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REVIEW

Selective Advantages Conferred by the High Performance Physiology of Tunas, Billfishes, and Dolphin Fish

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ABSTRACT. Tunas are extensively distributed throughout world's oceans and grow and reproduce fast enough to support one of the world's largest commercial fisheries. Yet they are apex predators living in the energy depauperate pelagic environment. It is often presumed that tunas evolved their specialized anatomy, physiology, and biochemistry to be capable of (a) high maximum swimming speeds, (b) high sustained swimming speeds, and/or (c) very efficient swimming, all of which help account for their wide distribution and reproductive success. However, a growing body of data on the energetics and physiological abilities of tunas do not support these assumptions. The three things demonstratively "high performance" about tunas, and probably other pelagic species such as marlin (*Makaira* spp. and *Tetrapturus* spp.) and dolphin fish (*Coryphaena* spp.), are (a) rates of somatic and gonadal growth, (b) rates of digestion, (c) rates of recovery from exhaustive exercise (i.e., clearance of muscle lactate and the concomitant acid load). All of these are energy consuming processes requiring rates of oxygen and substrate delivery above those needed by the swimming muscles for sustained propulsion and for other routine metabolic activities. I hypothesize that the ability of high performance pelagic species (tunas, billfishes, and dolphin fish) to deliver oxygen and metabolic substrates to the tissues at high rates evolved to permit rapid somatic and gonadal growth, rapid digestion, and rapid recovery from exhaustive exercise (abilities central to success in the pelagic environment), not exceptionally high sustained swimming speeds. COMP BIOCHEM PHYSIOL 113A;1:3–15, 1996.

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INTRODUCTION

Tunas (family Scombridae, subfamily Scombrinae, tribe Thunnini) (77) are distributed in the world's oceans from ≈40°N to ≈40°S, and from the surface down to ≈400 m (71,108,113). Tunas therefore occupy (in terms of volume) one of the largest habitats on the planet. Tunas also support one of the world's largest commercial fisheries landing roughly 2–3 × 10⁹ kg annually (71). Tunas have reproductive and growth rates capable of sustaining this level of fisheries mortality (plus high natural mortality) (89) even though they are top level carnivores living in an energy depauperate environment where patches of forage are widely scattered (8,109). If evolutionary success is defined as equal to reproductive success (i.e., the ability to grow and reproduce), tunas must be considered an extremely successful group. Two questions that have guided my research for a number of years are (a) "What anatomical,

physiological, and biochemical abilities permit this extreme evolutionary success?" and (b) "How do the physiological abilities of tunas (and other high performance pelagic species) act and interact to limit their movements, oceanographic distribution and vulnerability to specific fishing gears?" It is the purpose of this paper briefly to review what I have learned so far and suggest directions for future research.[1]

Tunas appear to be highly streamlined. Their bodies are fusiform (i.e., elongated egg shaped), which presumably minimizes both form and friction drag (42,82,122). Their paired fins fold flat against the body surface, and the first dorsal fin can be completely retracted into a slot (122). The surface of

[1]To keep this review a reasonable length, "the tunas" are treated as a relatively homogeneous group of species, although clearly they are not. Differences appear especially pronounced between the tropical (e.g., skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*) and the temperate species (e.g., bluefin tunas, *Thunnus thynnus* and *T. maccoyi*) (52,72). Most of the data presented are from skipjack and yellowfin tunas simply because they are the most studied. I have also purposefully excluded an extensive discussion of the advantages conferred by the body and cranial endothermy of tunas and billfishes because this topic has been comprehensively reviewed by Block (9) and Block and Finnerty (10).

the eyes, although large, are flush against the sides of the head. Their caudal peduncle is narrow with axe blade-like keels on either side, an adaptation that presumably minimizes resistance to lateral movement and disturbance to the water stream flowing over the tail (122). Tunas have stiff, large semi-lunate (i.e., high aspect ratio) tails which produce high thrust at minimum drag (82). Tunas also possess a series of finlets behind their second dorsal and anal fins. Although their exact function is not known, the finlets may act as flow fences which direct water flow over the tail and reduce form drag by preventing boundary layer separation (122,82).

