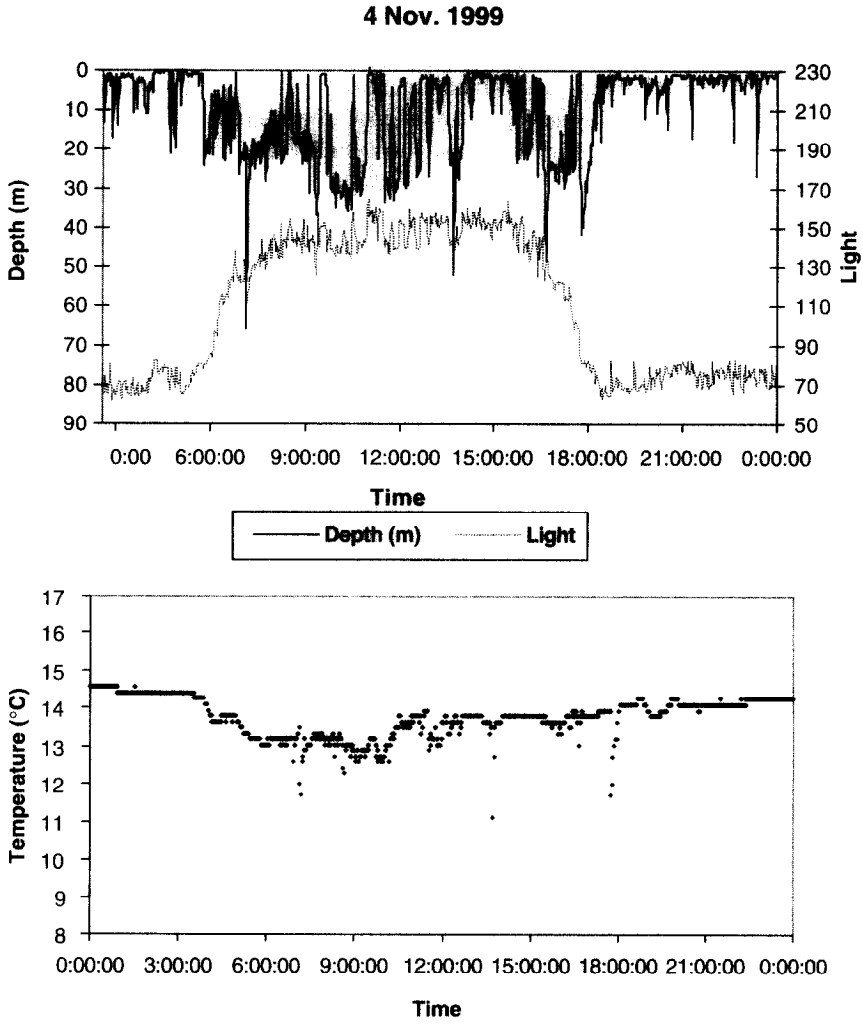


Fig. 7. Top graph shows depth movements 2 days after release of Pacific bluefin 99-473 in relationship to light. One day of the record is shown. Bottom graph shows water temperatures for the same period. Fish were maintained at 18–20°C for a year prior to release. To date small Pacific bluefin released from captivity have successfully carried the tags up to 4 months.

to increase their odds for survival in the wild. All tagged fish survived and their pop-up tags released 0.3–2 months after release. The captive yellowfin tuna PSAT tag released on day 7 reported a position 224 km to the south of Monterey Bay. All of the bluefin moved due south along the continental shelf of coastal California (Figure 6).

VI. FUTURE EFFORTS

The current level of success at maintaining captive tunas for research and exhibit has built upon the physiological knowledge of early researchers. Scombrids present challenges unique and appropriate to their level of biological sophistication. The future will undoubtedly see an expansion in these efforts that reflects the biological importance of what is perhaps the most highly evolved fish in the sea. Numerous physiological, growth, and development projects will emerge from the numerous facilities now keeping more diverse species spanning a larger range of the tunas natural history. Several species have not been kept long term in any facility (e.g., albacore and blackfin) and future efforts most likely will be focused on the challenges of keeping these species in captivity. The new intensive efforts to farm or ranch wild tunas will undoubtedly offer new opportunities for research. New techniques for handling tunas in land-based tanks and penning facilities will increasingly require novel techniques for transport, handling, and sedation. This most likely will improve research opportunities for larger specimens. The combination of physiologists and aquarists working together offers unique solutions for establishing the science and technology for maintaining, studying, and rearing captive species.

ACKNOWLEDGMENTS

Gratitude and thanks are due to many people who have given assistance with this chapter and with the maintenance of the TRCC facility. Without their support, guidance, and help this contribution would not have been possible. Barbara Block is responsible for including this chapter and without her continued contribution of support, guidance, and help with the writing, this effort would not have occurred. I thank Don Stevens for his helpful comments on a draft of the manuscript. Andrew Seitz and Tim Sippel, TRCC Research Technicians, contributed intellectually and in technical support. Roger Phillips and Eric Kingsley, Applied Research Department, MBA, have contributed through their efforts at providing water quality data necessary for the keeping of tunas in captivity and for Figure 1. Special thanks are due to the Block Laboratory and to Paul Sund, who has provided excellent daily care of the collection.

REFERENCES

Abe, Y. (1993). Rearing of four species: Bluefin tuna, *Thunnus thynnus,* yellowfin tuna, *Thunnus albacares,* skipjack tuna, *Katsuwonas pelamis,* and eastern little tuna, *Euthynnus affinis,* at Tokyo Sea Life Park. Proceedings, Third International Aquarium Congress, New England Aquarium, Boston, MA.

Altringham, J. D., and Block, B. A. (1997). Why do tunas maintain elevated muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200,** 2617–2627.

Anonymous (1974a). Proceedings Gas bubble disease. Gas Bubble Disease Workshop, Richland, WA, Technical Information Center, Energy Research and Development Administration.

Anonymous (1974b). "Annual Report of the Inter-American Tropical Tuna Commission." IATTC, La Jolla, CA.

Anonymous (1983). "Annual Report of the Inter-American Tropical Tuna Commission." IATTC, La Jolla, CA.

Anonymous (1994). "Annual Report of the Inter-American Tropical Tuna Commission," pp. 35–37. IATTC, La Jolla, CA.

Anonymous (1996). "Annual Report of the Inter-American Tropical Tuna Commission," pp. 29–33. IATTC, La Jolla, CA.

Anonymous (1997). "Annual Report of the Inter-American Tropical Tuna Commission," pp. 27–31. La Jolla, CA.

Aristotle (2350 B.P.). "History of Animals."

Bayliff, W. H. (1993). Growth and age composition of northern bluefin tuna, *Thunnus thynnus*, caught in the eastern Pacific Ocean, as estimated from length-frequency data, with comments on trans-Pacific migrations. *IATTC Bull.* **20**(9), 501–540.

Bayliff, W. H., Ishizuka, Y., and Deriso, R. B. (1991). Growth, movement, and attrition of northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean, as determined by tagging. *Bull. IATTC* **20**(1), 3–70.

Block, B. A., Keen, J., Brill, R. W., Castillo, B., Dewar, H., Freund, E., Marcinek, D., and Farwell, C. (1997). The thermal niche of yellowfin tuna, *Thunnus albacares*, in the northern part of their range. *Mar. Biol.* **130,** 119–132.

Block, B. A., Dewar, H., Farwell, C., and Prince, E. D. (1998a). A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proc. Natl. Acad. Sci. USA* **95,** 9384–9389.

Block, B. A., Dewar, H., Williams, T., Prince, E. D., Farwell, C., and Fudge, D. (1998b). Archival tagging of Atlantic bluefin tuna (*Thunnus thynnus thynnus*). *Mar. Tech. Soc. J.* **32**(1), 37–46.

Brill, R. W. (1999). The Kewalo Research Laboratory—Leading the way for more than 40 years. NOAA Tech. Memo., NMFS, Southwest Fisheries Science Center, Honolulu, HI. U.S. Dept. Commerce.

Buchanan, L. (1977). Ranching Atlantic bluefin. *Sea Frontiers* **23**(3), 172–180.

Butler, M. J. A. (1982). Plight of the bluefin tuna. *Natl. Geogr.* **162,** 220–239.

Carey, F. G., and Olson, R. J. (1982). Sonic tracking experiments with tunas. *Int. Comm. Cons. Atl. Tunas, Collect. Vol. Sci. Pap.* **17**(2), 458–468.

Carter, C. G., Seeto, G. S., Smart, S., and van Barnesveld, R. J. (1998). Correlates of growth in farmed juvenile bluefin tuna *Thunnus maccoyii* (Castelnau). *Aquaculture* **161,** 107–119.

Colt, J. (1986). Gas supersaturation—Impact on the design and operation of aquatic systems. *Aquacult. Engin.* **5,** 49–85.

Colt, J., and Bouck, G. (1984). Design of packed columns or degassing. *Aquacult. Engin.* **3**(3), 251–273.

Crockford, S. J. (1997). Archeological evidence of large northern bluefin tuna, *Thunnus thynnus*, in coastal waters of British Columbia and northern Washington. *Fish. Bull.* **95,** 11–24.

Davidoff, E. B. (1963). Size and year class composition of catch, age and growth of yellowfin tuna in the eastern tropical Pacific Ocean, 1951–1961. *IATTC Bull.* **8**(4), 381–416.

Ellerby, D. J., Altringham, J. D., Williams, T., and Block, B. A. (2000). Slow muscle function of Pacific Bonito during steady swimming. *J. Exper. Biol.* **203,** 2001–2013.

Foreman, T. (1996). Estimates of age and growth, and an assessment of ageing techniques, for bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean. *IATTC Bull.* **21**(2), 121.

Glencross, B. D., Barneveld, v. R. J., Carter, C. G., and Clarke, S. M. (1999). On the path to a manufactured feed for farmed southern bluefin tuna. *World Aquacult.* **30**(3), 42–46.

Glencross, B. D., Clark, S. M., Buchanon, J. G., Carter, C. G., and Barneveld, v. R. J. (2000). Growth dynamics of farmed, juvenile southern bluefin tuna during a production season. Pers. Comm.

Gooding, R. M., Neill, W. H., and Dizon, A. E. (1980). Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. *Fish. Bull.* **79**(1), 31–48.

Hackney, G. E., and Colt, J. E. (1982). The performance and design of packed column aeration systems for aquaculture. *Aquacult. Engin.* **1,** 275–295.

Harada, T. (1973). Artificial breeding of tuna and raising larvae. *Agric. Kinki Univ.* **6,** 109–112. Memoir Fac.

Harada, T., Kumai, H., Mizuno, K., Murato, O., Nakamura, M., Miyashita, S., and Hurutani, H. (1971). On rearing of young bluefin tuna. *Mem. Fac. Agric. Kinki Univ.* **4,** 153–157.

Harada, T., Kumai, H., and Nakamura, M. (1973a). On the rearing of bluefin tuna and bonito in wire netting cages. *Mem. Fac. Agric. Kinki Univ.* **6,** 117–122.

Harada, T., Murata, O., and Miyashita, S. (1973b). On the artificial fertilization and rearing of larvae in Hisada, *Auxis thazard. J. Agric. Dept. Kinki Univ.* **6,** 110–114.

Harada, T., Murata, O., and Oda, S. (1980). Rearing of and morphological changes in larvae and juveniles of yellowfin tuna. *Mem. Fac. Agric. Kinki Univ.* **13**(3), 33–36.

Hennemuth, R. C. (1961). Size and year class composition of catch, age and growth of yellowfin tuna in the eastern tropical Pacific Ocean. *IATTC Bull.* **5**(1), 1–112.

Holland, K. N., Brill, R. W., and Chang, R. K. C. (1990). Horizontal and vertical movements of yellowfin and bigeye tunas associated with fish aggregating devices. *Fish Bull. U.S.* **88,** 493–507.

Komiya, H. (2000). "Skeletal *Thunnus* remains, Jomon period 6000–4000 years BP." Natural History Museum & Institute, Chiba. Pers. Comm.

Koski, R. T. (1967). Age and growth determinations of bluefin tuna in the North Pacific Ocean. Thesis Biology Dept. Calif. State College, Long Beach, CA.

Maggio, T. (2000). "Mattanza." Perseus, Cambridge, MA.

Magnuson, J. J., and Prescott, J. H. (1966). Courtship, locomotion, feeding, and miscellaneous behavior of the Pacific bonito (*Sarda chiliensis*). *Anim. Behav.* **14**(1), 54–67.

Marcinek, D. J., Bonaventura, J., Wittenburg, J. B., and Block, B. A. (2001a). Oxygen affinity and amino acid sequence of myoglobins from endothermic and exothermic fish. *Am. J. Physiol. Regulat Integrative Comp. Physiol.* **280,** R1123–R1133.

Marcinek, D. J., Blackwell, S., Dewar, H., Freund, E., Farwell, C., Seitz, A., and Block, B. A. (2001b). Muscle temperature and behavior of Pacific bluefin measured with ultrasonic and pop-up satellite transmitters. *Mar. Biol.* **138,** 869–885.

Masuma, S. (1992). Breeding of yellowfin at Yaeyama Station. *In* "Annual Report of Japan Sea-Farming Association 1992," pp. 53–56.

Masuma, S. (1993). Breeding of yellowfin at Yaeyama Station. *In* "Annual Report of Japan Sea-Farming Association Annual (1993)," pp. 53–56.

Masuma, S., and Oka, M. (1996). Rearing of bluefin and yellowfin tuna in subtropical areas. Proceedings of Fourth International Aquarium Congress Tokyo, Tokyo, Japan, Congress Central Office of IAC '96.

Murai, T., Akiyama, T., Hirasawa, Y., Oshino, T., and Nose, T. (1982). Blood constituent levels and body composition of wild and cultured bluefin tuna juveniles. *Bull. Natl. Res. Inst. Aquacult.* **3,** 51–59.

Olson, R. J., and Scholey, V. P. (1990). Captive tunas in a tropical marine research station: Growth of late-larval and early juvenile black skipjack. *Fish. Bull.* **88,** 821–828

Pliny (1950 B.P.). "Natural History."

Spotte, S. H. (1970). "Fish and Invertebrate Culture. Water Management in Closed Systems." Wiley-Interscience, New York.

Suwa, Y. (1989). "Bluefin Feeding, Growth." Taiyo Fishery Co. Pers. Comm.

Suzuki, K., Nishi, G., Shiobara, Y., Inoue, M., and Iwasaki, Y. (1972). Studies on culture and domestication of tuna, billfish and other large-sized oceanic fish—II. *J. Oceanogr. Dept. Tokai Univ.* **6**(2), 79–88.

Wheaton, F. W. (1993). "Aquacultural Engineering." Krieger, Malabar, FL.

Wild, A. (1986). Growth of yellowfin tuna, *Thunnus albacares,* in the eastern Pacific Ocean based on otolith increments. *IATTC Bull.* **18**(6), 63.

Yukinawa, M., and Yabata, Y. (1967). Age and growth of the bluefin tuna, *Thunnus thynnus* (Linnaeus), in the North Pacific Ocean. *Rep. Nankai Regional Fish. Res. Lab.* **25,** 1–18.

11

TUNA CONSERVATION

CARL SAFINA

I. Introduction
II. Synopsis of Current Management Regimes
  A. Atlantic Tuna Commission
  B. Southern Bluefin Commission
  C. Indian Ocean Tuna Commission
  D. Inter-American Tropical Tuna Commission
  E. Moving toward Management in the Central and Western Pacific Ocean
  F. Newly Emerging Global Standards
III. Major Tunas—Status and Trends
  A. Skipjack
  B. Yellowfin
  C. Albacore
  D. Bigeye Tuna
  E. Bluefins
IV. Bycatch in Tuna Fisheries
  A. Purse Seining Bycatch
  B. Longline Bycatch
V. Southern and Atlantic Bluefin Tunas—Case Histories
  A. Southern Bluefin
  B. Atlantic Bluefin
VI. Summary, Conclusion, and Emerging Trends

In general, "conservation" is the struggle for long-term sustainability. Two broad generalizations can be made about tuna conservation: (1) conservation needs tend to vary inversely with species fecundity, and need increase with average size and the money paid for individual fish, and (2) conservation needs are most serious in the Atlantic, followed by the Pacific and then Indian oceans, in direct relation to the history and intensity of industrial-scale exploitation in each ocean. The Atlantic foreshadows what might be expected in other oceans if the Atlantic's lessons go unheeded. Half the world's tuna are taken from the central and western Pacific, where no fully implemented international management regime yet exists for waters of the high seas.

Tuna : Volume 19
FISH PHYSIOLOGY

Copyright © 2001 by Academic Press
All rights of reproduction in any form reserved.

In terms of economic or political importance, the major tunas are the skipjack, yellowfin, bigeye, albacore, and northern and southern bluefins. Skipjack account for roughly half the annual world catch of these six tunas. Overexploitation of skipjack seems to have been reached in specific areas of the Atlantic. Exploitation of Pacific skipjack stocks appears low to moderate. Yellowfin landings appear close to the maximum sustainable yield (MSY) level in the Atlantic, where fishing effort and mortality may be in excess of levels associated with MSY. Pacific yellowfin exploitation rates are considered moderate. In the eastern Pacific, recent assessments suggest that increased effort directed at juvenile tunas is probably reducing economic yield and sustainability for bigeye and yellowfin. Indian Ocean yellowfin catches are increasing. Albacore are overfished in the North Atlantic, and South Atlantic albacore are considered fully exploited. Albacore exploitation in the central and western Pacific is relatively low and sustainable. Atlantic and Pacific bigeye tuna populations have declined rapidly.

Bluefin tunas are everywhere depleted, and their recovery has not been allowed anywhere. The case of the bluefin shows that when an animal is worth enormous money, politics will go to great lengths to disfigure science.

I. INTRODUCTION

Virtually anyone who sees a living tuna is moved by the beauty of a life so energized and yet so mysteriously cloaked by the sea. Tuna provoke an intensity of interest that few other creatures engender. They have inspired Aristotle's prose, Salvador Dali's painting, Pablo Neruda's poetry, contemporary literature, international diplomacy, some of the highest prices paid for any creature, bitter policy disputes, lawsuits, and fistfights. Not least, tuna have inspired science; their lives remain largely unknown, beckoning our fascination. Unfortunately, study of these superlative creatures for the sheer fascination of their exquisite beauty and extreme biology is increasingly overshadowed by concern about their continued existence in robust and viable populations. Can tunas bear the appetite of a world with 6 billion people?

Perhaps a few words about the term "conservation" are in order. Conservation can mean any of several things. Here I use it to refer to actions meant to prevent long-term decline, to restore depleted populations, or to manage human activities so as to achieve the sustainable use and continued robustness of natural populations. Conservation can take the form of a concept (ecosystem integrity), a policy (sustainable yield, say, or recovery), or an action (not setting a purse seine around small juvenile yellowfin tuna).

Two broad generalizations can be made about tuna conservation: In general, conservation need is inversely related to species fecundity, and need increases with average size and the money paid for individual fish. (This can also be viewed with regard to the relative fecundity of tropical vs. temperate tunas. Tropical tunas

breed two-thirds of the year and may breed as early as age 2. This is distinct from a southern bluefin that matures at age 12 and has a specifically restricted breeding season and location.) Also in general, conservation needs are most immediate in the Atlantic, followed by the Pacific and then Indian oceans, in direct relation to the duration and intensity of industrial-scale exploitation in each ocean.

A third generalization is that, as for many fishes, much uncertainty exists about population sizes, fishing mortality rates, natural mortality rates, and sustainable catch levels for tunas, and less is known of effective stock structure (i.e., not just genetic stock structure, which can be homogenized by low levels of gene flow, but behavior—actual movements, migration patterns, residence times, and average rates of mixing or behavioral separation of fish in populations). One reason for biological uncertainties is that research funding has generally been dismal—sometimes less than 1% of the value of the catch total (Anonymous, 1998b). Of money that is spent on scientific activity, stock assessments often take nearly all. A reasonable rule of thumb might be for agencies to spend on basic biology 1/10th of the money spent on stock assessments.