Tunas have lost the ability to pump water over their gills by opercular and buccal movements and are, therefore, obligate ram ventilators (103). This also may reduce hydrodynamic drag and lessen the energetic costs of ventilation (122,110). Tunas have internalized the red muscle fiber portions of their myotomes (i.e., those fibers used for sustained swimming) and possess vascular counter-current heat exchangers to maintain red muscle fiber temperatures significantly above ambient (37,34,52). Tunas' red muscle fibers contain elevated myoglobin levels (27). Elevated temperature and high myoglobin levels increase the rate of oxygen diffusion from the capillaries to the mitochondria (111). Internal placement may also enhance the mechanical performance of the red muscle fibers (9,10). Tunas have gill surface areas approximately an order of magnitude larger, and gill thickness approximately an order of magnitude less, than other active teleosts such as rainbow trout (62,63,64). They also have ventricle masses and cardiac outputs roughly four to five times larger than those of other active fishes (19,32). Billfishes (family Istiophoridae) and dolphin fishes (family Coryphaenidae), although much less studied, also appear to be high performance pelagic species and share anatomical and physiological characteristics with the tunas (122,94,90,40). There are, however, significant differences in muscle anatomy, biochemistry, and swimming modes between tunas and billfishes (10,44).

Based primarily on the anatomy of tunas, three characteristics would seem obvious. Tunas (and perhaps also billfishes and dolphin fishes) should be capable of:

1. exceptionally high maximum swimming speeds,
2. exceptionally high sustained (i.e., cruising) speeds,
3. very efficient swimming.

Indeed, much has been written about the unique abilities and exceptional swimming performance of tunas and other large pelagic fishes (e.g., 122,34,52,82,111,9,10,41,42).

Research on live subadult skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas in held in captivity (conducted mostly at the National Marine Fisheries Service's Kewalo Research Facility, Honolulu, HI, USA), however, casts doubt on the first two conclusions and shows the third may be valid only under a very specific definition of the term "efficiency." In this review I will briefly discuss the evidence that

is counter to the above hypotheses, then describe the aspects of tuna, billfish, and dolphin fish biology which I consider to be clearly "high performance" and truly unique among the teleosts. Mention should be made however that, because of their extremely large size, the physiology of adult tunas (and billfishes) is almost unstudied. It is possible that many of the conclusions I draw here may not hold for adult fishes. The recently constructed Tuna Research and Conservation Center (a joint project of Stanford University's Hopkins Marine Laboratory and the Monterey Bay Aquarium), with its ability to hold adult tunas, and the advanced ultrasonic telemetry techniques being developed at the Monterey Bay Aquarium Research Institute to study tunas and other large pelagic fishes in the open ocean, may eventually remedy this situation.

DISCUSSION
Maximum Swimming Speeds

Maximum swimming speeds are limited by the duration of the contraction-relaxation cycles of the swimming muscles. In other words, fish can complete a tail beat cycle no faster than the muscles on opposite sides of the body can contract and relax. Maximum tail beat frequencies (F_t) can be calculated from the time required to reach maximum contraction (T_{max}) measured in isolated muscle blocks (124).

$$F_t = 1 \cdot (2 \cdot T_{max})^{-1} \tag{1}$$

Maximum swimming speed (U_{max}) can, in turn, be estimated from maximum tail beat frequencies and stride lengths (SL; i.e., the distance moved per tail beat cycle usually expressed as fractions of a body length) (124)

$$U_{max} = SL \cdot (2 \cdot T_{max})^{-1}. \tag{2}$$

As shown in Fig. 1 (upper panel), isolated white muscle blocks from skipjack tuna (*Katsuwonus pelamis*) are not capable of exceptionally high rates of contraction when compared to other equal sized teleosts and corrected for differences in measurement temperatures (21). Skipjack tuna are capable of maximum tail beat frequencies higher than those of the other species only because their muscles operate at higher temperatures (i.e., skipjack tuna usually occupy the surface waters of warm tropical oceans). Tuna stride lengths are ≈0.7–0.8 body lengths per tail beat (132,82,22,104,42), which match those of many other fishes (121). Predicted maximum burst speeds of skipjack tuna (Fig. 1, lower panel), therefore, are not exceptional if compared to other active teleosts at similar body sizes and muscle temperatures (21,121).