In the next decade, new technology using electronic tags (e.g., Block *et al.*, 1998a,b; Gunn and Block, this volume) will provide new views and expanded data frameworks for understanding the movements of fish and the distinctions between populations in the sea.

Information about population trends, sustainable yields, and fishing mortality is generally more developed in the Atlantic, followed by the Pacific and then Indian oceans—again in direct relation to the length of history of industrial-scale exploitation and therefore the extent and history of efforts to establish monitoring and management regimes in each ocean.

Therefore, information presented in this chapter will be most extensive for the Atlantic, where a longer time series of information is available. As the world human population has grown and industrialized, humans have become essentially one "stock" thanks to globalization of markets and the effects of modern transport on the flow of genes and diseases. Consequently, the Atlantic's tuna history is not only a foreshadowing of what could happen in other oceans but a harbinger of the political difficulties of bumping against biological limits in a world that refuses to contain its technological, numerical, or economic growth.

We hear much about the increasing need to "feed the hungry from the seas." It may seem ironic that the less important a fish is as food for large numbers of people, the more contentious its management. Tunas provide perhaps the best example of this irony—particularly the highest-priced bluefin and adult bigeye, whose depletion is almost entirely driven by the Japanese sashimi market. On the world markets the bluefins (and to some extent bigeye tuna) are "boutique species" commanding excessive prices among a few people with excessive appetites for luxury and status-enhancing displays of wealth. For all the difficulty with management politics, in no sense can these fisheries be considered as producers of Food for the Masses.

In the case of the bluefin, particularly, we see the effects on nature, politics, and science resulting from the tyranny greed imposes. In important local cases, such as the east coast of the United States, recreational or sport fisheries targeting juvenile bluefin (for charter boat sportfishing businesses or for private recreation and home consumption) have evolved into politically organized alliances. Some recreational sectors now exhibit a degree of shortsighted self-interest paralleling the worst of the commercial fisheries, and with the same results: all user groups exert political force to prevent tighter regulation of themselves, resulting in management's failure to follow the best scientific information available (or even the law), depleted populations prevented from recovering (from becoming more biologically and economically productive), and scientific assessment processes at times corrupted.

Ironically, catches from populations rebuilt to levels capable of supporting maximum sustainable yield would in many cases be higher than current catches, and are always higher than replacement yields from merely stabilized but depleted populations.

So why is management of tunas worse for those species meaning less as food? For other species—sharks, say—it is because they are deemed not worth enough money to bother with. For bluefin and bigeye perhaps the same is true in a perverse way: no one will starve if bluefin and bigeye go commercially extinct, and no major economies will be seriously hurt. Those people benefiting from large profits invest enough of their money into political influence to affect management decisions. Not enough people care enough for recovery. There exists also an extreme resistance by many fisheries management agencies—often led by Japan—to actively acknowledging the concerns of conservation organizations. Japan's resistance to conservation extends even to those few governments, like Australia and New Zealand, who seek a more conservative approach to already-depleted resources in need of rebuilding (United Nations, 2001a). In the United States, conservation groups are now accorded more room "at the table" than they were a few years ago, but agencies usually yield more to user groups and demands of the fishing sector.

Various tunas and tuna-like fishes (e.g., mackerels and wahoo) are caught in world fisheries. In this chapter I will be focusing on the six most heavily exploited larger tunas—northern and southern bluefin (*Thunnus thynnus, Thunnus maccoyii*), bigeye (*Thunnus obesus*), yellowfin (*Thunnus albacares*), albacore (*Thunnus alalunga*), and skipjack (*Katsuwonus pelamis*)—rather than smaller, less widely distributed, and less heavily targeted species such as frigate tuna (*Auxis thazard*), bullet tuna (*Auxis rochei*), blackfin tuna (*Thunnus atlanticus*), or several others.

Also outside the scope of this chapter is aquaculture. Breeding tunas for commercial purposes, or growing wild-caught juveniles to more valuable market size ("ranching"), has in recent years been attempted or is practiced in several parts of the world, including Japan, Australia, Mexico, the United States, and the Mediter-

ranean. While these fish contribute to the market, their availability has not seemed to alter the intensity of fishing for wild fish. Hence aquaculture has not really matured in the mix of issues affecting conservation of wild tuna populations and species, and will not be further explored here.

This chapter will briefly synopsize international management structures, synopsize the status of the species, briefly discuss bycatch, delve a bit deeper into case histories of the bluefins, summarize, and then consider the future.

II. SYNOPSIS OF CURRENT MANAGEMENT REGIMES

The major international management regimes for tunas are the International Commission for the Conservation of Atlantic Tunas (ICCAT), whose purview covers the North and South Atlantic; the Inter-American Tropical Tuna Commission (IATTC), covering primarily the eastern tropical Pacific; the Commission for the Conservation of Southern Bluefin Tuna (CCSBT); and the Indian Ocean Tuna Commission (IOTC). These commissions are created by international treaties that set the parameters for their functioning. Other international bodies such as the Secretariat for the Pacific Community (formerly South Pacific Commission) and Forum Fisheries Agency coordinate information exchange and access agreements in national waters of many Pacific Island nations but have no management mandate. Beside international regimes, many countries have national laws governing tuna fishing (at least on paper) in their Exclusive Economic Zones (EEZs), usually within 200 miles of their shores. Some national entities cover immense geographic areas; for example, the Western Pacific Regional Fisheries Management Council has jurisdiction of the U.S.-exclusive economic zone surrounding the main Hawaiian Islands, most of the northwest Hawaiian chain, and waters surrounding all U.S. possessions in the central and western Pacific. However, no international management convention currently exists for the high seas region of the western and central Pacific, though an agreement is in development.

A. Atlantic Tuna Commission

The International Commission for the Conservation of Atlantic Tunas (ICCAT) was created by treaty in 1966 and commissioned in 1969. Its founding was prompted by rapidly expanding tuna fisheries in the eastern Atlantic and increasing competition between purse seiners and longliners there, as well as by concern about possible depletion of west Atlantic bluefin tuna. ICCAT assumed scientific and management authority throughout the Atlantic and Mediterranean for "tunas and tuna-like species." In practice this has included both tunas and such taxonomically more distant species as marlins (Istiophoridae) and swordfish (*Xiphias gladius*)—in effect Atlantic tunas and billfishes.

The commission is composed of roughly two dozen Atlantic-rim countries, plus Japan (which is a major fisher, importer, and consumer of Atlantic tunas) and China (on behalf of Taiwan). The commission's scientific committee, the Standing Committee on Research and Statistics, is composed of scientists from several countries and compiles catch statistics and models population trends. The commission's managers—also organized by national delegations—are responsible for setting fishing management policy, ostensibly based on scientific advice. The policies take the form of recommendations. Each country is then responsible for implementation, monitoring, and enforcement. The effectiveness of implementation and compliance thus varies.

The commission's charter obliges it to coordinate research and management so that Atlantic tunas and billfishes can be maintained at population levels that permit the maximum sustainable catch (i.e., B_{msy}, or the population or biomass that will allow production of maximum sustainable yield). But the majority of the fishes under ICCAT's purview are overfished and/or depleted, including several tunas, blue and white marlin, and swordfish. Berkeley (2001) provides a comprehensive review (see also bluefin case histories section later in this chapter).

B. Southern Bluefin Commission

The Commission for the Conservation of Southern Bluefin Tuna, or CCSBT, was formed by Australia, New Zealand, and Japan in 1994, after a decade of informal cooperation. This formalization was hastened into existence by increasing fishing pressure by other countries and increasing scrutiny of the southern bluefin situation by environmental groups, who began discussing listing southern bluefin under the Convention on International Trade in Endangered Species (CITES) as a possible means of addressing ineffective management of southern bluefin. CCSBT's sole purpose is to manage fishing for southern bluefin tuna. In the late 1990s serious disputes over sustainable catch levels occurred between Japan and New Zealand/Australia (see bluefin case histories section later in this chapter).

C. Indian Ocean Tuna Commission

The Indian Ocean catch of tunas increased in the 1990s from 18% of the world total to 24%. In the late 1980s the Indian Ocean catch exceeded the Atlantic catch by 20%; by the late 1990s it exceeded the Atlantic by 75%.

The Indian Ocean Tuna Commission (IOTC) grew out of a United Nations (UN)-supported Indo-Pacific Tuna Development and Management Programme, founded in 1982 (though it did not have a management mandate). IOTC, which has a management mandate, was established in the late 1990s.

IOTC covers 16 species of "tuna-like" fishes (primarily tunas and billfishes). Catches of these species have exceeded a million tons of reported catches (vessels

flagged for convenience usually do not report) since the early 1990s, 85% of which is tunas.

The Indian Ocean is unique in that artisanal fisheries take as much as industrial fleets. Artisanal fisheries use gill nets, troll lines, and pole-and-line. The importance of artisanal fisheries has actually increased in recent years.

Longlining, which started in the Indian Ocean in 1952, had spread over the entire Indian Ocean by the mid-1970s. Longlines now take about a quarter of the Indian Ocean catch. Their portion of the catch has the highest value, because they take mostly large fish for Japan's high-priced sashimi market. Purse seining, which started in the early 1980s and now takes about 360,000 metric tons (mt), takes smaller fish mostly for canning (IOTC, 2001).

D. Inter-American Tropical Tuna Commission

The Inter-American Tropical Tuna Commission (IATTC) was created in 1950 under a convention between the United States and Costa Rica. Present members also include France, Japan, Nicaragua, Panama, Vanuatu, Mexico, and Venezuela. Its original mission was to carry out research into effects of fisheries and natural events on fish stocks in the eastern Pacific Ocean, and to make management recommendations. In the late 1970s IATTC became heavily involved in research on the incidental mortality of dolphins in purse seine sets made on tunas associating with dolphins. Currently IATTC has a tuna–billfish program to study dynamics of these fishes and estimate the effects of fishing, and to recommend actions that will keep populations high enough to allow maximum sustained catch. It also has a tuna–dolphin program to monitor dolphin abundance and fishing-related mortality, and to recommend practices minimizing fishing-related mortality to dolphins.

In 1995, representatives of 12 governments, including most IATTC members except Japan, signed the Panama Declaration. This declaration commits nations to a legally binding Agreement to Conserve Dolphins, contingent on U.S. law changing to reopen U.S. markets to tuna caught in purse seine sets made around dolphins in accordance with the agreement (Allen, 2001).

Some observers believe the Panama Declaration has created an important opportunity for conserving the region's fish populations, reducing the bycatch associated with its tuna fisheries, and building a transparent and participatory fisheries management regime. In addition to containing measures designed to protect the region's dolphin populations, the declaration includes a number of key mandates that build upon the conservation requirements of the UN Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks. The declaration: (1) calls for the adoption of management for tuna populations that will ensure levels capable of producing maximum sustainable yield, based upon the best available science and a precautionary methodology; (2) requires the establishment of measures that will avoid, reduce, and minimize the bycatch of sea life; (3) mandates the adoption

of cooperative measures to ensure compliance with the declaration's terms; and (4) requires transparency in the declaration's eventual implementation.

The only wrinkle is that dolphin populations are not recovering at the expected rate. Some speculate that the stress involved in chasing them to exhaustion to get a net around them causes miscarriages or separation and loss of small juvenile dolphins (Hall, 1998). Consequently, animal defense groups have sued to block efforts by the U.S. government to change the definition of "dolphin safe." The definition change would be necessary to implement the Panama Declaration and again allow import into the U.S. of tuna caught by setting nets around dolphins.

E. Moving toward Management in the Central and Western Pacific Ocean

The large pelagic fish populations of the Pacific Ocean are among the most economically important in the world. Roughly half the world's tuna comes from the western and central Pacific region, which encompasses some 10 million square miles of ocean. As the demand for these fish continues to escalate, concern for the future of these populations is growing. Most are subject to little or no active management, and reliable information as to their status is largely sketchy.

Currently there is no fully implemented international management regime for tuna or other large pelagic fisheries of the central and western Pacific. The Secretariat of the Pacific Community (SPC; formerly the South Pacific Commission), formed in 1947, is an international organization based in Nouméa, New Caledonia. Its mission is to provide technical assistance to the Pacific Islands to improve the economic and social welfare of the peoples of the South Pacific. Its 22 member countries are spread across 30 million square kilometers from 130°E to 130°W and 25°N to 30°S (commonly termed the central and western tropical Pacific). Over 98% of this area is ocean, much of which is within Exclusive Economic Zones of members. SPC's five main program areas are fisheries, health, community education, agriculture, and socioeconomic statistical services—though fisheries is the largest program, and the oceanic portion of that program (as opposed to coastal) is focused on tuna (Lewis, 2001).

The main role of the commission is statistical monitoring, biological research (e.g., yellowfin age and growth, reproduction, tagging, stock structure, bycatch), and stock assessment (Lewis, 2001). The SPC is not a management or conservation organization. Its geographic area, the western and central Pacific Ocean, has no fully implemented international management body to deal with tuna fisheries in the vast international waters of the high seas (Lewis, 1999). However, the region has very large tuna fisheries with a variety of different gears, local artisanal and larger international fleets, and recreational fisheries.

Fisheries in the western and central Pacific have expanded rapidly. Catches of roughly half a million tons in 1980 expanded throughout the 1980s as purse seine fisheries developed, and purse seine catches peaked in 1998 at just under 1.2 mil-

lion mt. Regional catches totaled nearly 1.8 million mt in 1998, when western and central Pacific catches represented 77% of the total Pacific Ocean tuna catch of 2.3 million mt, and 52% of the total 3.4 million mt world tuna catch (Hampton *et al.*, 1999).

By the end of the 1990s purse seines in the western and central Pacific caught an estimated 860,000 mt, the pole-and-line catch took 240,000 mt, and the long-line fishery caught 187,000 mt (Anonymous, 1998a). Domestic and artisanal fisheries took less than 10% of the catch. The catch was mostly skipjack (60–70% by volume) and yellowfin (20–30%), with much lesser amounts of albacore (2–6%) and bigeye (4–6%; Lewis, 1999).

From 1980 to the end of the 1990s, the purse seine fleet in the region went from just 14 Japanese vessels to almost 200 boats, mainly from Japan, the United States, Korea, Taiwan, and the Philippines (Anonymous, 1998a). Japan's catch shrank by more than half from 1980 to 1994 (Morishita, 2001) due to changing patterns of effort. New fishing forces such as China and Indonesia are emerging rapidly in the region. Further, the region is filled with diverse and often conflicting commercial fisheries, subsistence fisheries, recreational fisheries, and environmental conservation groups.

A complicated series of events has developed momentum in the region to formalize and strengthen cooperative agreements aimed toward conservation. A Multilateral High-Level Conference for the Management of Tunas was held in December 1994, the first of several meetings to develop a body for conservation and management of the tunas in the central and western Pacific region (Morishita, 2001). An Interim Scientific Committee for Tunas and Tuna-like Species in the North Pacific Ocean (ISC) was held in 1996 (Morishita, 2001). The ISC is conceived as the scientific groundwork for a possible future management body (Morishita, 2001). Activities include establishment of swordfish, bigeye tuna, and northern bluefin tuna working groups (Morishita, 2001). Eventually, management will require development of stock-specific reference points against which stock status can be measured. But current levels of funding for data collection, research, and stock assessment of tuna fisheries of the western and central Pacific are "insufficient . . . to allow fisheries to be guided by good science" and total less than 1% of the value of the catch (about $1.7 billion annually; Anonymous, 1998b).

Countries of the western and central Pacific region, along with the United States, Korea, Japan, China, and Taiwan, met in June 1997 in the Marshall Islands to discuss the possibility of developing a management regime for the region's tunas and other highly migratory species based on the new UN treaty. The prime motivation to develop a management regime stems from increasing fishing pressure on yellowfin and bigeye tuna in the region as new vessels from China, Taiwan, and other nations have entered the fishery.

The parties agreed to a detailed negotiating schedule aimed at reaching final agreement in three years. The parties issued a declaration of intent (the Majuro

Declaration) that announced their commitment to undertake a number of crucial activities, including applying the precautionary approach to the management of large pelagics, collecting and sharing data in accordance with the UN Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks, and cooperating in monitoring, control, and surveillance of fishing activities.

The Majuro Declaration charted an ambitious agenda for conserving the pelagic fisheries of the western and central Pacific through the development of a new regional fisheries management organization. It represents a major breakthrough and opportunity to establish a precedent-setting regional agreement for the conservation of pacific pelagics.

In June 1998, a third session of the Multilateral High-Level Conference met and developed a revised draft for a convention on the conservation and management of highly migratory fish stocks in the western and central Pacific. Many laudable provisions were featured in "Article 5, Principles for Conservation and Management." This section states that contracting nations shall, among other things, "protect biodiversity in the marine environment," "apply the precautionary approach," "assess the impacts of fishing, other human activities, and environmental factors on target stocks and non-target species . . . and species associated with the target stocks," "take into account the interests of artisanal and subsistence fishers," and "adopt measures to ensure long-term sustainability." Though good language is just a starting point, these are reasons for optimism.

In September, 2000, the seventh session of the Multilateral High-Level Conference adopted a Convention on the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean. Importantly and unfortunately, Japan and Korea opposed, and China and two others abstained. The convention has now been signed by 13 states, including the U.S., and Taiwan ("Chinese Taipei"). This important convention, which covers all highly migratory stocks in a vast ocean area where tunas are the primary commercial resource, is the first to follow the format of the United Nations Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks.

The implementation of this agreement in the next few years will govern the management of half the world's tuna, and roughly 10 million square miles of ocean. The agreement will also establish an important precedent for the management of other pelagic species in other parts of the Pacific and the world. The fisheries of the western and central Pacific rest at a precarious moment in history. In the coming decade we will either repeat the mistakes of the Atlantic or fashion a regime that ensures the long-term sustainability of these important fishing activities and the health of their associated ecosystems.

F. Newly Emerging Global Standards

The UN Convention on the Law of the Sea gives coastal states jurisdiction over all resources, including living resources, in an Exclusive Economic Zone that

can extend up to 200 nautical miles from their coasts. Under the Law of the Sea, the UN in 1995 concluded the Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea Relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks. The UN states, "preservation and management of rapidly dwindling fisheries resources are the underlying objectives of the Agreement" (United Nations, 2001b).

Often referred to as the Agreement on the Conservation and Management of Straddling and Highly Migratory Fish Stocks, this new global treaty is intended to guide management of fishing for large pelagic species and other types of fish that occur in international waters. This agreement will not enter into force until the requisite number of nations officially ratify it (30 are required; at this writing 27 have ratified, and updates can be seen at www.un.org/depts/los/los164st.htm).

The agreement sets out acceptable standards and mechanisms for cooperation, monitoring, control, and surveillance. The new UN treaty requires countries to cooperate to manage these fish through methods aimed at preventing overfishing, minimizing waste and bycatch, and conserving nontarget fish, marine birds, and other marine wildlife. These conservation requirements apply both within and outside of zones of national jurisdiction.

Importantly, the agreement embodies the precautionary approach (acting conservatively in the face of uncertainty to fulfill policy requirements and minimize risk of damaging resource viability). This approach is now contained in various international policy instruments. Support for the approach has grown, following recognition that many world fisheries are depleted and that more cautious management could have prevented this. The agreement also states that management must be based on the best available science.

The agreement attempts to achieve conservation objectives by establishing a framework for cooperation. This includes international minimum standards for conservation and management; and measures designed to ensure compliance and enforcement on the high seas. It also requires countries to cooperate or join regional fisheries management bodies. When the agreement is fully entered into force, there will no longer the freedom to fish the high seas without obligation to cooperate in management toward more sustainable fishing (Edwards, 2001).