Wardle and Videler (127) have shown that it is hypothetically possible for tunas to reach exceptionally high maximum burst speeds by doubling their stride lengths. However, there are yet no data showing that tunas do indeed have this ability. The maximum speeds of yellowfin tuna claimed by Walters and Fierstine (123) require unrealistically high muscle contraction speeds (128) and/or stride lengths (121). Others have
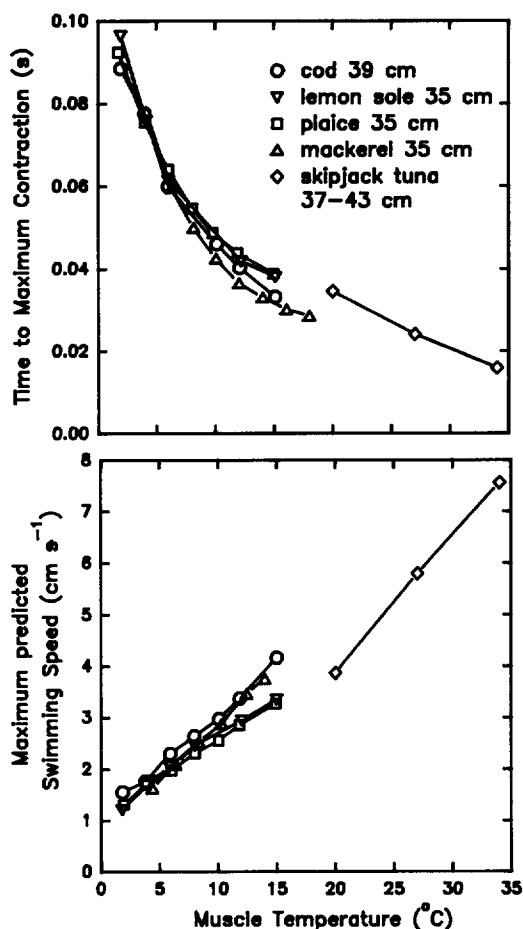
FIG. 1. Effect of temperature on the time for isolated muscle blocks to reach maximum contraction (upper panel) and predicted maximum swimming speeds (lower panel) of plaice (*Pleuronectes platessa*), lemon sole (*Micorstomus kitt*), cod (*Gadus calarias*), mackerel (*Scomber scombrus*), and skipjack tuna (*Katsuwonus pelamis*). Figure redrawn from data presented in Wardle (126) and Brill and Dizon (22).

argued that tunas may reach exceptionally high burst speeds because the temperatures of the white fiber muscle portions of the myotomes may be elevated significantly above ambient temperature (34,52,55,42). Thermal profiles of muscle (23) and telemetered muscle temperatures (20) show that in 2 kg skipjack tuna the temperature of the bulk of the white muscle portions of the myotome is not significantly elevated, even when the fish are chased to exhaustion and red muscle temperatures have increased from ≈2°C to ≈8°C above ambient temperature.

In summary, a statement in a recent book on fish swimming by Videler (121) seems appropriate ". . . estimates of maximum speeds of the fastest fishes desperately need confirmation by actual measurements." Moreover, I feel that the interesting question is not "How do tunas reach exceptional maximum burst swimming speeds?" because indeed they may not.

Rather, questions relating to factors that limit maximum rates of muscle force development and why maximum rates of force development appear the same in a wide variety of teleosts would seem more fertile.

Maximum Sustained Swimming Speeds

Although Jeff Graham and colleagues (57,58,41,42,43,53,79) have met with remarkable success studying several species of tunas swimming in a large (3000 l volume) water tunnel, the maximum sustained swimming speeds of tunas are yet to be directly measured. Mathematical models of maximum oxygen extraction rates from the ventilatory water stream (Fig. 1) and maximum rates of oxygen delivery to tissues (78) attainable by tunas' cardio-respiratory systems both predict that the maximum sustained speeds of 1.5–2 kg skipjack and yellowfin tunas (*Thunnus albacares*) are in the range of 2 to 4 body lengths $\cdot$ s^{-1} (Fig. 2). These speeds are not exceptionally above the maximum sustainable swimming speeds of other active teleosts (121), and are well below the exceptionally high sustained speeds of tunas (10 body lengths $\cdot$ s^{-1}) claimed by some authors (e.g., 122,133,82).

A summary of sustained swimming speeds determined by following fish carrying ultrasonic transmitters in the open ocean (28) also showed that tunas are not exceptional, but rather have maximum sustained speeds similar to those of other fishes (≈3–5 body lengths $\cdot$ s^{-1}, 121) and in the range predicted by the mathematical models of Bushnell and Brill (29) and Korsmeyer et al. (78). Furthermore, speed measurements determined by the distances covered by fish carrying ultrasonic telemetry devices in a given time period are complicated because what is really measured is speed over ground, not swimming speed (i.e., speed relative to the water). Brill et al. (24) have shown that, for striped marlin (*Tetrapturus audax*) at least, speed over ground and direction can be strongly influenced by oceanic currents (i.e., speed over ground and swimming speed may be significantly different). The same could be expected for tunas. Direct measurement of the maximum sustained speeds of tunas are, therefore, clearly needed.

The red muscle fiber portions of the myotomes of tunas (those responsible for powering sustained swimming, 22) do have several unusual characteristics. One, the bulk of red fibers are internal and adjacent to the spinal column, rather than laterad and against the body surface as in other fishes (75,56,9). Two, their temperatures are maintained significantly above ambient due to the presence of vascular countercurrent heat exchangers that break the inevitable linkage of muscle metabolic heat production and gill heat loss occurring in other teleosts (36,112,20). Three, the red muscle fiber portions of the myotomes of tunas have elevated myoglobin levels (≈18–35 mg $\cdot$ g^{-1}, 86,27,45) compared to other fishes (≈4–15 mg $\cdot$ g^{-1}, 27,45). Four, the capillarity of tuna red muscle fibers is significantly elevated (84) compared to that
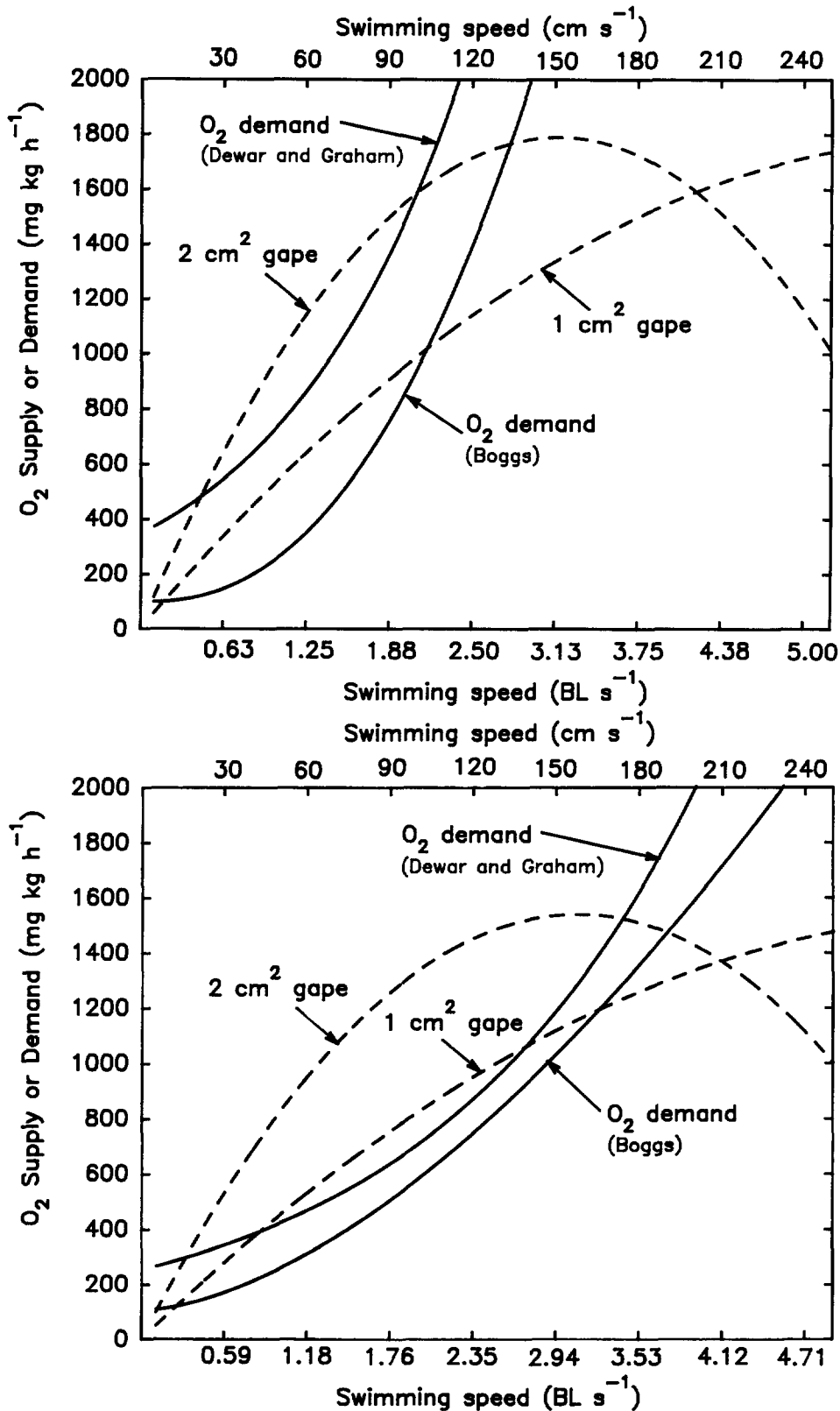
FIG. 2. Oxygen demands (solid line) and predicted maximum rates of oxygen extraction from ventilatory water stream (i.e., "supply," dashed lines) by the cardio-respiratory systems of skipjack tuna (upper panel) and yellowfin tuna (lower panel). Data for oxygen demand were taken from Boggs (11) and Dewar and Graham (41), and for oxygen supply from Bushnell and Brill (29). Values are based on 48 cm (fork length, 2.1 kg) skipjack tuna and 51 cm (2.2 kg) yellowfin tuna. "Gape" refers to tunas' cross-sectional mouth area which is a prime determinant of ventilation volume in these obligate ram ventilating fishes.