III. MAJOR TUNAS—STATUS AND TRENDS

In terms of economic or political importance, the major tunas are the skipjack, yellowfin, bigeye, albacore, and northern and southern bluefins. Longlines and purse seines take most of the catch. Longlines take mostly larger adult yellowfin as well as larger bigeye and bluefin (Anonymous, 1998a). Purse seine technology and efficiency increased substantially during the 1980s and 1990s, with innovations and advances such as bird-locating radar; omni-scan sonar; Doppler current

meters; satellite-derived sea surface temperature information; radio buoys; net depth recorders; deeper nets and more powerful winches, power blocks, and associated deck machinery; increased ability to store very large catches (up to 300 tons per set); and increased reliance on fish aggregating devices (FADs).

What purse seiners set the net around is the major determinant of fish size. Setting around free-swimming schools, or dolphins, takes larger fish. Sets around FADs, logs, or other floating objects catch considerable numbers of smaller fish, notably younger yellowfin and bigeye (Itano, 1998; Miyabe and Takeuchi, 1998), as well as high bycatch of many species. Most of the modifications to purse seine technology in the western Pacific during the late 1980s and 1990s were designed to increase ability to capture free schools feeding at the surface and unassociated with objects or mammals, and to be able to quickly load and refrigerate large catches (Itano, 1998).

In Garcia's 1994 review of 20 stocks of bluefin, yellowfin, albacore, bigeye, and skipjack, 14 were then overfished or depleted. Stocks believed not fully exploited at that time were Atlantic albacore, western and central Pacific yellowfin, and skipjack worldwide. This situation is somewhat changed. Fishing pressure for Atlantic skipjack appears now to be at or above maximum sustainable levels. Albacore are overfished and fully exploited in the North and South Atlantic, respectively. Increasing effort directed at juvenile Pacific yellowfins appears problematic.

A. Skipjack

The skipjack is the most tropical of the tunas targeted by major fisheries, has the highest metabolic requirements of all the tunas, and tends to remain shallower than other tunas (Brill, 1994; ICCAT, 1998). They spawn year-round over vast ocean areas in equatorial waters, and seasonally where the 24–26°C isotherm extends (Anonymous, 1998a). They grow at variable rates depending on area, maturing at about 42–45 cm in the Atlantic (ICCAT, 1998).

Worldwide, skipjack account for roughly half the annual catch of the major commercially exploited tunas (skipjack, yellowfin, albacore, bigeye, and southern and northern bluefin; IATTC, 1999a). Virtually all skipjack are taken by surface gears (ICCAT, 1998).

Important changes in Atlantic skipjack fisheries in the early 1990s included intensive use of artificial floating objects to concentrate fish, resulting in record high catches. Atlantic effort has declined in terms of vessel capacity but increased in terms of effective vessel effort, due to technology enhancements. No quantification of effective effort exerted on Atlantic skipjack is currently available, though it is known to have increased overall for the Atlantic (ICCAT, 1998).

In the Atlantic ICCAT has established eastern and western management units due to lack of trans-Atlantic tag returns. ICCAT has no quantified estimates of maximum sustainable yield, population size, or relative fishing mortality for At-

lantic skipjack tuna (ICCAT, 1998). No assessments of the west Atlantic stock have ever been performed, and stock status relative to quantified MSY-based reference points is unknown (Mace, 1997). Catch per unit of effort seems to have fluctuated without trend since the 1980s, suggesting that catches are sustainable in the west Atlantic (Mace, 1997).

In the East Atlantic, purse seines take the majority of skipjack, followed by baitboats. Most fishing is done by western European, north African, South American, and Caribbean nations. Vanuatu also fishes the Atlantic for skipjack (ICCAT, 1998).

ICCAT's 1998 scientific committee reports that

> there has been a declining catch in recent years, despite sustained fishing effort and increases in efficiency associated with fishing objects. Most of the catches have been made in a specific area, the equatorial area, where remarkable decreases have been noted in the sizes and average weights of the fish caught. These could be indications of a local over-exploitation of skipjack. (p. 25)

ICCAT (1998) concluded, "in spite of the characteristics of this species, a state of over-exploitation of skipjack seems to have been reached, at least in specific areas" of the Atlantic (mostly the tropical eastern Atlantic).

Skipjack have high fecundity, relatively rapid growth, and high natural mortality at younger ages. Such a life history pattern is a powerful buffer against high fishing mortality. That fishing power exerted on this species over such a vast area of the Atlantic could apparently be enough to cause "remarkable decreases" in fish size says much about the ability of modern fleets to muster ocean-transforming levels of pressure on various components of wild communities.

Skipjack constitute 66% of the western and central Pacific tuna catch (Hampton *et al.*, 1999). From 1980 to the early 1990s skipjack catches there doubled, and now total 1.8 million mt annually (purse seines take about two-thirds of this; Anonymous, 1998a). Skipjack catch per unit of effort (CPUE) fluctuated at around the same level from 1980 to the late 1990s, with an increase to an all-time high in 1995 (Anonymous, 1998a). Technological advances and retirement of less efficient vessels may have caused the increase in CPUE. Current catches are thought to constitute a low to moderate exploitation level for western and central Pacific skipjack. Skipjack are almost certainly not overfished in the eastern Pacific (IATTC, 1999a).

B. Yellowfin

Yellowfin tuna is a cosmopolitan species of tropical and subtropical seas. Juveniles form mixed schools with skipjack and juvenile bigeye tunas, and tend to

remain in surface waters (ICCAT, 1998). Yellowfin can often be found deeper in the water than skipjack.

There appear to be two Pacific stocks: eastern and west-central Pacific (Anonymous, 1998a). Exploited sizes run the range from small juveniles (30 cm) to adults (e.g., 170 cm; ICCAT, 1998). They are caught trolling, on handlines, longlines, and rod and reel, with purse seines, and by baitboats. Yellowfin compose roughly 35% of the world tuna catch (IATTC, 1999b).

In the Atlantic a single yellowfin stock is assumed due to rates of trans-Atlantic tag recoveries. The main spawning zone in the Atlantic is the equatorial Gulf of Guinea, and after spawning the fish are presumed to move west. Longline catches show them distributed throughout the tropical Atlantic (ICCAT, 1998).

While Atlantic yellowfin recruitment has fluctuated without trend since the 1980s, spawning biomass has generally declined (Figure 1). Fishing pressure on juveniles increased significantly in the early 1990s when increased Atlantic purse seining operations employing fish aggregating devices and targeting fish associated with floating objects resulted in increased catches of juvenile yellowfin, juvenile bigeye, and skipjack. Atlantic yellowfin catches peaked in 1990 at 184,000 mt, and then declined 30% by 1997 (ICCAT, 1998).

Eighty percent of east Atlantic yellowfin catches are purse-seined, while in the west Atlantic 40% is taken by purse seiners, 30% by longliners, and 15% by baitboats. Longline effort increasingly targeting deep bluefin and bigeye tuna has resulted in yellowfin being a smaller portion of the Atlantic longline catch (ICCAT, 1998).

Reported Atlantic yellowfin landings appear close to the MSY level, and fishing mortality may be in excess of levels associated with MSY (Figure 1). ICCAT's scientific committee said

> it is important to ensure that effective effort does not increase further. . . . Therefore the Committee reaffirms its previous recommendation that measures to reduce overall effort, or at least to freeze it at current levels, should be initiated immediately. . . . The Committee also continues to recommend that effective measures be found to reduce fishing mortality of small yellowfin. (ICCAT, 1998, pp. 18–19)

There are insufficient data to fully evaluate the effects of a voluntary moratorium, begun in 1997, on fishing on floating objects. ICCAT (1998) continues to recommend this and other measures to reduce effort on small fish.

In 1973, nearly 3 decades ago, the commission recommended a minimum size of 3.2 kg, with a 15% tolerance for smaller fish in the catches. But overall percentages of undersized yellowfins are currently running about 60% for all gears in the Atlantic, with baitboats catching 80% undersized fish. Most of these small fish are caught in the east Atlantic where they school with, and are caught with, skipjack (ICCAT, 1998).

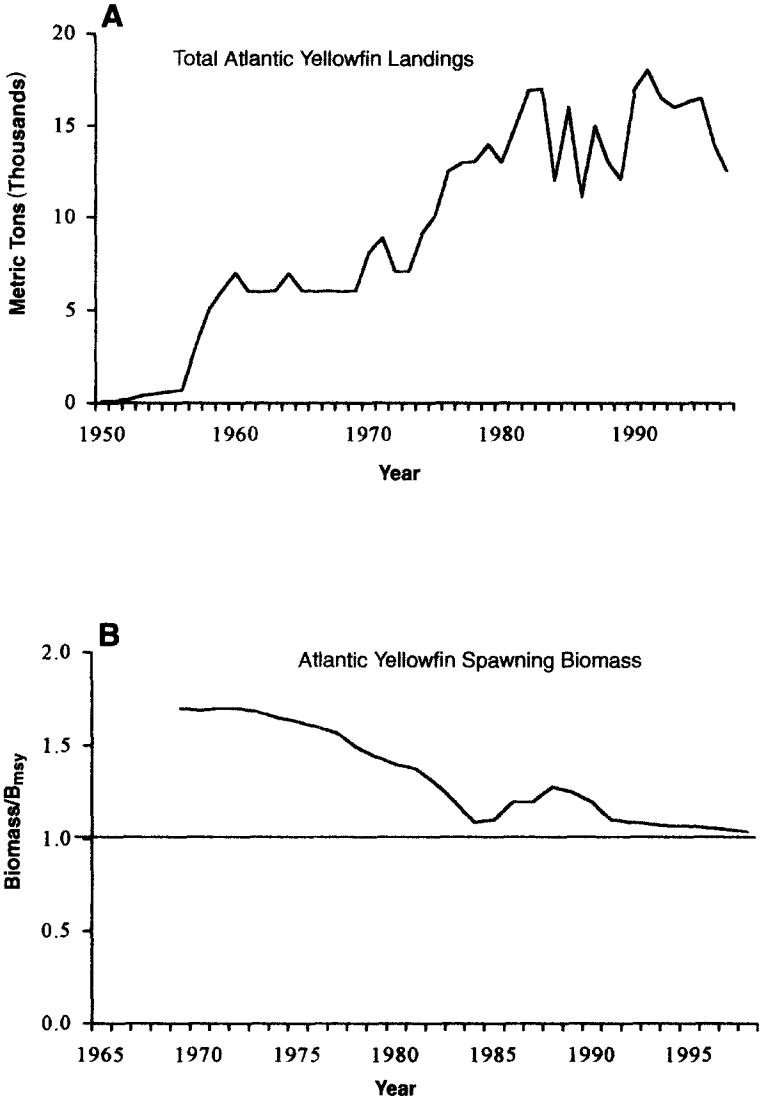


Fig. 1. Trends in Atlantic yellowfin tuna landings (A) and spawning biomass (B). Y axis in B is biomass relative to that required to support maximum sustainable yield. Data from ICCAT (1998).

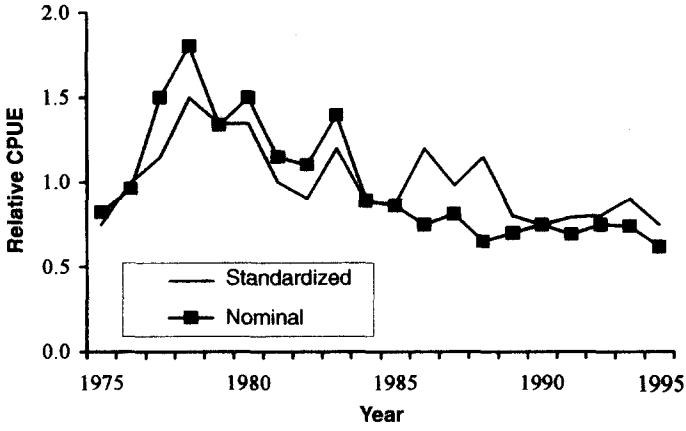


Fig. 2. Trend in catch per unit of effort for central Pacific yellowfin tuna. Y axis scale is relative to base year 1976. Data from Anonymous (1998a).

Exploitation rates for Pacific yellowfin are considered moderate (Anonymous, 1998a). In the eastern Pacific, yellowfin tuna are the most important species taken by purse seiners (IATTC, 1999b). Central Pacific yellowfin CPUE has fluctuated greatly since the early 1980s (Figure 2), with no clear trend for purse seiners (which catch mainly juveniles) or temperate-zone longliners (which catch mainly adults), but with a declining trend for longliners in the tropical zone (Anonymous, 1998a).

Patterns of increasing fishing development in the western Pacific and Indian Ocean are reflected in yellowfin catches (IATTC, 1999b). The approximate percentages of the world total yellowfin catch for different areas in the early 1970s versus the early 1990s are as follows: eastern Pacific ocean, 45% versus 27%; western Pacific, 25% versus 35%; Atlantic, 20% versus 12%; and Indian, 8% versus 26% (IATTC, 1999b).

In the eastern Pacific, yellowfin abundance underwent a sharp decline in the early 1960s and 1970s, but recovered strongly in the 1980s and has remained relatively high since. However, effort increased 27% in the last half of the 1990s, bringing effort to a level higher than necessary to take the maximum sustainable yield (overcapitalization), and possibly enough to cause a population decline (IATTC, 1999b). Further, increased effort directed at floating objects and fish not associated with dolphins is taking smaller fish, "probably causing the sustainable catch of yellowfin in the eastern Pacific Ocean to decline" (IATTC, 1999b). IATTC now limits the catch of yellowfin tuna taken in the eastern Pacific Ocean purse seine fishery to roughly 225,000 mt.

C. Albacore

The albacore is a widely distributed, mostly subtropical to temperate tuna. Albacore tend to spawn in subtropical waters, though they do spawn in tropical waters in some places. Albacore mature at about 5 years of age and 90 cm (fork length) in the Atlantic, and somewhat smaller in the Mediterranean (ICCAT, 1998). Albacore are rather temperate in their distribution, and are considered to constitute separate north and south stocks in both the Pacific and the Atlantic. ICCAT also recognizes a Mediterranean stock.

Various fishing methods targeting albacore include trolling, baitboats, drift nets, pelagic pair trawls, and longline. Other gears make minor catches. Juveniles tend to remain shallower than adults (ICCAT, 1998). Consequently, juveniles tend to be caught in surface gear, and adults tend to be caught more on longlines (ICCAT, 1998).

The total Atlantic catch has declined following declining total effort since the 1960s (due to longlines shifting to more lucrative and deeper bigeye tuna), though effort and catch in one component—the new surface fisheries—has increased markedly since the late 1980s (ICCAT, 1998). Spain, Ireland, Portugal, France, and the United Kingdom are among the more important fishing countries in the North Atlantic, while South Africa, Namibia, Brazil, Taiwan, Japan, and Portugal fish the South Atlantic. Boats from Italy and Greece, mainly, fish for albacore in the Mediterranean (ICCAT, 1998).

For the North Atlantic, abundance of adult fish (age 5+) declined during the late 1970s to mid-1980s, falling through the level needed to support MSY and remaining there. Spawning biomass is currently only about half the level needed to support MSY (Figure 3). Fishing mortality has generally been increasing recently and now appears to be between 25 and 40% higher than that which would generate MSY. ICCAT has highlighted the need to limit North Atlantic fishing effort at current levels (ICCAT, 1998).

For the South Atlantic, abundance of adult fish declined markedly from the mid-1970s to the mid-1990s. Recent estimates suggest spawning stock and fishing mortality variously above and below the level associated with MSY. These differences arise from revised catch data and trend changes in different indexes of abundance. Considering these differing results and uncertainties, South Atlantic albacore are considered roughly fully exploited relative to MSY (ICCAT, 1998).

In 1998 ICCAT implemented a South Atlantic albacore catch limit of 22,000 mt, and most albacore-fishing countries implemented corresponding regulations (this is designed to limit catches to 90% of the average annual catch between 1989 and 1993; ICCAT, 1998).

No ICCAT regulations exist for the Mediterranean (ICCAT, 1998). Mediterranean catches are considered minor and no assessment has been done due to insufficient information (Mace, 1997). In 1998 the European Union adopted a regulation phasing out drift nets entirely by 2002 (ICCAT, 1998).

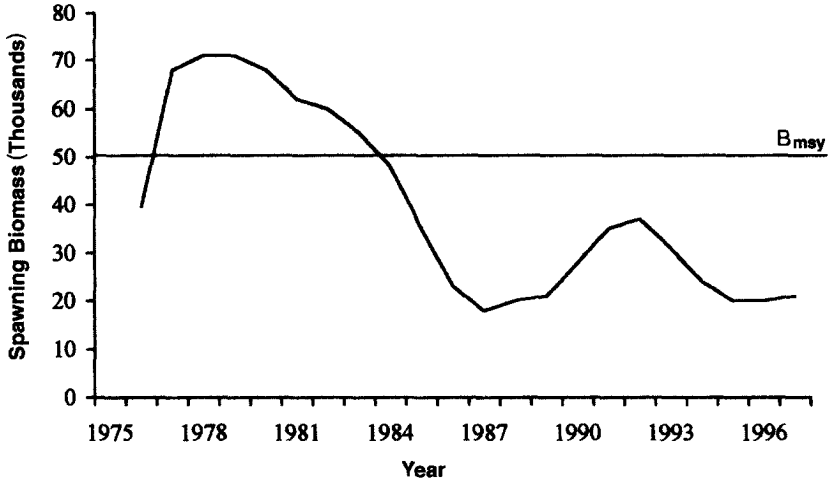


Fig. 3. Trend in spawning biomass (age 5+) for North Atlantic albacore. Horizontal line is spawning biomass required to support maximum sustainable yield. Data from ICCAT (1998).

Pacific Albacore CPUE is relatively low or declining in many areas compared with data from earlier years of the Pacific fishery, though recruitment seems relatively stable and estimates of adult biomass seem strong (Anonymous, 1998a). Though albacore are relatively slow growing and long lived compared to tropical tunas, it is believed that the current exploitation rate in the central and western Pacific is relatively low (probably less than 10%/year.) and sustainable (Anonymous, 1998a).

D. Bigeye Tuna

Bigeye tolerate the lowest dissolved oxygen and water temperatures among the major species in commerce (skipjack, yellowfin, albacore, and bigeye; Brill, 1994). Bigeye make extensive vertical movements and often feed deeper than other tunas (ICCAT, 1998). The bigeye tuna is a generally understudied tuna despite its increasing value and intensifying importance in tuna fisheries.

Bigeye mature at the beginning of their third year, at a fork length of about 100 cm (ICCAT, 1998). They spawn largely in tropical waters, and growth is relatively rapid (ICCAT, 1998). Their Pacific stock structure is poorly known (Anonymous, 1998a).

In the Atlantic, the Gulf of Guinea is a major nursery area. Young fish often mix in shallow schools with yellowfin and skipjack tunas, often in association with drifting objects or sea mounts. At larger sizes, bigeyes move into more temperate waters and their proclivity for associations with other tunas and objects diminishes (ICCAT, 1998).

ICCAT manages bigeye based on the assumption of a single Atlantic-wide stock but notes the possibility of separate North and South Atlantic populations (ICCAT, 1998). A recent genetic analysis of Pacific Ocean bigeye populations by the Pelagic Fisheries Research Program (PFRP) was unable to detect major subdivisions (PFRP, 1998). Some bigeye move considerable distances, for example, 5% of bigeye tagged by the South Pacific Commission in the early 1990s moved more than a thousand miles (PFRP, 1998). Yet bigeye also demonstrate considerable site fidelity—a considerable number of bigeye were captured at the release site after more than 5 years at liberty (PFRP, 1998).

Bigeyes are killed primarily by longlines, baitboats, and purse seines. Longlines catch bigger fish (45–50 kg), baitboats take small to medium fish (20–30 kg), and purse seines take small fish (5 kg; ICCAT, 1998).

In the Atlantic, most baitboats operate in the eastern North Atlantic, where they take significant amounts of medium to large bigeye tuna; baitboats in other oceans tend to take smaller fish. Japan and Taiwan operate enough longliners in the Atlantic to take half the bigeye catch. Purse seiners targeting primarily yellowfins take significant numbers of bigeye tuna, again mostly in the eastern Atlantic—primarily in the Gulf of Guinea nursery area—but also off Venezuela (ICCAT, 1998).

For Atlantic bigeye tuna, fishing mortality rates have increased "sharply" since the early 1990s for both juveniles and adults (ICCAT, 1998). ICCAT's calculations are that the Atlantic bigeye tuna spawning population has declined rapidly since about 1993. In the mid-1990s, the Atlantic bigeye catch reached a record of 115,000 mt, declining to about 90,000 mt in the late 1990s. Increased use of drifting logs, fish aggregation devices, and other floating objects, and technological advances in sonar, deeper nets, and bird radar (for spotting feeding flocks), all helped increase purse seine effectiveness and thus the catch of small fish through the mid-1990s. Despite a minimum size regulation of 3.2 kg adopted in 1980, fully 70% of the fish caught in 1996 were undersized. Apparent reduction of juvenile abundance led to a voluntarily observed seasonal and area closure on FAD fishing in 1997, which continues today. The voluntary regulation has been deemed "very effective in reducing fishing mortality for juvenile bigeye" (ICCAT, 1998).

ICCAT (1998) has calculated the maximum sustainable yield for Atlantic bigeye at around 70,000 to 90,000 mt, but estimates that since 1993 (except in 1997), the total catch of bigeye in the Atlantic has been near or over 100,000 mt, an increase of 30,000 mt since the late 1980s/early 1990s due to increased fishing effort by all three major gear types. According to ICCAT (1998, pp. 21–22; see Figure 4),

> The total [Atlantic] catch has been higher than the upper boundary of the likely range of MSY since 1993, suggesting that the stock has declined considerably. . . . The estimated current biomass is below B_{msy} [biomass required to support maximum sustainable yield] by 20–40%, and current

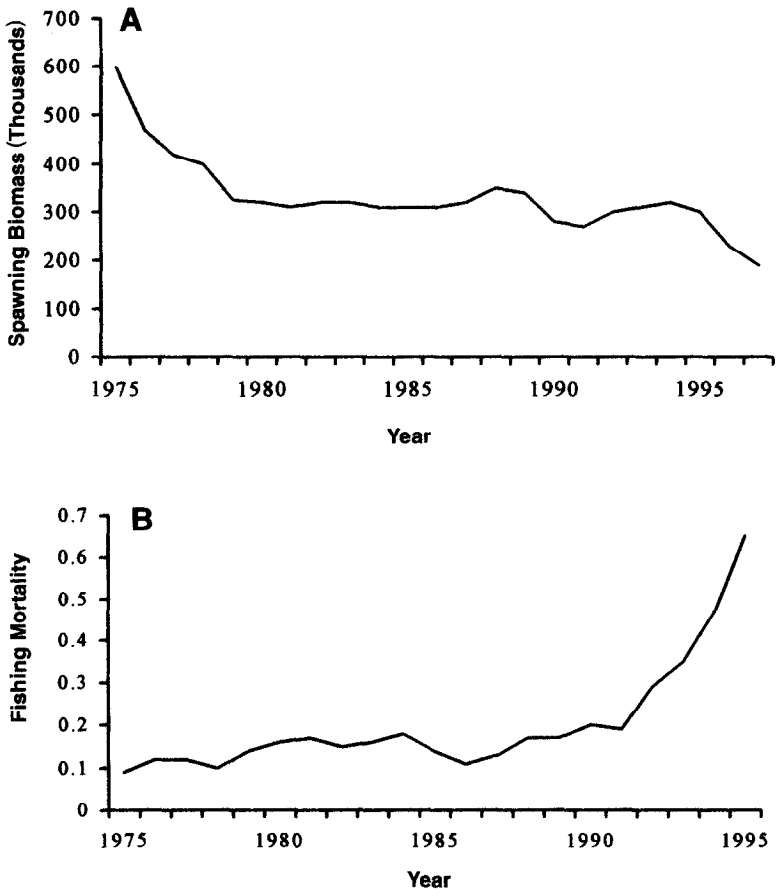


Fig. 4. (A) Atlantic bigeye tuna abundance estimates and (B) fishing mortality rates. Data from ICCAT (1998).

F [fishing mortality rate] estimates surpass F_{msy} [fishing mortality rate associated with MSY] by 50 to 120%. . . . The bigeye stock is already overexploited. In addition, current spawning stock biomass-per-recruit is lower than 20% of its maximum, which corresponds to a threshold at which recruitment overfishing may occur. . . . [Y]ields would be expected to decline in the near future to levels below MSY. . . . Although MSY levels are not well determined, the recent high catch surpasses estimates from all models considered. It is highly likely that this catch level cannot be sustained in the long term and may result in substantial declines in stock size [in the Atlantic].

Eastern Pacific bigeye longlining began in the 1950s (IATTC, 1999c), and until the 1990s Pacific bigeye were caught mainly by this gear (IATTC, 1999b). During the 1990s, sharply increased catches of bigeye resulted from increasing use of fish aggregating devices by purse seiners (IATTC, 1999c). Pacific bigeye have been subject to large and increasing surface catches of small and medium fish during the late 1990s (Anonymous, 1998b). Five to 10% of purse-seined Pacific "yellowfins" are misidentified bigeyes, and purse-seined bigeye catches have increased sharply along with the sharp increase in fleet capacity (Anonymous, 1998a). Purse seine catches of bigeye in the eastern tropical Pacific are estimated to have grown from 5000 mt in 1992 to over 50,000 mt in 1997 (PFRP, 1998). CPUE for bigeye in the eastern tropical Pacific has declined to low levels in recent years (PFRP, 1998). In 1999 IATTC passed a resolution to limit the catch of bigeye tuna taken in the eastern Pacific Ocean purse seine fishery to 40,000 mt. When this limit is reached, purse seine sets on floating objects are prohibited.

Declines similar to those noted in the eastern Pacific are not yet detectable in the western Pacific, but such declines are expected as the level of juvenile catches of bigeye by surface fisheries increases (PFRP, 1998).

Total bigeye catch in the eastern Pacific doubled between the early 1970s and late 1990s, and "the productivity of the stock has almost certainly changed due to the increased exploitation of younger fish" (IATTC, 1999c). Biomass of bigeye in the eastern Pacific generally declined during the 1990s (IATTC, 1999c).

Overall, Pacific bigeye numbers have declined significantly (Anonymous, 1998a; see Figures 5 and 6). Recent catches—about 150,000 mt per year Pacific-wide (IATTC, 1997)—are approximately at or above the maximum sustainable yield (Anonymous, 1998a). However, deficiencies in knowledge about bigeye stock structure hinder conclusions about stock status relative to overfishing reference points (Anonymous, 1998a).

E. Bluefins

Taxonomy recognizes three bluefin tuna species. The southern bluefin ranges from waters off New Zealand and Australia throughout the Indian Ocean and into the South Atlantic. The northern bluefin ranges primarily throughout the North Pacific and North Atlantic, mainly in temperate and subtropical waters. Atlantic and Pacific northern bluefin are genetically dissimilar enough to be considered separate species *Thunnus thynnus* and *Thunnus orientalis* (Collette, 1999).

Bluefins are by far the largest tunas, reaching 650 kg, and living upward of 20 years. They are characterized by late maturation, slow growth, cool-water life histories, and long generation times. Atlantic bluefin spawn from mid-April to June in the Gulf of Mexico and Florida Straits, and late May to July in the Mediterranean (ICCAT, 1998). Bluefin make some of the most extensive migrations of any fish; their physiological adaptations allow exploitation of environments ranging from subtropical spawning areas to subarctic feeding zones.

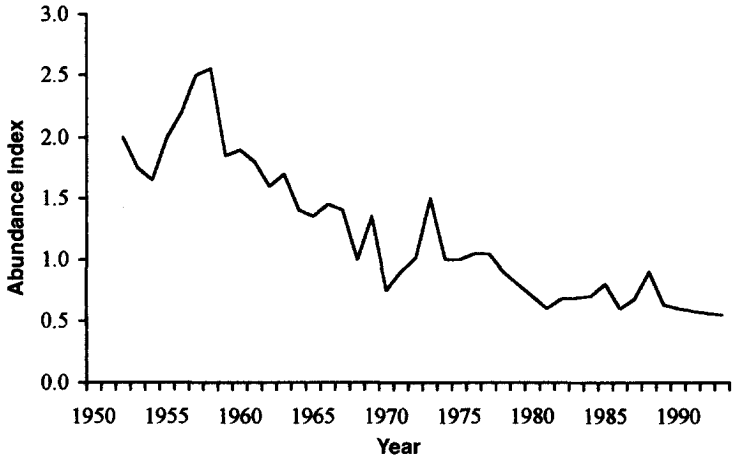


Fig. 5. Relative abundance index estimates for Pacific bigeye tuna. Data from Anonymous (1998a).

Southern bluefins and Pacific northern bluefins are taken mostly by longline. Atlantic northern bluefins are caught by longline, purse seine, handline, harpoon, rod and reel, and trap.

Pacific northern bluefin tuna are known to breed (based on larval distribution) only between the Philippines and southern Japan, and in the Sea of Japan. From

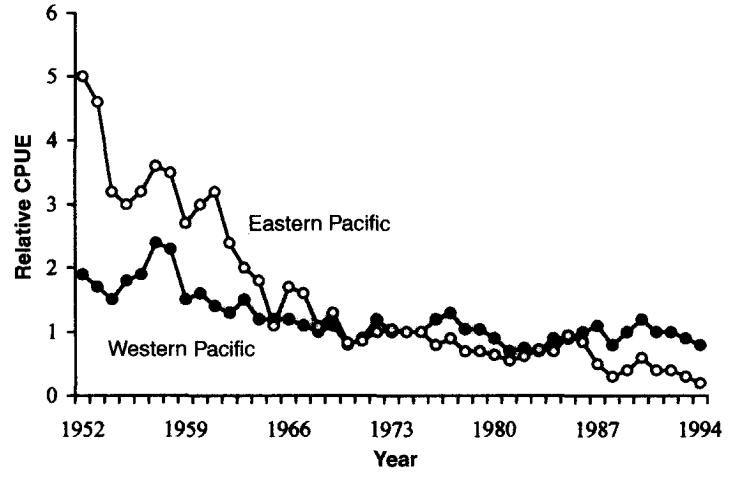


Fig. 6. Relative catch per unit of effort for Pacific bigeye tuna. Data from Anonymous (1998a).

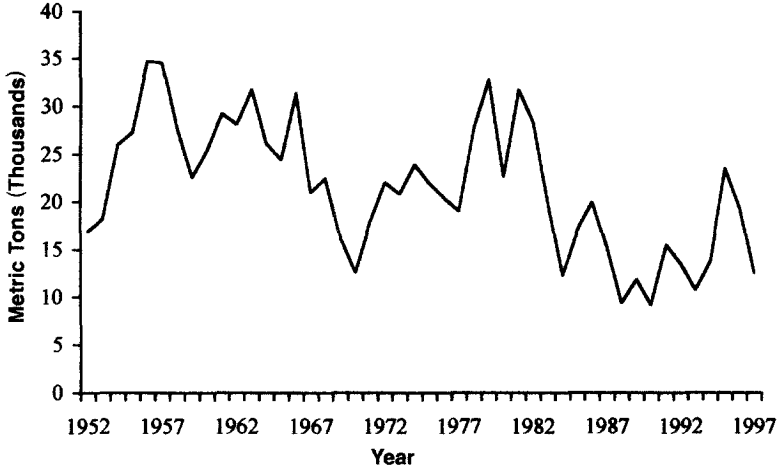


Fig. 7. Pacific catches of northern bluefin tuna. Data from IATTC (1999a).

those only known origins, they inhabit much of the temperate north Pacific, east to North America. In the eastern Pacific Ocean nearly the entire catch of bluefin tuna is made by purse seiners fishing not far offshore from California and Baja California (IATTC, 1999a).

Catches of Pacific northern bluefin tuna were as high as 35,000 mt as early as 1956, and as low as 9000 mt in 1990. But as recently as 1995 fluctuating catches went as high as 24,000 mt (IATTC, 1999a). Though recruitment has been judged not to have declined significantly, IATTC (1999a) states, "fishing has greatly reduced the abundance of mature [northern] bluefin in the Pacific Ocean" (Figure 7).

Southern bluefin tuna inhabit three oceans in the southern hemisphere. The only known spawning ground is an area south of Java and northwest of Australia. Juveniles migrate along the Australian coast, extending their range as they grow until they are distributed throughout the circumpolar South Pacific, Indian, and South Atlantic oceans. They mature at about age 8. A significant number of large fish are more than 25 years old—and the maximum known age is 42 (ICCAT, 1998).

IV. BYCATCH IN TUNA FISHERIES

While this chapter is about tuna conservation, tuna fisheries create collateral conservation issues. One prefacing comment is needed: an information sheet put out by the Oceanic Fisheries Program of the Secretariat of the Pacific Community

notes that vessel logbooks in one of the area's tuna fisheries put the bycatch at 9% of the catch, while observers report 45%. Honesty in reporting and information quality and reliability are important and contentious issues in themselves. Suffice to say there is considerable misinformation—some of it intentional. The following is a brief overview of some bycatch issues in tuna fisheries where data are relatively reliable.

A. Purse Seining Bycatch

The most widely publicized tuna bycatch is the dolphins in the eastern tropical Pacific purse seine fishery. This complicated topic has been reviewed in detail by Hall (1998) and Gosliner (1999). Perhaps the best publicized bycatch issue involved the estimated 400,000 dolphins that were caught annually while netting yellowfin tuna in the eastern tropical Pacific. Over the three decades after the tuna industry mechanized and went from pole-and-line fishing with large crews to purse seine netting with small crews around 1960, the eastern spinner dolphin (*Stenella longirostris*) population fell 80%, and that of the offshore spotted dolphin (*Stenella attenuata*) fell more than 50%. This led to the United States' dolphin safe policy which began in 1990, banning imports of tuna caught by netting around dolphins. The success of this in reducing direct kill of dolphins in the nets has been excellent. Dolphin kills went from just under 100,000 in 1989 to 3000 in 1997 (Gosliner, 1999). To simplify a complicated story, let it suffice to say that some netters shifted from netting around dolphin schools to netting around logs and floating objects. Unfortunately, "dolphin safe" netting methods are not tuna, billfish, turtle, or shark safe.

Netting around objects can entail hundreds of times the bycatch that netting around dolphins does. Hall calculates that because many kinds of marine animals congregate around drifting objects, including juvenile tunas, saving 1 dolphin was traded off against approximately 16,000 discarded small tunas, 380 mahimahi (*Coryphaena hippurus*), 190 wahoo (*Acanthocybium solanderi*), 20 sharks and rays, 1200 triggerfish and other small fishes, 1 marlin, and other animals.

The preseining pole-and-line fishery entailed essentially no significant bycatch and did not catch dolphins. Going back to pole and line would entail hiring back the numbers of people who were laid off when the fishery became mechanized. Considering that regulations are always resisted by the fishing industry on the grounds that they would hurt employment, it is interesting how eager boat owners are to embrace any new technology that will allow them to reduce their payroll. However, the reality is not that simple. Purse seining has greatly extended the range of trips because there is no need to return to coastal waters to refresh bait supplies, and in the past the fisheries had some difficulty sustaining bait fishing (Hall, 1998). Many believe the solution is to refocus purse seining on dolphin schools where that is possible, using new techniques that greatly reduce dolphin

deaths. But as noted above, dolphin populations are not recovering at the expected rate, leading to speculation that the stress involved in chasing them to exhaustion in order to net them, to catch the associated tuna, causes separation and loss of small juvenile dolphins, miscarriages, or other problems (Hall, 1998). A change in the U.S. government's definition of "dolphin safe" would be necessary to implement the Panama Declaration (see Section II.D) and again allow import into the United States of tuna caught by setting nets around dolphins. When the United States has attempted to make that change, animal defense groups have taken the definition of "dolphin safe" back to the courts and blocked the effort.

Purse seining in most other areas does not involve setting around dolphins because the tuna–dolphin association is not cosmopolitan. But most purse seining involves considerable bycatch of undersized tunas and other species. Bailey *et al.* (1996) report that in the western Pacific, tuna purse seines catch up to 7% bycatch, with the most common species being amberjack (*Seriola rivoliana*), mackerel scad (*Decapterus macarellus*), rainbow runner (*Elagatis bipinnulata*), drummer (*Kyphosis cinerascens*), mahimahi, and ocean triggerfish (*Canthidermis maculatus*).

B. Longline Bycatch

High seas longline fisheries for tunas and billfishes deploy some 750 million hooks annually into the world's oceans (Bonfil, 1994). The Atlantic, Indian, and Pacific oceans have major tuna longline fisheries targeting bluefin, yellowfin, bigeye, and albacore tuna. Some of the fisheries, for example, the North Atlantic, target mixed tunas and swordfish (*Xiphias gladius*).

Longline tuna fisheries incur significant bycatch and discard of sharks and other elasmobranchs, bony fishes, undersized target species, prohibited and protected species, and various mammals, birds, and turtles. Hoey (1995) examined bycatch in western Atlantic pelagic longline fisheries in five regions from the Grand Banks to the Gulf of Mexico. Discards ranged from 40 to 65% of the catch. Of these, dead discards ranged between 15 and 35%. Discards included mahimahi, lancetfish (*Alepisaurus* sp.), oilfish (*Ruvettus pretiosus*), wahoo, various sharks, undersized swordfish [about a quarter of all swordfish caught; National Marine Fisheries Service (NMFS), 1999], and some birds, mammals, and turtles. Threatened and endangered marine turtles are occasionally caught and most are released alive, but they probably incur significant mortality from ingested hooks (estimated at 30%; Aguilar *et al.*, 1992). Twice as many turtles are caught when light sticks are used (NMFS, 1997). NMFS (1997) has concluded that "sea turtle takes are documented everywhere the fishery occurs."

The Hawaiian longline fishery has significant interactions with marine turtles (NMFS/SWFSC, 1997). NMFS determined that Hawaiian longline interactions with sea turtles "adversely affects green, leatherback, loggerhead, olive ridley and

hawksbill turtles" and found that these species may not be able to sustain the current level of estimated take on a continuing basis (NOAA, 1994). Rapid expansion of the Hawaiian longline fleet from 37 vessels in 1982 to 166 in 1992 led to interactions with endangered monk seals (*Monachus schauinslandi*). As a result, a 50-NM (nautical mile) no-longlining zone was created around the northwest Hawaiian Islands (NMFS/SWFSC, 1996). Small cetaceans reportedly occasionally take bait or catch, and rumors of shooting seem plausible.

Hawaii has also seen skyrocketing retention of fins of sharks caught incidentally to tuna fishing (i.e., sharks that were once released are now killed, and most carcasses are discarded). Numbers of sharks "kept" rose from an estimated 2300 in 1991 to 61,000 in 1998, as retention went from 3 to 61% (Camhi, 1999). Bonfil (1994) estimated the total high seas longline bycatch of sharks at 8.3 million animals annually, almost a third of the world catch of elasmobranchs reported by the UN Food and Agriculture Organization (FAO) in 1991. Of the total, he estimated over 4 million were blue sharks. Most sharks caught by tuna boats in most of the world are killed for their fins. Estimates for shark bycatch total numbers in tuna fisheries are very poor for most regions (Bonfil, 1994).