seen in more sluggish species like carp (68), although it is not the highest seen in fishes (69,85).

Elevated temperatures, high myoglobin levels, and high capillarity are clearly adaptations for increasing rates of oxygen delivery. If tunas are so highly streamlined why would they need adaptations apparently directed at increasing maximum rates of aerobic energy production in the red muscle portions of the myotomes? Low drag and high rates of aerobic energy production in the red muscle portions of the myotomes should combine to give tunas highly elevated maximum sustained speeds. Indeed, Stevens and Carey (111) have argued that these adaptations enable tunas to have maximum sustained swimming speeds well above those of other teleosts. However, (as already mentioned) these are yet to be routinely observed either in the field or in tunas swimming in a water tunnel (28,57,58,41,42).

I therefore propose an alternative explanation for the elevated temperatures, high myoglobin levels, and high capillarity of tuna red muscle fibers. They ensure that the red muscle fiber portions of the myotomes never function anaerobically (i.e., never accumulate an oxygen debt). Because tunas are

obligate ram ventilators, they depend on continuous forward motion to force water over their gills. [They are also negatively buoyant and must maintain minimum swimming speeds to keep from sinking (i.e., maintain hydrostatic equilibrium) (83). Minimum hydrostatic equilibrium speeds appear to be above those needed for gill ventilation, however (29).] Because tunas must maintain a constant forward velocity, the red muscle fibers which power sustained swimming function in a way analogous to cardiac muscle, another muscle that contracts continuously throughout life. Interestingly, tuna red muscle fibers have a mitochondrial volume density per capillary length and capillary volumes similar to those seen in mammalian cardiac muscle (85).