Bailey *et al.* (1996) also note that western Pacific longline bycatch data are very poor, but report that over 50 fish, including 21 species of sharks, 7 species of nontarget scombrids, 6 species of billfishes, and 21 other fishes, have been reported. The shark catch often equals the tuna catch, and most are blue sharks (*Prionace glauca*).

Many thousands of seabirds are killed annually in southern hemisphere longline fisheries. Sixteen species of seabirds were recorded taken in the Australian Fishery Zone between 1988 and 1995. Many of these were albatrosses. Other bird species reported killed on longlines are petrels, skuas, gulls, kittiwakes, fulmars, shearwaters, and penguins (Ornithological Council, 1997). In some cases, catches of shearwaters and petrels considerably exceed albatross catches. But it is only for albatrosses, with their extremely low reproductive potential, that longline bykill is known to be driving population declines. The Japanese southern bluefin tuna fleet alone was estimated in 1990 to be killing 44,000 albatrosses annually (Brothers, 1991).

Most longline fishing occurs on the high seas, and several nations longline in the Southern Ocean with no regulations or reporting requirements (Hayes, 1997). There are no data for seabird catch from the tuna longline fleets of Taiwan, China, Korea, and others (Earle and McKay, 1997).

In the wandering albatross (*Diomedea exulans*), adult females' foraging behavior brings them into contact with the southern bluefin tuna longline fishery more than does males' (Weimerskirch and Jouventin, 1987). In 1995 Australia declared longline bycatch a "key threatening process" to seabirds under its Endangered Species Protection Act of 1992. The Macquarie Island subspecies of wandering albatross was listed as endangered in 1995. The wandering albatross is listed on the World Conservation Union's (IUCN) Red List as endangered, and the

gray-headed albatross as vulnerable. Gales (1993) called direct fishing mortality "the most serious threat facing albatross populations."

The southern bluefin tuna fishery alone may have accounted for South Georgia's annual mortality of 2–3% of adult wandering albatrosses and 14–16% of South Georgia's immatures between 1980 and 1986 (Croxall *et al.*, 1990; Croxall and Prince 1996). This is enough to account for observed declines. Longline fishing is the only identified cause of decrease in these populations. Longline fishing for southern bluefin tuna also affects survival of wandering albatrosses breeding on the Crozet Islands in the southern Indian Ocean (Weimerskirch *et al.*, 1997). Pelagic as well as bottom longline fisheries take birds. Longlining contributes to and may drive observed declines in northern Pacific albatrosses (Flint, 1995).

The Convention for the Conservation of Southern Bluefin Tuna imposes no gear regulations to mitigate bycatch, so increased quotas such as Japan has proposed for that severely depleted population would also lead to increased seabird bycatch (Earle and McKay, 1997). The CCSBT's awareness of the albatross bycatch problem is reflected in its creation of its Ecologically Related Species Group, but so far seabirds have not been a decisive factor in decisions on catch limits (Earle and McKay, 1997). Australia requires the use of a variety of bycatch mitigation devices on Australian and Japanese vessels. Because albatrosses take bait that might otherwise be eaten by a tuna worth thousands of dollars, the fishing industry has some financial stake, though albatross mortality is calculated to cause only a low percentage of income loss (1% of its catch, valued at $5 million per year). Estimates of up to five baits lost per hooked bird suggest the reason why boats have been willing to use streamer lines to frighten birds away, as well as mechanical bait-throwing devices to remove slack from branch lines and speed sinking. Hooking rates can be sharply lowered by using streamers to scare the birds (and save baits). Japanese vessels using *tori* (bird) lines and setting at night have catch rates less than 0.02 birds per thousand hooks (Hayes, 1997).

V. SOUTHERN AND ATLANTIC BLUEFIN TUNAS—CASE HISTORIES

The bluefin tuna is emblematic for failure to find the political resolve to act toward recovery of severely depleted fish despite having generally reliable scientific information. Scientists will find much in these case histories to suggest why it is important for them to maintain professional vigilance over management processes that claim to be science-based.

Bluefins' life histories of late maturation (up to 12 years) and restricted spawning areas make them more vulnerable to overfishing and slower to recover from population reductions than faster maturing and more widely spawning species. Because the prices surrounding them run so high, bluefins are depleted everywhere they swim.

Management of bluefin has gotten more complicated than management of probably any other species. Wherever fishing quotas for bluefins exist, the quota has always been kept too high to allow recovery. The resulting management controversies keep managers busy making more complex rules for marginally sustainable quotas. It is as though a pilot whose plane is losing altitude concentrated not on trying to gain altitude but on flying more and more precisely closer and closer to the ground. In some cases bluefin management has become absurdly complicated, like the United States' Atlantic size categories of small school, school, large school, small medium, large medium, and giant, with different regulations on different days of the week and closings and reopenings at different (but unpredictable) times of the year as different quotas for different local areas fill for parts of the season, and those areas are closed and then reopened.

These unnecessarily complex regulations result from one simple fact: catches are too high. Bluefins everywhere are too desired to be allowed to thrive.

Southern bluefin and the Atlantic northern bluefin are the two cases that best highlight the recalcitrance of countries that have conceptually good management frameworks in place and painstakingly developed scientific information available. But, because of political pressure to keep bluefin catches as high as possible in the short term, the countries fail to use those frameworks for recovering depleted populations or maximizing sustainable yields.

The following case histories are detailed because the arguments over scientific information and use of science in management have long and well-developed histories. They are instructive about the fate of scientific information in management disputes.

Conservation biology is usually defined as "science in the service of conservation" (Noss, 1993). That prompts the question, what is conservation? While good conservation policies start with well-articulated goals and excellent scientific information, conservation is not science alone. Conservation is mostly politics—politics in the service of living nature. Conservation policies are only as good as the goals and the tools available. A goal like "sustainable use" cannot be achieved without adequate scientific tools with which to design management. But even perfect information will never find its way into management without a constituency advocating use of high-quality science to guide human activities. The efforts of that constituency of science advocates constitute much of what can be called conservation work. Usually, "conservation" becomes the struggle for long-term sustainability—the struggle to infuse management with long-term versus short-term thinking and interests.

What authorizes us to judge management? Management is inherently value-free until performance standards are agreed upon. Just as science becomes "bad science" if it fails to conform to agreed standards of objectivity and repeatability, management becomes "bad management" if it fails to conform to legally agreed performance standards (almost all of which are science-based) such as maximum

sustainable yield, recovery targets, biodiversity preservation, the precautionary approach, or best science. "Sustainable use" and "use of best available science" have emerged as the most widespread standards for natural resource exploitation. These standards are explicitly stated in legal instruments such as national laws, regional agreements, global treaties, and tuna management conventions.

In the world tuna fisheries, the bluefin tunas best illustrate this tension between science, legal requirements, and commercial politics.

A. Southern Bluefin

Southern bluefin have been heavily exploited for nearly 5 decades, mainly by commercial fleets from Japan and Australia (ICCAT, 1998). They are caught primarily far offshore Australia, New Zealand, and South Africa. The catch peaked back in 1961, at 81,605 mt, with the Japanese longline fishery taking 78,000 mt (96%; ICCAT, 1998). Thereafter, catch per unit of effort decreased during 2 decades of intensifying effort (Edwards, 2001). By 1980 the catch declined to 45,000 mt and there was already serious scientific concern over the status of the population. Australian surface gear catches, which take younger fish than longlines, peaked in 1982 with 21,500 mt (Edwards, 2001).

Australia, New Zealand, and Japan have had a quota system since 1986. The first annual quota was 38,650 mt, "too high and too late to avert further decline" (Edwards, 2001)—the familiar pattern of unwillingness to apply enough restraint to get ahead of the problem.

In 1994 Australia, New Zealand, and Japan entered into a treaty creating the Commission for the Conservation of Southern Bluefin Tuna, or CCSBT. This formalization followed a decade of informal cooperation, and was finally hastened into existence by a combination of increasing fishing pressure from other countries and increasing scrutiny by environmental groups who were discussing international action to ban international trade of the species.

The parental biomass is estimated at 5 to 8% of the virgin biomass (Edwards, 2001), and parental and younger age classes are facing increasing fishing pressure—"cause for serious concern" (ICCAT, 1998). A strong year class in 1987 was fished hard rather than protected as a way of increasing parental biomass (ICCAT, 1998). (Shepherding the last strong year class into adulthood to stimulate more egg production was the linchpin of the recovery of U.S. east coast striped bass, in my opinion the world's most successful recovery yet of a depleted fish due to strong management. Unfortunately, this simple principle is not universally applied.)

The population seems to have stabilized at a low level recently, but catches by other countries are showing "marked and continuous increase" (ICCAT, 1998). No consensus exists on whether the population will further decline, remain stable, or increase. The Australian government calculates only a 36% chance, under cur-

rent quotas, of southern bluefin recovering in the next 25 years to levels capable of supporting maximum sustainable yield.

Australia, Japan, and New Zealand take 11,750 mt under quotas (5265, 6065, and 420, respectively), but recent actual catches have totaled about 16,000 mt (ICCAT, 1998) due to catches taken by countries not party to the CCSBT (e.g., Taiwan, Indonesia, and Korea reportedly take 1400, 2200, and 1600 mt per year, respectively). These countries have entered discussions about possibly joining the CCSBT in the future. Their catches have been demoralizing to the CCSBT countries. Success in including all the fishing countries is seen by some as crucial to the credibility and ability of CCSBT to manage.

Japan's market drives the fishing (most commercial bluefin fishing is driven by the Japan market), and so Japan could limit imports as a way of forcing other nations to join and abide by CCSBT conservation measures.

Unfortunately, Japan does not itself appear to strongly support CCSBT conservation measures. Japan had proposed an *increase* in the total allowable catch in 1995. After Australia and New Zealand would not agree to increase Japan's quota, Japan refused to agree to be limited by a total allowable catch quota (TAC) in 1996. [Additionally, in 1996 New Zealand and Australia sought agreement on actions that could be taken to, among other things, minimize mortality to albatrosses endangered in the southern bluefin fishery. Japan would not agree on a course of action, saying further work was necessary (Edwards, 2001).] When no agreement to an increased TAC was reached, Japan began in 1998 an "experimental fishing program" in which it reportedly caught additional "experimental" catches of 1500 to 2000 mt in 1998 and 1999—more than 25% beyond its quota.

In 1999 Australia and New Zealand took Japan to an international tribunal in Hamburg, Germany, under the UN Convention on the Law of the Sea, for fishing over its quota. Japan stood accused of violations of the Convention for the Conservation of Southern Bluefin Tuna, and of the Law of the Sea. Japan insisted that it's 65-vessel "experimental" bluefin tuna fishing program, operating off Australia's west coast, was not to be bound by its quota limit because it was "scientific." Australia and New Zealand charged the program was for commercial, rather than scientific, purposes (Japan makes the same specious claim of "scientific" hunting of Antarctic whales, and following that lead, ICCAT has long disingenuously referred to all the commercial and sport fishing for west Atlantic bluefin as being done under its "scientific monitoring quota"). Obviously, Japan was using the pretense of science simply to increase its quota of a commercially valuable fish.

The two plaintiff countries claimed increased fishing by Japan threatened "serious or irreversible damage to the southern bluefin tuna population," and they sought a temporary injunction to halt Japan. Japan argued before the tribunal that bluefin were increasing in Indian and Southern ocean waters, and their "experimental" catch was sustainable.

The court agreed with Australia and New Zealand, ruling by 20 to 2 that Japan

must consider any fish it catches as part of its quota (the 2 dissenting judges cited technicalities, not the legal theory of the case). In addition, Japan may continue an experimental fishing program only if the other two countries agree, according to the court verdict (United Nations, 2001a). Whether Japan will comply remains to be seen.

The condition of the southern bluefin has attracted international criticism. IUCN added the species to its Red List of Threatened Animals, and prior to the tribunal decision, Australia itself had considered proposing listing it on the Convention on International Trade in Endangered Species of Wild Flora and Fauna.

B. Atlantic Bluefin

The Atlantic bluefin's uniquely lengthy management history constitutes another case study of disparity between consistent scientific findings and consistently unresponsive management (Mather, 1974; Safina, 1993, 1997; Berkeley, 2001).

Boats fish for Atlantic bluefin from the Gulf of Mexico to Newfoundland, from the Canary Islands to waters south of Iceland, and throughout the Mediterranean Sea (ICCAT, 1998). Formerly an active fishery existed in the North Sea. ICCAT manages Atlantic bluefin tuna as two separate stocks—east and west Atlantic—based on the existence of two widely separate spawning areas (Gulf of Mexico and Mediterranean), different ages and sizes at maturity (younger in the Mediterranean), tag returns showing only limited trans-Atlantic mixing (ICCAT, 1998), and absence in the Gulf of Mexico of fish of the sizes that breed in the Mediterranean Sea (Nemerson *et al.*, 2000).

1. Status in the East Atlantic and Mediterranean

The east and west Atlantic fisheries differ in various ways. Catches in the east Atlantic (which for this discussion includes the Mediterranean, where roughly three-quarters of the catch is taken) are far less controlled than those in the west Atlantic. Eastern markets for smaller fish are more diffuse, and the catch from the eastern population is greater than an order of magnitude more than that from the west—west Atlantic catches, including discards, have ranged during the late 1990s from 2200 to 3000 mt, while those in the east have exceeded 48,000 mt in recent years (ICCAT, 1998). (The disparate catches supportable by the two areas further suggest separate populations.) Catches have recently been near historic highs at around 40,000 mt, but projections indicate that they must be cut to 25,000 mt merely to halt the decline (ICCAT, 1998).

For conservation and management in the east, one of the greatest difficulties is monitoring—merely obtaining information from the various countries and points of landings. Italy and Greece have both gained reputations for unrestrained fishing and poor reporting.

A variety of fishing gears catch bluefin in the east Atlantic. Purse seining takes

75% (by weight) of the eastern catch. Since the mid-1990s Japanese longliners have been exploiting a new fishing area in the North Atlantic near 60° north latitude and 20° west longitude (ICCAT, 1998). Beginning in 1994, ICCAT adopted a regulation prohibiting large longliners from operating in the Mediterranean in June and July, but "there have been many reported activities by many longliners flying flags of convenience or without any country identification . . . during the closure period" (ICCAT, 1998). ICCAT (1998) observes that "the high demand for the Japanese market is without a doubt the reason" for longliners ignoring the closure.

Small fish are under heavy pressure in the Mediterranean (Mace, 1997). Seiners routinely target age 0 fish. Fish under the 6.4-kg minimum size constitute 40 to 60% of overall catches in the east Atlantic and Mediterranean (ICCAT, 1998). ICCAT (1998) reports that recent area closures have helped reduce the percentage of undersized fish taken in the Mediterranean, but Raymakers and Lynham (1999) contend that in Spanish landings half of the bluefin tuna from the eastern Atlantic Ocean and over 80% of the bluefin from the Mediterranean Sea are below ICCAT's minimum size.

For the eastern Atlantic and Mediterranean, ICCAT (1998) noted "a strong decline in number and biomass of older fish (spawning stock) since 1993. . . . The current catch level is not sustainable. . . . The committee continues to be concerned about the intensity of fishing pressure on small fish. . . . Additionally, recent abrupt increase of catches of large fish is of grave concern" (pp. 35–36; Figure 8).

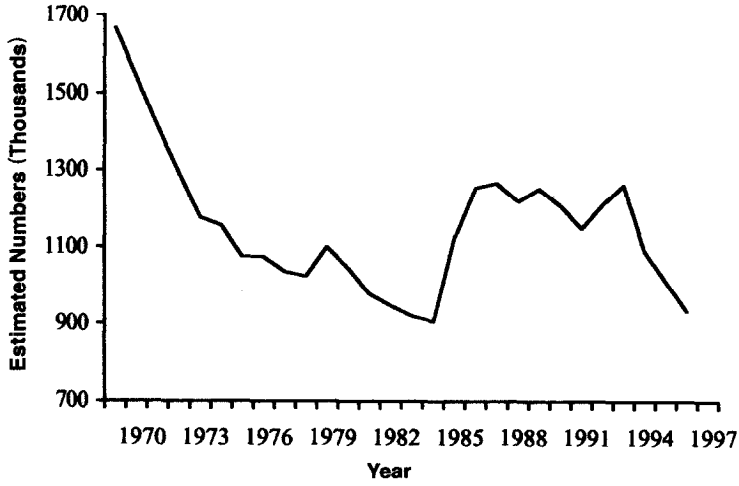


Fig. 8. Population trend estimates for eastern Atlantic (including Mediterranean) bluefin tuna (age 5+). Data from National Marine Fisheries Service.

In 1994 the commission recommended a 25% reduction in bluefin catches in the East Atlantic and Mediterranean (ICCAT, 1998). The most recent catches are 3 to 8% *higher* than in 1994 (ICCAT, 1998).

Fishing mortality as of the mid-1990s was considered "far in excess" of fishing mortality associated with maximum sustainable yield (Mace, 1997). Additionally, the 1995 spawning biomass was estimated at only 19% of that corresponding to B_{msy}, the biomass needed to support maximum sustainable yield (Mace, 1997). Thus the eastern Atlantic bluefin population is considered "severely overfished" (Mace, 1997).

Maximum sustainable yield for eastern Atlantic bluefin is considered to be about 40,000 mt, which is near recent landings (Mace, 1997). However, to rebuild the spawning population within 20 years to levels that can support that catch long-term, catches should be about 20,000 mt (Mace, 1997).

2. Deficiencies at ICCAT

The bluefin problem in the Atlantic results largely from ICCAT's structure and approach (though the recently formed CCSBT's short history is in some ways worse due to large catches by nonparty members and Japan's noncompliance). ICCAT's stock assessments and scientific analyses are conducted by the Standing Committee on Science and Statistics, which is composed of whomever the member countries designate to be on their delegation. This committee makes recommendations to ICCAT's managers, who likewise represent the various member countries in respective delegations. These managers make recommendations intended to be policy, for implementation by member countries. Implementation of these recommendations is essentially voluntary, and the quality of compliance and enforcement varies among countries. Fishing by certain nonparty countries further exacerbates problems.

ICCAT's science has generally been of high quality over its history (with the notable exception of its 1998 west Atlantic bluefin assessment, discussed later). Its management, however, has often responded inadequately to the advice of its scientists. Consequently, the commission has failed to prevent the depletion of most species of tunas and billfishes under its purview.

Berkeley (2001, p.136) says of ICCAT, "although science is supposed to be impartial and objective . . . even at the scientific level, national agendas and industry objectives are paramount and . . . color the analyses and interpretation of the results." Scientific results are often reported equivocally and in unclear language, reflecting a reluctance to restrict fishing. As situations worsen over years and solutions require more decisive action, restrictions become more difficult. "If there is insufficient support to implement management in the initial stages of stock decline, when sacrifices are minimal, there will certainly be little support to do so if substantive reductions in catch and effort are required. This is how the downward spirals that are so evident began" (Berkeley, 2001).

Is ICCAT a net benefit for Atlantic tunas and billfishes? That's debatable. Without ICCAT some species' status might be even worse (Berkeley, 2001). But it is also possible that some species might be better off without ICCAT. The fishing industry in the United States succeeded in getting the U.S. Congress to adopt a law preventing the United States from setting more restrictive quotas in its own waters than the ones ICCAT gives the United States. In practice this has prevented the country from setting more restrictive quotas for west Atlantic bluefin and swordfish within the U.S. EEZ (which contains major breeding, nursery, migration, and foraging grounds for both species).

The fishing industry argues that these species compose one pan-Atlantic "stock" and that unilateral management could not affect a species' population trajectory. Is this true? In the early 1970s the United States unilaterally banned sale of swordfish because of mercury levels. ICCAT's data indicated that Atlantic swordfish population recovered almost to pre-longlining levels in only about 6 years, and declined again when the United States relaxed mercury standards and the fishery reopened. This unintended experiment suggests potential efficacy of unilateral management in at least some cases.

Denial and conflict avoidance are major characteristics of ICCAT's political atmosphere. As Berkeley (2001, p. 136) notes,

> there is a tremendous inertia in the system. The *status quo* is always the path of least resistance. . . . Considering the condition of the stocks under its jurisdiction, it appears that ICCAT has lost sight of its original goal of maintaining stocks at MSY and has instead focused on keeping the process operating smoothly.

As with many management agencies, procedure becomes the chief product.

ICCAT activity increased in the 1990s. It established requirements that bluefin in international trade be accompanied by a statistical document that travels with each fish (allowing illegally caught fish to be better tracked) and enacted a system for identifying countries fishing in contradiction of or outside of ICCAT recommendations (and sanctioning several of them). Berkeley (2001) notes that ICCAT accomplished little until it came under outside scrutiny, particularly by nongovernmental organizations: "the most significant change in ICCAT has been brought about by the involvement and oversight of conservation groups." These changes have been mostly too little and too late, however. [In the case of west Atlantic bluefin, where the truly significant changes involved quota cuts, ICCAT has since reversed itself. As the immediate threat of outside intervention from the Convention on International Trade in Endangered Species (CITES) has seemed to lessen (see next section), ICCAT has put the quota essentially back up to where it was during the 1980s.]

ICCAT's charter requires management to maintain populations at levels capable of producing the "maximum sustainable catch," but east and west Atlantic

bluefin, north and south Atlantic albacore, bigeye tuna, swordfish, blue marlin, and white marlin all have fishing mortalities above MSY and biomass below that needed to produce MSY. If one compares ICCAT's performance with its charter, it is clear that this commission has not been effective.

3. Management in the Western Atlantic

West Atlantic bluefin is the most depleted species in ICCAT's portfolio. West Atlantic bluefins were fished intensively in the 1960s by purse seiners targeting small fish for canneries. Obvious depletion—less than a decade after industrialized commercial targeting—led to reduction in the east coast purse seine fleet from more than 20 vessels to 5 (and led in part to the creation of ICCAT in the late 1960s). West Atlantic bluefin catches averaged roughly 8000 mt during the 1960s and 5500 mt during the 1970s. During the 1970s, commercial targeting switched to large fish for export. Effort intensified and longlining on the western breeding ground increased, prompted by Japanese prices often averaging U.S. $10,000, and as high as $30,000, per fish and more.

ICCAT managers long rejected their scientific committee's advice to reduce catches. In 1981 the Commission's Standing Committee on Research and Statistics concluded that the western Atlantic's bluefin tuna population was depleted and that catches "should be reduced to as near zero as feasible." But the commission's managers set a 1160-mt annual quota for 1982, ostensibly for "scientific monitoring." The next year, ICCAT doubled this "scientific" quota to 2660 mt due to political pressure.

The first quota in 1982 brought mortality rates down considerably and might have stemmed the population decline. Under the 1983 quota, however, the population continued to drop. (The quota is shared by Canada, Japan, and the United States, which gets the major share.)

Large fish were targeted for export and immature fish targeted by U.S. recreational boats (which catch about half the fish, by number). Throughout the 1980s, lax U.S. government monitoring left catches untallied until the following year, allowing extensive overruns in the recreational sector's catch of juveniles.

The excessive quota, intensified effort, and poor monitoring and enforcement caused another spike in fishing mortality in the late 1980s. Because the population was rapidly shrinking and the quota —though higher than ICCAT's scientists had advised—was not, high fishing mortality continued. By 1990 the breeding population was at an all-time low. The mainstream "environmental" community got involved in Atlantic bluefin conservation in 1991, asking ICCAT to reduce the quota to a level that would allow recovery, and asking the U.S. government to tighten monitoring on recreational catches of juveniles, to avoid overruns. ICCAT managers clung to the quota it had implemented in 1983, and the United States was sluggish in responding to overruns in the juvenile allocation.

Consequently, the National Audubon Society petitioned the U.S. government

to list west Atlantic bluefin tuna under the Convention on International Trade in Endangered Species, on Appendix 1 (Safina, 1993). Such a listing would have prohibited international trade in the species. Virtually the entire market for large fish is in Japan. Without export to Japan, the price would collapse and far fewer people would incur the expense of fishing.

Proposals to CITES can only formally be made by governments of party nations. The United States declined to carry the proposal after the U.S. fishing industry and their congressional representatives opposed the idea. The proposal was then made by Sweden, which at one time had considerable bluefin landings but whose fishery collapsed.

Sweden was pressured to withdraw the CITES proposal, but first extracted nonbinding language that ICCAT would act on its scientific information and reduce the quota low enough to initiate recovery (Safina, 1997). Threat of listing under CITES led ICCAT to implement a modest quota cut in 1992 (reduced from 2660 to 2394 mt).

With increased scrutiny and the threat of eventual CITES action usurping their authority, ICCAT made several other improvements. ICCAT instituted a requirement for documentation to accompany each fish in international trade. This mimicked the requirement of a CITES Appendix 2 listing; ICCAT was trying to blunt the argument that CITES would do needed things ICCAT was unwilling to do. Such documentation made illegal export and import more difficult. Increased visibility also caused U.S. enforcement to improve significantly during the 1990s, with better monitoring and seasonal closures when the U.S. cap was reached. A new prohibition on sale of most juvenile bluefins by recreational boats (requested by several conservation and recreational fishing groups and fought by commercial interests) made reductions of possession limits more feasible; consequently the United States sharply reduced daily possession limits for juveniles.

Under continued threat of CITES action, ICCAT agreed in 1992 to cut the west Atlantic bluefin quota to roughly half its long-standing 2660-mt quota, but gave themselves another 2 years to phase it in, first reducing the quota in 1993 to 1995 mt.

The National Research Council (NRC) convened a team to review the bluefin science. The NRC review highlighted gaps in relevant biological knowledge and stimulated a new infusion of funding toward important basic research. The NRC report (NRC, 1994) confirmed the history of depletion. It chose, however, to highlight the fact that in the prior 5 years or so the population appeared to have stabilized—albeit at or near all-time lows (Figure 9). That opinion was interpreted by the industry and its political lobbyists as a finding of "no decline." This led to widespread misinterpretation (Sissenwine *et al.*, 1998)—and allowed ICCAT to rescind the 50% cut before implementing it.

After that, ICCAT increased the quota several times. By 1999 it was 2500 mt, including discards. This is close to where it was from 1983 to 1992, when the breeding population had initially been roughly twice as large.

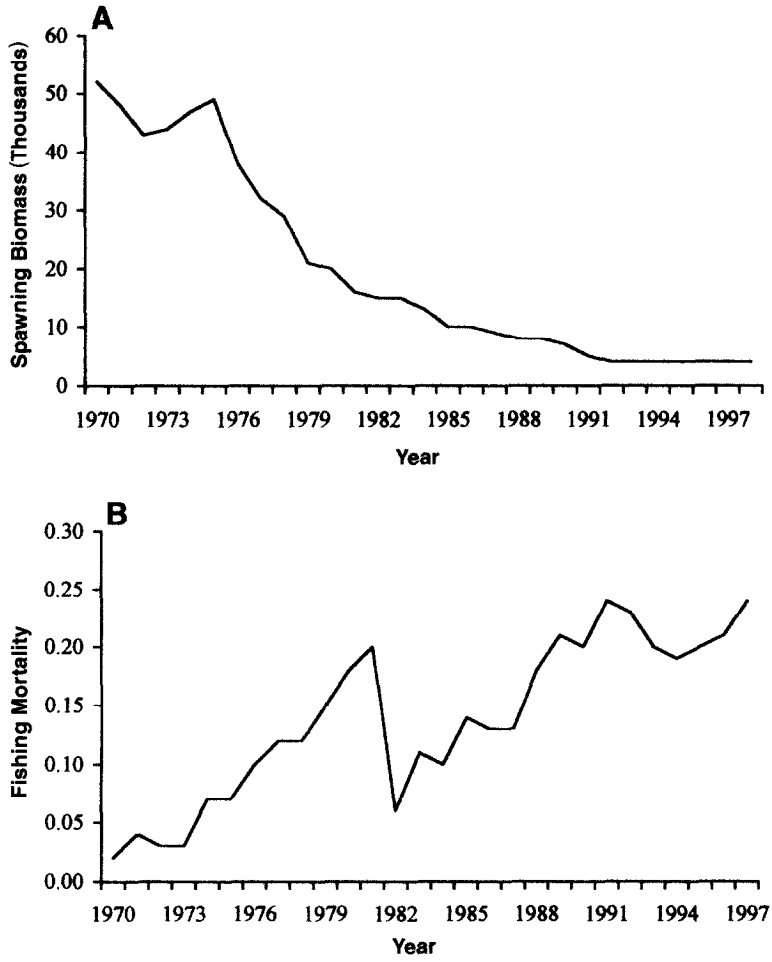


Fig. 9. (A) Population (age 8+) and (B) fishing mortality rate trend estimates for West Atlantic bluefin tuna. Biomass in 1975 was long considered a proxy for the spawning biomass required to support maximum sustainable yield. Data from ICCAT (1998).

Recent assessments estimate "spawning" (age 8+) biomass at only 13 to 18% of that considered the target to support MSY. Thus the western Atlantic bluefin population is considered "severely overfished" (Mace, 1997).

To summarize, after falling steadily during the 1960s and into the 1970s, west Atlantic bluefin have been managed under a series of catch quotas since the early 1980s. Spawning biomass shrank roughly 85% between 1975 (the initial year for

quantitative population estimates) and the late 1990s, with biomass of fish aged 8 and higher falling from an estimated 42,000 to 7,000 mt. Despite advice by ICCAT's scientific committee for a quota "near zero" in the early 1980s, ICCAT has kept quotas averaging roughly 2300 mt. Under these quotas, the spawning biomass fell sharply and remains near all-time lows.

4. 1998: One Regime Shift Claimed, Another One Established

ICCAT's science has generally been exemplary. Virtually all the conservation groups' positions on quotas have been based entirely on ICCAT's own science. And ICCAT's internal dichotomy has often been characterized as "good science and unresponsive management." In 1998, events surrounding ICCAT's bluefin assessment changed that characterization, at least regarding bluefin, to "bad science and bad management."

The U.S. Sustainable Fisheries Act of 1996 requires the National Marine Fisheries Service to publish an annual list of overfished species. A recovery plan must be developed for all species listed as overfished. West Atlantic bluefin are now listed as "overfished."

Thus in 1998 ICCAT was faced by the U.S. delegation with needing to develop a recovery plan that would satisfy U.S. legal requirements.

By prior arrangement, ICCAT's Standing Committee on Research and Statistics had agreed to conduct its bluefin assessment using a Beverton–Holt model. Beverton–Holt projections indicated that: (1) the current catch of 2500 mt could not be sustained, (2) 2000 mt was likely sustainable, but to have a 90% chance of maintaining the current population level the catch would have to be reduced to 1500 mt, (3) a 2000-mt annual catch would have about a 50% chance of leading to a slight increase in breeding biomass (at the end of 20 years the spawning population would be about 20% of its 1975 level—still quite overfished), and (4) to recover the west Atlantic bluefin to the biomass associated with maximum sustainable yield within 20 years (the goal required by ICCAT's charter and the timetable resulting from U.S. law), median trajectories indicated the need for reducing the catch to about zero.

Faced with such a bleak assessment, a scientific and management cat-and-mouse game ensued whereby the task became, essentially, "can we satisfy the legal need for a 'recovery plan' without reducing fishing?"

Consequently, a scientist who works as consultant for the main industry lobbying association, and whose presence on the U.S. delegation has been arranged by the commercial fishing industry, introduced a new model late in the assessment workshop.

Any model predicting whether a population will increase or decline requires estimates of the relationship between parental "stock" and reproductive success or recruitment, and most such estimates are based on past observations of year class strength and parental abundance ("stock/recruitment relationship").

The stock/recruitment function used in the Beverton–Holt model indicated higher chances of good recruitment when spawning biomass is higher. Such a relationship is the general rule with fish. Myers and Barrowman (1996) studied nearly 400 data sets from different species, asking a series of questions: (1) Are the largest groups of young fish entering a fishery produced by the highest populations of spawners? (2) Are the smallest groups of young fish entering a fishery produced by the lowest populations of spawners? (3) Are above-average groups of young fish entering a fishery produced by above-average populations of spawners? Their findings were that "the answer to all three questions is almost always 'yes.'" More to the point, such a relationship for bluefin has existed within ICCAT's own bluefin data (Figure 10).

The model introduced by the industry-paid scientist was a so-called "2-line model." While the Beverton–Holt model is a well-known standard, the "2-line" model is an ad hoc model that has apparently never been used outside of ICCAT, nor has it been independently peer reviewed or published.

Actually the models are so similar that it might be difficult to conclude which model might be superior. Given the same data input, they would likely produce similar output. But they produced very different results when ICCAT used them in 1998 for bluefin.

The disparity in output arose mainly from the omission of data. In running the 2-line model, the committee omitted data from the 1970s—when estimated breeding biomass and recruitment were higher.

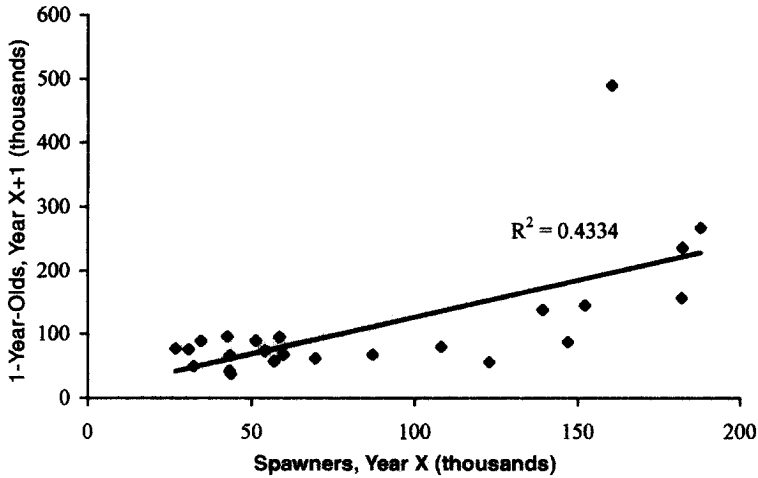


Fig. 10. Relationship between estimated numbers of spawning-aged west Atlantic bluefin tuna and year classes of 1-year-old recruits they produced. Estimated numbers of breeders in a given year (year X) are plotted against estimated numbers of 1-year-olds of the following year (year X+1). Data from ICCAT and National Marine Fisheries Service.

All of the data (1970–1994) were used to estimate the stock/recruitment parameters employed in running the Beverton–Holt model, whereas only data from 1981 to 1994 were used to estimate the stock/recruitment parameters employed in running the 2-line model. *Essentially, for running the 2-line model they discarded all the information showing that higher bluefin tuna breeding populations produced larger year classes of young fish.*

Thus, predictions of recruitment from the 2-line model's results could not attain levels as high as those estimated in the bluefin population's actual history for the 1970s. Consequently, estimates of biological reference points, such as MSY or B_{msy}, must correspondingly be lower than those based on higher possible levels of recruitment in the discarded data. So the 2-line model reached its conclusion through the committee's discarding parts of ICCAT's data set that indicated higher recruitment in years when parental abundance was much higher.

Because it assumes that recruitment is much less dependent on parental biomass, the 2-line's recovery goal is about half the breeding population recovery goal level identified for the last 2 decades by ICCAT. The 2-line model's results predict that a catch of 2000–2500 mt—roughly the current catch—had about a 50% probability of reaching this new, halved B_{msy} in 20 years. (The Beverton–Holt run indicates a catch of about zero would be required to reach B_{msy} in 20 years.) The 2-line's projected MSY is 2800 mt; in other words, we are already near MSY (the Beverton–Holt run indicates MSY would be about 7700 mt, so we have a long way to go to rebuild).

Thus output from the 2-line model suggests that at catches near current levels, within 20 years there is only about a 50% chance of reaching a goal that is only half the prior goal. The recovery goal is much lower because the 2-line model output suggests that bluefin recruitment would not—cannot—increase with increasing parental biomass. These conclusions resulted from discarding the parts of the existing data set showing higher recruitment with higher parental biomass.

Proponents justified discarding almost half the data by claiming that a "regime shift" in the Atlantic had lowered the ocean's carrying capacity for bluefin. They claimed as evidence the fact bluefin recruitment has been consistently poor in recent years. Rather than concluding—based on the data set—that recent poor recruitment may be related to the severely depleted parental biomass, they "assumed" poor recruitment was occurring because the ocean must have changed, and discarded a large part of the "old" data from back when the ocean must have been different (as evidenced by better recruitment). They also ignored the fact that virtually every other fish or bivalve in the North Atlantic for which fishing pressure has been reduced by management has shown an almost immediate population increase, including among others New England cod, haddock, Atlantic herring, sea scallop, and Atlantic mackerel; mid-Atlantic striped bass, weakfish, sandbar shark, and summer flounder; and king mackerel and redfish off the southeast United States (herring and mackerel, key foods for bluefin, have recovered to very high levels.)

Thus the marked difference in estimates of MSY and rebuilding resulted from data input choices. There was no revision in the diagnosis that bluefin were severely depleted. In 1998 ICCAT estimated spawning biomass at only around 15% of the 1975 level (and bluefin were already heavily fished by the 1970s). ICCAT's 1998 scientific report even noted continued high fishing mortality: "A regulatory recommendation stating that contracting parties should limit the fishing mortality to recent levels came into force in 1975. Catch reductions have not been sufficient to reduce fishing mortality rates to comply with this regulation." (p. 33) If ICCAT had based its rebuilding plan on the same modeling choices it had followed consistently prior to 1998, it would have had to mandate a significant catch reduction.

ICCAT chose the most risk-prone of all the assessments produced; even the output they chose projects a 10% chance of extinction by 2012. It predicts less than a 50% probability that the population will rebuild even to the much lower new "target." ICCAT chose not to use the Beverton–Holt results because they indicated that B_{msy} was higher, that recruitment was related to spawning population, that the sustainable catch was much lower, and that rebuilding would require very low catches in the near term.

The key point is that ICCAT's scientific committee confounded the question of choice of model with the intentional omission of data. Thus many observers have been under the impression that the choice of model, not the choice of data, resulted in the disparity of results between the two models' output. One wonders whether the ad hoc 2-line model was introduced specifically so the report could conclude that it had no basis for deciding which *model* was superior, to call attention away from the fact that much of the data had been dumped to produce the 2-line model's very different output. Inability to distinguish which model was superior was how it was portrayed in the scientific committee's report to the managers, and that is the reason the managers gave for choosing the results produced from the 2-line model.

By introducing and pressing use of the 2-line model and discarding the bluefin data showing the positive stock/recruitment relationship, the industry had figured out a way of corrupting the scientific process enough to construct a justification for leaving the existing catch in place.

As a result of all the above, the committee's 1998 report says, "to move with about a 50% chance of reaching biomass levels supporting MSY [the 2-line's new, much lower MSY] within 20 years, current catches need not be reduced under the 2-line stock-recruitment relationship." (p. 34)

Yet ICCAT's management delegations voted to *raise* the quota slightly, to 2500 mt.

Thus, ICCAT's "recovery" plan lowered the recovery goal by half, allowed only a 50% probability of reaching this halved goal, and raised the quota slightly. The 1998 quota returned catches to virtually the same levels that had been in place during 1982–1992, when the population declined from a much higher level to remain near all-time lows.