Swimming Efficiency

Tunas, at all sustainable speeds, have metabolic rates above those of other similarly sized active teleosts (e.g., sockeye salmon, *Oncorhynchus nerka*) swimming at equivalent speeds, even when the data are corrected for temperature differences (Fig. 3). Moreover, Videler (121) has compiled data
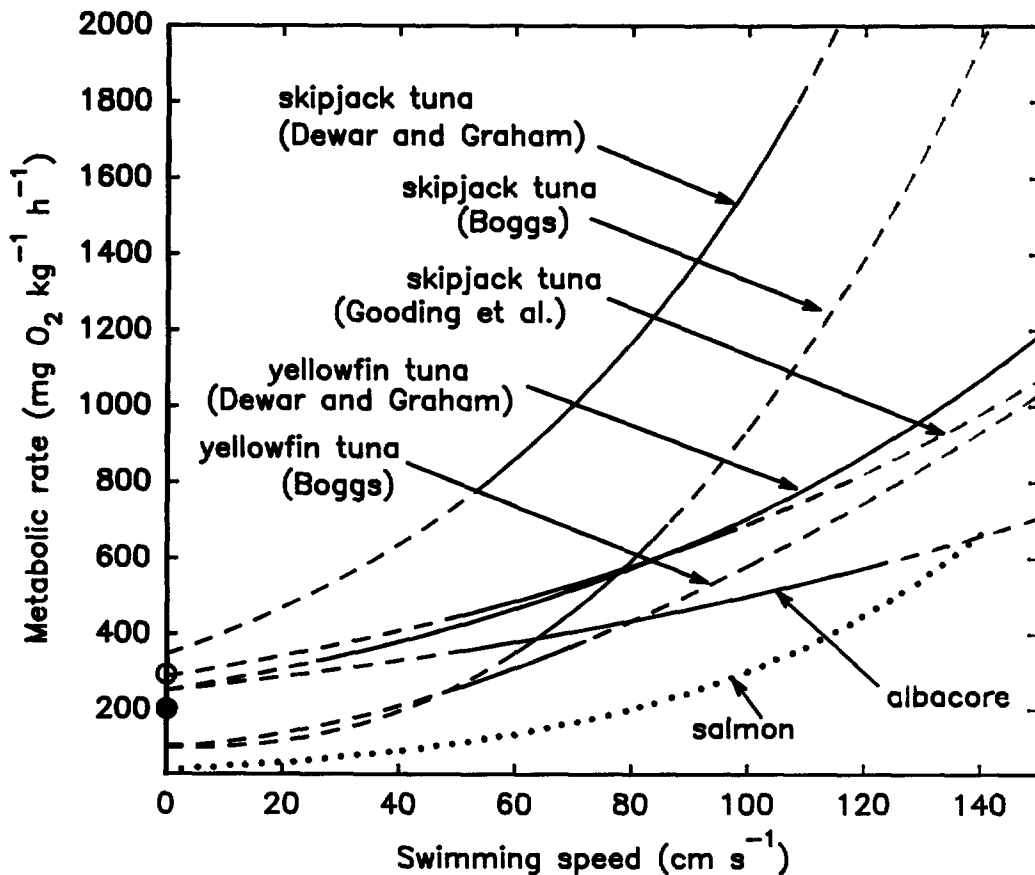

FIG. 3. Effect of swimming speed on metabolic rates of skipjack tuna, yellowfin tuna, albacore, and salmon. Speeds over which data were collected are shown by solid lines. Data are from Brett (14), Gooding *et al.* (51), Boggs (11), Graham *et al.* (58) and Dewar and Graham (41). The directly measured standard metabolic rates of skipjack tuna (solid circle) and yellowfin tuna (open circle) are also plotted. SMR data are from Brill (17). Measurements for skipjack and yellowfin tunas were made at 23–25°C, albacore at 13.5–18°, and salmon at 15°C.
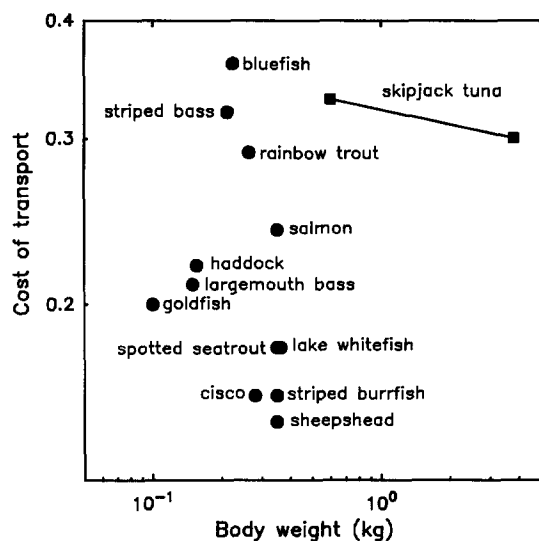
FIG. 4. The nondimensional cost of transport (at optimal swimming speeds) for various teleosts including skipjack tuna. Data were taken from Table 9.2 in Videler (121). Species names are as follows: bluefish = *Pomatomus saltatrix*, cisco = *Coregonus artidii*, goldfish = *Carassius auratus*, haddock = *Melanogrammus aeglefinus*, lake whitefish = *Coregonus clupeaformis*, largemouth bass = *Micropterus salmoides*, rainbow trout = *Oncorhynchus mykiss*, salmon = *Oncorhynchus nerka*, sheepshead = *Archosargus probatocephalus*, skipjack tuna = *Katsuwonus pelamis*, spotted seatrout = *Cynoscion nebulosus*, striped bass = *Morone saxatilis*, striped burrfish = *Chilomycterus scoepfi*.