In my opinion, data were omitted from the analysis to comply with an *a priori* determination to develop a seemingly scientific way to avoid reduction of the quota. The "assumption" that the higher recruitments of the 1970s are no longer achievable (because of a "regime shift") was not a scientific assumption as we understand the term: a logical assumption based on the best objective consideration of all relevant known factors. Rather, this "assumption" was merely an excuse because these "scientists" were working for the fishing industry to do everything they could to keep catches high.

This was their best response to the question, "how can we come up with a recovery plan without reducing fishing?" Flimsy and transparent as this was, complicity by other scientific representatives caused both by intense U.S. congressional pressure and other nations' proclivities allowed the scientific committee and managers to claim that they had no basis for deciding which of the two models yielded more realistic results.

The U.S. Magnuson–Stevens Fisheries Conservation and Management Act (FCMA) mandates that within 1 year of a stock being listed as overfished, the Secretary of Commerce is legally obligated to prepare "a fishery management plan, plan amendment, or proposed regulations . . . to end overfishing . . . and to rebuild the affected stocks" to population levels capable of producing "maximum sustainable yield." The peculiar 1998 bluefin plan slashes the recovery goal in half, has a poor probability of reaching even the lowered goal, and raises the annual catch. Contrary to U.S. law, the "recovery plan" fails to project rebuilding as required and allows overfishing to continue. In fact, even if accepting the definition of overfishing derived from the 2-line model, the "recovery plan" allows a fishing mortality rate higher than the one calculated as the threshold that constitutes overfishing *for 15 years of the 20-year recovery period.* The "recovery plan" thus appears illegal (Audubon v. Daley, 1999).

In every substantial way, this was a United States-driven plan. The scientific results and report were driven by the industry's hired consultant on the U.S. scientific delegation, and the management position was driven or complied with by commissioners representing U.S. fishing interests. The United States introduced this plan and brokered its adoption. Japan was happy to avoid quota reductions (and initially suggested an even higher quota). Canada initially pressed for real rebuilding even though it would mean catch cuts, giving the United States another opportunity to do the right thing. Canada capitulated to the U.S. position only later in negotiations.

As a recovery plan it is at best a misnomer, because rather than claiming to recover the west Atlantic bluefin, it claims first that the fish cannot recover due to a regime shift, and then plans to "recover" them to a much lower target by increasing the quota. In practical terms, it's not possible. Even by its own calculation it allows a fishing mortality rate in excess of its overfishing threshold for 15 years out of the 20-year period. And quite simply, how can one expect recovery at the

same catch level that coincided with a major decline from a much larger population level over 2 decades?

VI. SUMMARY, CONCLUSION, AND EMERGING TRENDS

The status of tunas around the world is poorest in the Atlantic, better in the Pacific, and perhaps better still, though least known, in the Indian Ocean. Fishing pressure for Atlantic skipjack and yellowfin appears now to be at or above maximum sustainable levels. Albacore are overfished and fully exploited in the North and South Atlantic, respectively. Atlantic bigeye have rapidly declined.

Pacific skipjack are under low to moderate levels of exploitation; yellowfin stocks are under generally moderate exploitation pressure, though increasing effort directed at juvenile yellowfins and bigeye appears problematic. Albacore exploitation appears low. As in the Atlantic, Pacific bigeye populations have declined rapidly. Indian Ocean tuna fisheries and management and monitoring are all at earlier stages of development, but fishing is increasing. Bluefin tunas are everywhere depleted.

A striking aspect of this survey is that the sea is not so large, nor the human population so small, to exempt even extremely fecund and very widely distributed organisms such as skipjack and yellowfin tuna from concern about sustainability. Fishing pressure is now developed enough to drive long-term declines even on the scale of ocean basins. Just a few years ago it would have seemed highly unlikely that even Atlantic skipjack and Pacific bigeye would suffer declines that appear attributable to fishing.

Future recovery of depleted populations, and sustainable management of all, will require much better commitment and better scientific understanding than have been applied to tuna conservation and management until now. Scientific activity is increasing and new technologies promise large advances in biological understanding in the near future. The challenge is particularly clear for the central and western Pacific high seas and the Indian Ocean, where management regimes are emerging. We must help ensure that these management regimes will learn from and greatly improve upon, rather than repeat, the performance of ICCAT with regard to Atlantic tunas and CCSBT with regard to southern bluefin. Recent signs of increased responsibility and improved management by New Zealand, Australia, and central Pacific countries are encouraging. Implementation of the 1995 UN agreement on high seas and straddling stock fisheries would further help harmonize and improve performance standards for management, conservation, and recovery of tuna populations.

Where else might the future take us? Up to now, fishery management, when practiced, has been the near-exclusive domain of governmental agencies regulat-

ing catches by tonnage and season. One large exception was the consumer movement in the United States that brought its concern over dolphin deaths to the marketplace so forcefully that major tuna canners pledged that their products would henceforth be "dolphin safe." The consequent U.S. legislation prohibiting import of tuna netted under dolphins merely followed where the marketplace had already gone. New consumer education campaigns currently underway may widen the role of consumer choice in fishery management, and management may become increasingly company-driven rather than government-driven if it increasingly responds to consumer demand for more "environmentally responsible" tuna and other seafood products. A seafood specialty niche for ecofriendly seafood similar to the niche for organic vegetables may soon appear, prompted by organized consumer education efforts, and this will probably favor relatively abundant, low-bycatch sources. These market changes are likely to be first evident in the United States, where consumer interest, conservation organizations, and information availability are currently most developed.

Whether market forces will further affect tuna management remains to be seen, but swordfish present an illustrative case. A consumer boycott of Atlantic swordfish organized by the United States-based Natural Resources Defense Council and SeaWeb affected prices enough to gather crucial momentum toward a recovery plan for depleted swordfish in the Atlantic. Partly as a result of the visibility and pressure, ICCAT cut the catch quota significantly. The U.S. Atlantic swordfish/tuna longline industry then entered talks with environmental groups and recreational fishing interests to negotiate a government buyout and permanent retirement of a significant part of the fleet. Further, recent U.S. legislation (the Sustainable Fisheries Act of 1996) mandates that "essential fish habitat" be identified for all fish under management plans. Delineation of spawning, nursery, and migration routes (NMFS, 1998), together with the act's bycatch-minimization mandates, helped prompt several environmental groups to sue the U.S. government for failing to reduce bycatch of undersized swordfish. This led the U.S. National Marine Fisheries Service to propose a very extensive permanent longline closure in the U.S. Exclusive Economic Zone from just below Cape Hatteras to southern Florida, and a large part of the Gulf of Mexico (Department of Commerce, 1999). For all practical purposes, this is a proposed marine nursery reserve for swordfish. This would equally affect tuna longlining. This is probably the first extension of the marine reserve concept to pelagic fish species. The outcome of the proposals and the buyout discussion are uncertain at this writing.

These unfolding events point to trend changes in perceptions and changes in the way fisheries are viewed and valued. The other, countervailing trend is the simple continued expansion of the human population. The biggest question for the future is whether new values enlightened by recognition that the sea is finite will be outpaced by sheer increasing demand. The future remains unwritten.

ACKNOWLEDGMENTS

The comments of David Wilmot, Ellen Pikitch, and Josh Eagle; suggestions by Barbara Block and Don Stevens; and David Itano's thoughtful review of an earlier manuscript greatly improved this chapter.

REFERENCES

Aguilar, R., Mas, J., and Pastor, X. (1992). Impact of Spanish swordfish longline fisheries on the loggerhead sea turtle, *Caretta caretta,* population in the western Mediterranean. Presented at the 12th Annual Workshop on Sea Turtle Biology and Conservation, Feb. 25–29, Jekyll Island, GA.

Allen, R. (2001). The Inter-American Tropical Tuna Commission. *In* "Getting Ahead of the Curve: Conserving the Pacific Ocean's tunas, billfishes, and sharks." (Hinman, K., Ed.). National Coalition for Marine Conservation, Leesburg, VA.

Anonymous (1998a). "The Status of the Stocks: Are We Maintaining Sustainable Yields?" Oceanic Fisheries Program, South Pacific Commission, Nouméa, New Caledonia.

Anonymous (1998b). Report by the Chairman of the Standing Committee on Tuna and Billfish. Workshop on Precautionary Limit Reference Points for Highly Migratory Fish Stocks in the Western and Central Pacific Ocean. Report to the Third Multilateral High Level Consultation on the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean. South Pacific Commission, Nome, New Caledonia.

Audubon v. Daley (1999). National Audubon Society versus Daley et al. Case 1:99CV01707 RWR.

Bailey, K., Williams, P. G., and Itano, D. (1996). "By-catch and Discards in Western Pacific Tuna Fisheries: A Review of SPC Data Holdings and Literature." South Pacific Commission, Oceanic Fisheries Program Tech. Rep. 34. South Pacific Commission.

Baker, C. S., and Palumbi, S. R. (1994). Which whales are hunted? A molecular genetic approach to monitoring whaling. *Science* **265,** 1538–1539.

Berkeley, S. (2001). ICCAT: A case study from the Atlantic. *In* "Getting Ahead of the Curve: Conserving the Pacific Ocean's tunas, billfishes, and sharks." (Hinman, K., Ed.). National Coalition for Marine Conservation, Leesburg, VA.

Block, B. A., Dewar, H., Williams, T., Prince, E. D., Farwell, C., and Fudge, D. (1998a). Archival tagging of Atlantic bluefin tuna (*Thunnus thynnus*). *Mar. Technol. Soc. J.* **32,** 37–46.

Block, B. A., Dewar, H., Farwell, C., and Prince, E. D. (1998b). A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proc. Natl. Acad. Sci.* **95,** 9384–9389.

Bonfil, R. (1994). "Overview of World Elasmobranch Fisheries." FAO Fisheries Tech. Pap. 341. FAO, Rome.

Brill, R. W. (1994). A review of temperature and oxygen tolerance studies of tuna pertinent to fisheries oceanography, movement models and stock assessments. *Fish. Oceanogr.* **3,** 204–216.

Brothers, N. (1991). Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biol. Conserv.* **55,** 255–268.

Camhi, M. (1999). "Sharks on the Line II: An Analysis of Pacific State Shark Fisheries." National Audubon Society, Islip, NY.

Croxall, J. P, and Prince, P. A. (1996). Potential interactions between wandering albatrosses and longline fisheries for Patagonian toothfish at south Georgia. *CCAMLR Sci.* **3,** 101–110.

Croxall, J. P., Rothery, P., Pickering, S., and Prince, P. C. (1990). Reproductive performance, recruitment and survival of wandering albatrosses *Diomedia exulans* at Bird Island, South Georgia. *J. Anim. Ecol.* **59,** 775–796.

Department of Commerce (Dec. 15, 1999). Atlantic highly migratory species pelagic longline management: proposed rule. *Fed. Register* **64**(240), 69982–69987.

Earle, M., and McKay, B. (1997). Whither the albatross? *In* "Albatross Biology and Conservation" (Robertson, G., and Gales, R., Eds.). Surrey Beatty and Sons, Chipping Norton, NSW.

Edwards, M. (2001). Progress and problems: The operation of the convention for the conservation of southern bluefin tuna. *In* "Getting Ahead of the Curve: Conserving the Pacific Ocean's tunas, billfishes, and sharks" (Hinman, K., Ed.). National Coalition for Marine Conservation, Leesburg, VA.

Flint, E. N. (1995). Albatross populations and conservation issues in the Northern Hemisphere. *In* "Abstracts of the First International Conference on the Biology and Conservation of Albatrosses," p. 9. CSIRO, Hobart, Tasmania.

Gales, R. (1993). "Cooperative Mechanisms for the Conservation of Albatrosses." Australian Nature Conservation Agency, Hobart, Tasmania.

Garcia, S. M. (1994). "World Review of Highly Migratory Species and Straddling Stocks." FAO Fisheries Tech. Pap. 337. FAO, Rome

Gosliner, M. L. (1999). The tuna-dolphin controversy. *In* "Conservation and Management of Marine Mammals" (Twiss, J. R., Jr., and Reeves, R. R., Eds.). Smithsonian Institution Press, Washington, DC.

Hall, M. A. (1998). An ecological view of the tuna-dolphin problem: Impacts and trade-offs. *In* "Reviews in Fish Biology and Fisheries," Vol. 8, pp. 1–34.

Hampton, J., Lewis, A., and Williams, P. (1999). "The Western and Central Pacific Tuna Fishery: Overview of the fishery and Current Status of Tuna Stocks." Secretariat of the Pacific Community, Oceanic Fisheries Programme.

Hayes, E. A. (1997). "A Review of the Southern Bluefin Tuna Fishery." TRAFFIC Oceanea, Sydney.

Hoey, J. (1995). Bycatch in the western Atlantic pelagic longline fisheries. *In* "Solving Bycatch Considerations for Today and Tomorrow." Univ. of Alaska Sea Grant College Program 96-03.

IATTC (1997). Assessment studies of bigeye tuna in the eastern Pacific Ocean. Background Paper 5, 58th Meeting of the IATTC, 3–5 June, 1997. IATTC, La Jolla, CA.

IATTC (1999a). Assessment of bluefin tuna in the eastern Pacific Ocean. Background Paper 8, 63rd Meeting of the IATTC, 8–10 June, 1999. IATTC, La Jolla, CA.

IATTC (1999b). Assessment of yellowfin tuna in the eastern Pacific Ocean. Background Paper 2, 63rd Meeting of the IATTC, 8–10 June, 1999. IATTC, La Jolla, CA.

IATTC (1999c). Assessment of bigeye tuna in the eastern Pacific Ocean. Background Paper 5, 63rd Meeting of the IATTC, 8–10 June, 1999. IATTC, La Jolla, CA.

ICCAT (1998). "Report of the Standing Committee on Research and Statistics (SCRS)." ICCAT, Madrid.

IOTC (2001). Indian Ocean Tuna Commission [on-line]. Available [May 3, 2001] on-line: www.seychelles.net/iotc.

Itano, D. G. (1998). Notes on the improvement of fishing power and efficiency in the western tropical Pacific tuna purse seine fishery. Working paper presented to Eleventh Meeting of the Standing Committee on Tuna and Billfish, Honolulu.

Lewis, A. D. (2001). The South Pacific Commission. *In* "Getting Ahead of the Curve: Conserving the Pacific Ocean's tunas, billfishes, and sharks" (Hinman, K., Ed.). National Coalition for Marine Conservation, Leesburg, VA.

Mace, P. M. (1997). The status of ICCAT species relative to optimum yield and overfishing criteria recently proposed in the United States, also with consideration of the precautionary approach. ICCAT working document SCRS/97/74. ICCAT, Madrid.

Mather, F. (1974). The bluefin tuna situation. *In* "Sixteenth Annual International Game Fish Research Conference," pp. 93–106. Woods Hole Oceanographic Institution contribution 3304. Woods Hole Oceanographic Institution. Woods Hole, MA.

Miyabe, N., and Takeuchi, Y. (1998). Exploring VPA analysis on Pacific bigeye tuna. Working paper

presented to Eleventh Meeting of the Standing Committee on Tuna and Billfish, Honolulu. Available from Western Pacific Regional Fisheries Management Council, Honolulu, HI, www.wpcouncil.org.

Morishita, J. (2001). The interim scientific committee for tuna and tuna-like species in the North Pacific Ocean. *In* "Getting Ahead of the Curve: Conserving the Pacific Ocean's tunas, billfishes, and sharks." (Hinman, K., Ed.). National Coalition for Marine Conservation, Leesburg, VA.

Myers, R. A., and Barrowman, N. J. (1996). Is fish recruitment related to spawner abundance? *Fish. Bull.* **94,** 707–724.

Nemerson, D., Berkeley, S., and Safina, C. (2000). Determining spawning site fidelity in Atlantic bluefin tuna *Thunnus thynnus:* The use of size-frequency analysis to test for the presence of migrant east Atlantic bluefin tuna on Gulf of Mexico spawning grounds. *Fish. Bull.* **98,** 118–126.

NMFS (1997). Memorandum on Section 7 Consultation on the Atlantic Pelagic Fishery, May 29, 1997. NMFS/NOAA, Silver Spring, MD.

NMFS (1998). "Highly Migratory Species Essential Fish Habitat (EFH)." National Marine Fisheries Service, Silver Spring, MD.

NMFS (Dec. 22, 1999). Draft supplemental environmental impact statement: Regulatory amendment to the Atlantic tunas, swordfish, and sharks fishery management plan. Reduction of bycatch and incidental catch in the Atlantic pelagic longline fishery. NMFS, Silver Spring, MD.

NMFS/SWFSC (1996). "Draft Marine Mammal Stock Assessment for the Pacific Region," pp. 89–91. NMFS, Silver Spring, MD.

NMFS/SWFSC (1997). "Annual Report under the Biological Opinion of June 25, 1994, Concerning the Take of Sea Turtles in the Hawaii Longline Fishery." NMFS, Silver Spring, MD.

NOAA (1994). Formal Section 7 Consultation on the fishery management plan for the pelagic fisheries of the western Pacific region: Long-term operation of the Hawaii central North Pacific longline fishery. NMFS memorandum from Rolland Schmitten, Assistant Administrator for Fisheries. NOAA, Washington, DC.

Noss, R. F. (1993). Whither conservation biology? *Conserv. Biol.* **7,** 215–217.

NRC (1994). "An Assessment of Atlantic Bluefin Tuna." NRC, National Academy Press, Washington, DC.

Ornithological Council (1997). Catching seabirds instead of fish: The effects of longline fishing on seabirds. *In* "Bird Issue Briefs," Vol. 1, no. 4. Ornithological Council, Washington, DC.

PFRP (1998). "Bigeye Tuna: Five-Year Research Plan. A Prospectus for Coordinated International Research." Pelagic Fisheries Research Program, Joint Institute for Marine and Atmospheric Research, University of Hawaii, Honolulu.

Raymakers, C., and Lynham, J. (1999). "Slipping the Net: Spain's Compliance with ICCAT Recommendations for Swordfish and Bluefin Tuna." TRAFFIC International, Cambridge.

Safina, C. (1993). Bluefin tuna in the west Atlantic: Negligent management, and the making of an endangered species. *Conserv. Biol.* **7,** 229–234.

Safina, C. (1997). "Song for the Blue Ocean." Holt, New York.

Sissenwine, M. P., Mace, P. M., Powers, J., and Scott, G. (1998). A commentary on western Atlantic bluefin tuna assessments. *Trans. Am. Fish. Soc.* **127,** 838–855.

United Nations (2001a). ITLOS Procedures and Cases [on-line]. Available [May 3, 2001] on-line: http://www.un.org./depts/los/ITLOS/ITLOSproc.htm#verbatim.

United Nations (2001b). Oceans and Law of the Sea Home Page [on-line]. Available [May 3, 2001] on-line: http://www.un.org./depts/los.

Weimerskirch, H., and Jouventin, P. (1987). Population dynamics of the wandering albatrosses *Diomedea exulans,* of the Crozet Islands: Causes and consequences of the population decline. *Oikos* **49,** 315–322.

Weimerskirch, H., Brothers, N., and Jouventin, P. (1997). Population dynamics of wandering albatross *Diomedia exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with longline fisheries: Conservation implications. *Biol. Conserv.* **79,** 257–270.

Index

A

abundance
  aerial survey, 174
  behavior and, 345
  catch per unit indexes, 218
  coordinated estimates of, 376–80,
  limited by oxygen and temperature, 158
  status and trends in, 423–35
acoustic tags, 167, 169–178, 200, 215–217, 378–380
adrenaline
  effect on heart and blood pressure, 97, 157
  effect on heat exchangers, 127
  interaction with calcium, 101
aggregation, size, 380
allometry see scaling
allozymes, 21, 27
applied science, 345, 384
aspect ratio of caudal fin, 275–6, 299, 302, 307, 317
archival tags, 58, 167, 178–202, 397, 406
Atlantic Tuna Commission, 192, 417–8, 443–53
atresia, 233, 243, 259–60
atropine, 90, 96, 110
autonomic nervous system, 97, 107, 157
axial muscle, 271, 277, 322

B

backbone, 271, 280–4, 300–5, 323, 336
basking, 187, 195, 202
behavior
  diving
    albacore, 373
    Atlantic bluefin, 192–196, 208
    bigeye, 173, 200, 372
    Pacific bluefin, 175, 407–409
    spike diving, 183
    southern bluefin, 186–192
    yellowfin, 172, 372
  feeding
    albacore, 328
    Atlantic bluefin, 195
    bigeye, 372
    effect of tagging on, 185
    metabolic cost, 65
    southern bluefin, 185, 188–189
    versus migration or traveling, 382, 384
    yellowfin, 372
  schooling, 174, 352, 380–1
biomechanics, 271–2, 289, 291, 301, 304, 307
blood
  oxygen, 52, 86, 90–91, 112
  pressure, 79, 82, 85–87, 91, 94, 98, 106–108
  viscosity, 79, 91, 92
  volume, 82
body shape, 141, 144, 271, 274
bonito, 1, 9–11, 39–41, 54, 59, 66, 140, 275, 282, 402–403
bradycardia, 45, 93, 94, 110
brain heater, 5, 12, 16, 130–137
breeding, see spawning
buffer capacity, 57
bulbus arteriosus, 79, 105–108
bycatch, 362, 366, 413, 430, 435–9

C

calcium, 98, 100
cannery, 352, 359, 362, 364

capillaries, 52–55, 85–87
captive tuna
  collection, 400
  display, 399–400
  farmed, 36, 236, 391, 392–394, 403
  feeding, 394, 403
  research, 394–9
  transporting, 393, 395, 402
cardiac output, 52, 84–86, 98
  contribution to high oxygen uptake 89–91, 94, 97
  during hypoxia, 45
  effect of exercise, 111
  effect of temperature 94, 110, 155–156
  magnitude of 82,
  sarcoplasmic reticulum, 103
cardiovascular system, 51, 79, 80, 82, 86, 106, 121, 155
Carey, 137
caudal fin
  kinematics, 333
  mechanical design, 271, 275–6, 317
  muscles and tendons 294–302, 338
  tendon as a spring 313, 335
CITES, 418, 443, 446–448
cladistics, 10, 18
classification, 1
  molecular, 18
  morphological, 1, 5, 18–19, 23, 26–29, 72, 139, 225
climate of the ocean, 345, 356, 367–71
collagen
  tendon, 271, 335
  myosepta, 277–278, 283, 287
  vertebrae, 304, 306
conservation, 413, 440
cooling rate, 145, 147, 156, 159
coronary artery, 93–94, 104
corselet, 11, 13–15, 316
counter current, see retia
courtship, 242, 243, 245, 256, 399
cytochrome, 19–20, 23–24, 27

D

Davy, 134, 136–137
deep scattering layer see, scattering layer
digestion
  temperature, 134, 142, 149, 173, 189
  evolution of endothermy, 69–70
  metabolic cost, 60–63
distribution, see zoogeography
diving
  albacore, 373
  Atlantic bluefin, 192–196, 208
  bigeye, 173, 200, 372
  Pacific bluefin, 175, 407–409
  spike diving, 183
  southern bluefin, 186–192
  yellowfin, 172, 372
dogtooth tuna, 11
dolphin
  "dolphin-safe" tuna, 419–420, 456
  evolution of tuna-dolphin association, 367
  purse seine, 362–363, 436–437
drag
  caudal fin, 302
  calculation of, 68, 274
  structures affecting, 315–317
  swimming efficiency, 45, 67

E

Excitation–contraction coupling, 79, 101–102, 156
ECOTAP, 346, 376
efficiency
  gas transfer, 82
  heat-exchanger, 127, 130, 132, 140, 147
  muscle power output, 277
  swimming at high speeds, 45, 315–318, 321
  swimming at moderate speeds, 47, 67–68, 325, 332
  tendon contribution to, 335
El Nino, 201, 240, 357
electromyograms, 330–3
endangered species
  bycatch
    albatross 438, 442
    seals, 438
    turtles, 437
  CITES, 418, 443, 446–448
  IUCN red list, 168
endothermy, 121, 326
  history, 134
  ontogeny, 152–153
energetics
  metabolic costs, 35, 37, 60–69, 140
  reproductive, 62, 225, 255–261, 372

ENSO warm/cold event, 356
enzyme
  aldolase, 27
  carnitine-palmitoyl transferase, 103
  citrate synthase, 54–58, 103, 148, 154
  HOAD, 103
  lactate dehydrogenase, 19, 54–57
  Na,K,ATPase, 66
Eschricht, 136
evolution
  caudal muscles, 299
  endothermy, 70–72, 121–123, 149–152
  locomotor morphology, 272–273, 283, 307
  Scombrid, 28–29
exploitation, 168, 192, 351–354, 384, 414–415, 426, 430, 456

F

FAD, see fish aggregating device
fat, 5, 155, 367, 375
fatty acids, 103–104
fecundity, 225, 250–253, 413–415, 425
feeding
  albacore, 328
  Atlantic bluefin, 195
  bigeye, 372
  effect of tagging on, 185
  metabolic cost, 65
  southern bluefin, 185, 188–189
  versus migration or traveling, 382, 384
  yellowfin, 372
fertilization, 225
fineness ratio, 275
finlets, 11, 299, 315–316
fish aggregating device, 171, 172, 173, 216, 362, 376, 378–380, 433
fisheries, 348–53
  atlas, 353
  baitboats, 359–61
  catch statistics, 358, 419, 421, 427–35, 442
  dolphin, fishing on, 362–363, 367, 420, 436
  longline, 350, 364–7, 437
  old-world, 371
  overfishing, 355, 365, 414, 424, 439, 449
  purse seines, 361–364, 436
  traditional, 371
  traps, 391–3, 417
frigate tuna, 13, 55, 416
functional morphology, 271–272, 274–275, 289, 291, 301

G

Gasterochisma, 1, 5, 17, 19, 21
geoposition, 179–181, 200, 205, 217
gill rakers, 5, 7–9, 12–17
gills
  heat loss at 130
  hypoxia, 45
  oxygen utilization, 38, 52, 82
  structure, 52, 66, 84, 89
glycogen, 56–57, 62–63, 65
gonad, development, 226
granulosa, 228–230
growth rate, 254, 257–258, 369, 406

H

habitat, 345
  fisheries, 372–377
  habitat preference, 193–198
  inhabit mixed layer, 171
  selection for endothermy, 152
  spawning distribution 237, 239–240
habits, 372–76
heart, 52, 82, 92, 93, 98, 103, 125
heart rate, 82, 88, 95, 97, 156
heat exchanger see retia
heat production, 126–127, 130–134, 141
hemal spine, 301–305
hematocrit, 64, 79, 82, 84, 90–92
hemoglobin, 79, 82, 84, 89, 157, 373
history,
  Greeks, 391
  endothermy studies, 121, 134–141
  metabolic studies, 35, 37–39
Phoenicians, 391
Romans, 391
tuna fisheries, 348–51, 358, 358
homoplasy, 1, 19, 21, 23, 25
hydrodynamics, 67, 81, 276, 313, 317–22
hypoxia
  blood oxygen content, 90
  coronary circulation, 93–94
  distribution of tuna, 349, 352
  heart rate, 110, 157

hypoxia (*continued*)
metabolic rate, 35, 44–45
myoglobin, 104
hypural plate, 5, 10, 139, 295, 300, 302, 307

I

ICCAT, see Atlantic Tuna Commission, 192
Indian Ocean Tuna Commission, 418
Inter-American Tropical Tuna Commission, 419

K

keel, caudal
hydrodynamics, 315–316
morphometric differences, 5, 8, 10–12, 14, 26, 307
structure, 284
kinematics, 272, 274, 313, 317–322, 338
Kishinouye, 136, 157, 283

L

lactate
blood, 103
muscle, 57, 62–63, 88, 104, 149
larval surveys, 236, 348
little tuna or little tunny, 399
locomotion
carangiform, 273
costs, 35, 47–52, 68, 147, 336
mode, 138, 150
swim speed, 91, 125, 139, 314
thunniform, 29, 45, 125, 150, 273, 307, 314, 317, 325, 337
undulatory, 273

M

Majuro Declaration, 422
Maldivian culture, 341
management, see also stock assessment, 440
maturation, sexual, 225, 232–236, 369, 372
meristic characters, 8, 11
metabolic scope, 39, 42, 60, 62–63, 65, 69
migration
annual, 200–201
Atlantic bluefin, 195, 211
oceanic, 124
seasonal, 198
southern bluefin, 189–191
telemetry to estimate local, 179–182, 184, 207
mitochondria density, 54–55, 104
mitochondrial DNA, 3, 18, 19, 21, 26–27
molecular genetics, 6, 18
morphology
caudal fin, 271, 294–302
muscle, 271, 277–302
tendon, 271, 277–302
vertebral, 271, 302–6
muscle
caudal, 295–301
fast white, 35
citrate synthase, 54
force, 293
function, 329, 340
general properties, 52–54, 323
metabolic rate, 36, 38, 56–59, 69
myoglobin, 53
recovery after burst exercise, 62–63, 88
shark, 67
temperature, 58
force, 293, 334–335
power, 148, 326–328
slow red, 10, 12, 43, 52–56, 125
action, 288–94, 305, 329, 336–8
morphology, 271, 280–2, 323–5
metabolism, 35
temperature, 59, 109, 123, 131, 143, 152, 173
muscular hydrostat, 271, 287–288, 290–294, 306
myocardium, 93–94, 98–101, 104
myoglobin, 53–54, 104, 124
myomere, 271, 277–280, 287, 290
myosepta, 271, 278, 283–7
myotomes, 138, 150, 153, 315, 322, 330–336, 339

N

niche, 149, 150, 374, 382

O

ocean monitoring, 355
oceanography, fisheries, 345, 348–351, 384
ontogeny, endothermy, 121, 153–153
oocyte, 225, 227–230, 250–253
otolith development, 6, 257
oxygen debt, 35, 38, 62–63
oxygen uptake
  history, 37
  maximal, 42, 45, 46, 47, 81, 89, 90
  routine, 41, 81
  standard, 40, 41, 81, 82

P

phylogeny, 1, 19–27, 151, 273, 283
pineal window, 7, 12
pop-up satellite tags, 167, 202–213, 215–217
postcardinal vein, 12, 16, 17, 133, 135, 147
primary production, 346

Q

Q_{10}
  cardiac output, 84, 109
  metabolic enzyme activity, 148
  muscle power output, 328
  tissue metabolism, 38
  whole animal metabolism, 44

R

ram ventilation, 40, 45, 51, 79, 81, 123
range, Rastrelliger, 7
range, Scomber, 6
range, Scomberomorus, 8
recruitment
  by species, 426–436
  El Nino role, 240
  life span effect on, 355
  miscalculation for Atlantic bluefin, 451–454
  southern bluefin's erratic, 348
  trade-offs, 382–383
reproductive strategy, 376
retia, 121, 129–134, 141, 147
  brain, 5, 12, 16, 123, 131, 133–134
  muscle, 12, 16, 53, 126–127, 130–137
  ontogeny, 152
  viscera, 61, 134
ryanodine, 98–101

S

sarcoplasmic reticulum, 79, 98, 111
scales, 5, 7, 11, 13–15
scaling and size effects
  cost of transport, 47
  gill area, 44
  maturity, 254
  metabolic rate, 35
  muscle mechanics and tail-beat frequency, 339
  red muscle heat production, 153
  red muscle mass, 125
  sexual dimorphism in size, 226
  standard metabolic rate, 43–44
scattering layer
  Atlantic bluefin, 196–197
  bigeye, 108, 172,
  invertebrates, 350
  southern bluefin, 191–192
  yellowfin, 372
SDA, see specific dynamic action
seasonal effects
  Atlantic bluefin, 198, 210,
  migration, 124, 346–352
  spawning, 236–237, 250–251
septum, horizontal, 271, 277–290
septum, vertical, 271, 302–306
Sertoli cells, 230
sex ratios, 225, 253–255
sexual dimorphism, 225, 253
sexual maturation, 225, 232–236, 253, 258
sonomicrometry, 333, 337
Southern Bluefin Commission, 413, 418
Spanish mackerel, 1, 5, 7, 9, 26, 148, 274
spawning, 225–227, 348, 449
  behavior, 225, 242–245
  costs, see also energetics, 62, 225, 255–261, 372
  frequency, 225, 245–250
  North Atlantic Subtropical region, 346–348
  spatiotemporal patterns, 225, 236–242
    Atlantic bluefin, 192, 198–201, 211–213
    southern bluefin, 181
specific dynamic action, 35, 60–61, 64, 406

spermatogenesis, 225, 230–232
spike dives, 183
standard metabolic rate, 35, 40–41, 63, 81–82
Starling curve, 94–96, 110–111
stock assessment
  Atlantic bluefin, 192, 444–450
  bigeye, 380
  contribution of fishing vessels to, 355
  tagging, 168
  uncertainties, 415
  yellowfin, 426
stomach, temperature
  Atlantic bluefin, 137, 173, 197
  captive tuna, 407
  digestive enzyme activity, 61
  feeding, 149
  shark, 137
  southern bluefin, 183, 186–191
stride length, 51, 272, 318
stroke volume, 79, 82, 93–97
  bulbous arteriosus, 105
  cardiac output contribution to, 84, 88–90, 111, 155–156
  hypoxia, 110
  muscle fiber morphology, 93
swim bladder, 6–16, 126, 314
swimming, see locomotion
sympatric, 6
system science, 378
systematics, 1, 5, 18, 136–168

T

tagging
  acoustic, 167, 169–178, 200, 215–217, 378–380
  archival, 58, 167, 178–202, 397, 406
  conventional, 178, 182, 192, 201–202, 231, 218, 369
  limitations, 167, 179–180, 201, 213–218, 369–370, 369–370, 374
  number deployed, 209, 214
  pop-up satellite, 167, 202–213, 215–217
  recovery rate, 202, 209–210, 214
tailbeat frequency, 216, 272, 317–319, 322, 326–329, 339
temperature
  gut
    Atlantic bluefin, 137, 173, 197
    captive tuna, 407
    digestive enzyme activity, 61
    feeding, 149
    shark, 137
    southern bluefin, 183, 186–191
  muscle, 59, 109, 123, 131, 143, 152, 173
tendon, 271, 282, 294, 334
  axial, 271, 282–287
  caudal, 271, 294–302, 307, 313, 334–336
testes, 225, 230–232, 249, 253–254
theca, 228–230
thermal inertia, 141, 144, 155
thermoregulation, 121, 141, 144, 155, 159, 197
transitions, 21, 24
transversions, 24
traps, see fisheries

U

ultrasonic, see tagging

V

ventilation, 45, 52, 65, 82, 84–85, 123
vertebrae, number, 5–14
vertebrae, structure, 12–14, 26, 271, 280, 300–305
vertical distribution, 108, 138, 173, 178, 350
visceral, temperature,
  Atlantic bluefin, 137, 173, 197
  captive tuna, 407
  digestive enzyme activity, 61
  feeding, 149
  shark, 137
  southern bluefin, 183, 186–191
vitellogenesis, 225, 229–230, 232
vulnerability, 255, 350–351, 357, 376, 439

Y

yolk, 227–229, 233, 256

Z

zoogeography, 108, 345, 376

OTHER VOLUMES IN THE FISH PHYSIOLOGY SERIES

VOLUME 1	Excretion, Ionic Regulation, and Metabolism *Edited by W. S. Hoar and D. J. Randall*
VOLUME 2	The Endocrine System *Edited by W. S. Hoar and D. J. Randall*
VOLUME 3	Reproduction and Growth: Bioluminescence, Pigments, and Poisons *Edited by W. S. Hoar and D. J. Randall*
VOLUME 4	The Nervous System, Circulation, and Respiration *Edited by W. S. Hoar and D. J. Randall*
VOLUME 5	Sensory Systems and Electric Organs *Edited by W S. Hoar and D. J. Randall*
VOLUME 6	Environmental Relations and Behavior *Edited by W. S. Hoar and D. J. Randall*
VOLUME 7	Locomotion *Edited by W S. Hoar and D. J. Randall*
VOLUME 8	Bioenergetics and Growth *Edited by W. S. Hoar, D. J. Randall, and J. R. Brett*
VOLUME 9A	Reproduction: Endocrine Tissues and Hormones *Edited by W S. Hoar, D. J. Randall, and E. M. Donaldson*
VOLUME 9B	Reproduction: Behavior and Fertility Control *Edited by W. S. Hoar, D. J. Randall, and E. M. Donaldson*
VOLUME 10A	Gills: Anatomy, Gas Transfer, and Acid-Base Regulation *Edited by W. S. Hoar and D. J. Randall*
VOLUME 10B	Gills: Ion and Water Transfer *Edited by W. S. Hoar and D. J. Randall*
VOLUME 11A	The Physiology of Developing Fish: Eggs and Larvae *Edited by W. S. Hoar and D. J. Randall*

VOLUME 11B The Physiology of Developing Fish: Viviparity and Posthatching Juveniles
Edited by W. S. Hoar and D. J. Randall

VOLUME 12A The Cardiovascular System
Edited by W. S. Hoar, D. J. Randall, and A. P. Farrell

VOLUME 12B The Cardiovascular System
Edited by W S. Hoar, D. J. Randall, and A. P. Farrell

VOLUME 13 Molecular Endocrinology of Fish
Edited by N. M. Sherwood arid C. L. Hew

VOLUME 14 Cellular and Molecular Approaches to Fish Ionic Regulation
Edited by Chris M. Wood and Trevor J. Shuttleworth

VOLUME 15 The Fish Immune System: Organism, Pathogen, and Environment
Edited by George Iwama and Teruyuki Nakanishi

VOLUME 16 Deep Sea Fishes
Edited by D. J. Randall and A. P. Farrell

VOLUME 17 Fish Respiration
Edited by Steve F. Perry and Bruce Tufts

VOLUME 18 Muscle Growth and Development
Edited by Ian A. Johnson

VOLUME 19 Tuna: Physiology, Ecology, and Evolution
Edited by Barbara A. Block and E. Donald Stevens

VOLUME 20 Nitrogen Excretion
Edited by Patricia A. Wright and Paul M. Anderson

Copyrighted Material

TUNA

PHYSIOLOGY, ECOLOGY, AND EVOLUTION

Volume 19 in the FISH PHYSIOLOGY Series
Series Editors: William S. Hoar, David J. Randall, and Anthony P. Farrell

EDITED BY

BARBARA A. BLOCK
Hopkins Marine Station, Stanford University, Monterey, California

E. DONALD STEVENS
University of Guelph, Ontario

Tuna are biologically fascinating, with many specializations such as endothermy (warm-bloodedness), aerobic capacity, and migratory abilities. The primary focus of this book is the physiology of tuna with respect to biomechanics, thermoregulation, and morphology. An evolutionary and phylogenetic backdrop illustrates the importance of comparative perspectives. Because of the economic importance of tuna, a secondary focus of the book is tuna aquaculture and conservation.

RELATED TITLES

Randall/Farrell – **Deep Sea Fishes** (1997, ISBN: 0-12-350440-6)
Iwama/Nakanishi – **The Fish Immune System** (1997, ISBN: 0-12-350439-2)
Eastman – **Antarctic Fish Biology** (1993, ISBN: 0-12-228140-3)
Perry/Tufts – **Fish Respiration** (1998, ISBN: 0-12-350441-4)
Johnston – **Muscle Development and Growth** (1999, ISBN: 0-12-350442-2)

ACADEMIC PRESS
A Harcourt Science and Technology Company
San Diego San Francisco New York
Boston London Sydney Tokyo

Printed in the United States of America

Copyrighted Material