on the energy demands of a wide variety of teleosts and calculated the nondimensional cost of transport (Joules · Newton^{-1} · m^{-1}) at each species' optimal swimming speed. This is clearly the most unbiased way of comparing energetic costs of transport in fishes. As shown in Fig. 4, the cost of transport for skipjack tuna is above those of other teleosts. These data imply that tunas: (a) are less efficient at converting chemical energy to kinetic energy, (b) have caudal fins which are less efficient at converting lateral motion to forward thrust, or (c) experience high hydrodynamic drag in spite of what appears to be obvious streamlining. None of these possibilities seems likely to me. Rather, I postulate that the exceptionally high standard metabolic rate (SMR, i.e., the metabolic rate at zero overt muscular activity) of tunas is the explanation (16,17,57,41) (Fig. 5). In other words, it is the elevated SMR of tunas (Fig. 5) that accounts for their elevated active metabolic rate (Figs. 3 and 4).

As also shown in Fig. 5, the SMR of dolphin fish (*Coryphaena hippurus*) is equivalent to those of both skipjack and yellowfin tunas and much higher than that of salmon. (The SMR of other large pelagic species such as billfishes is yet to be determined.) Although the data for salmon were taken at 20°C, the 5°C temperature difference is unlikely to account for the disparity, because the effect of temperature on SMR has a Q$_{10}$ of approximately two (87,17,131). SMR has been

postulated to be set by the diffusing capacity of the respiratory system, whole blood sugar concentration, the rate at which the circulatory system can deliver substrates and oxygen to the cells, and the rate of proton leak across inner mitochondrial membranes (107,118,119,39,129,63,120,13,38). Whether one or a combination of these factors causes the high SMR of tunas and dolphin fish is still an open question.

I postulate, however, that the high SMR of tunas and dolphin fish are, in major part, a direct result of these species having the large thin gills (i.e., high gill oxygen diffusion capacity, see 99) necessary to achieve high maximum oxygen extraction rates from the ventilatory water stream. In other words, the ability to achieve high maximum oxygen extraction rates from the ventilatory water stream is linked to high SMR because the necessary large thin gills engender high osmoregulatory costs (i.e., high SMR). As shown in Fig. 6, SMR and gill surface areas appear correlated for a number of teleost and elasmobranch fishes. Calculated and measured values for the cost of osmoregulation for fish in seawater range from approximately 10–30% of the SMR (102,91,74). Calculating the cost of osmoregulation requires data on drinking rates, unidirectional sodium efflux, and branchial potential difference (74). None of these have been measured in tunas or dolphin fish, nor has the cost of osmoregulation. Osmoregulatory costs can be estimated based on the metabolic rate of isolated gills, because the gills are the main sites of active salt extrusion. Clearly, the metabolic rates of isolated gills from tunas, billfish, and dolphin fish needs to be measured, as has been done for cod (*Gadus morhua*) (67).

Tunas have 30–80% more mitochondrial protein per gram of muscle tissue than carp, *Cyprinus carpio*, due to densely packed mitochondrial cristae (88). Tunas also have exceptionally high cardiac outputs [115–132 ml min^{-1} kg^{-1} in paralyzed skipjack and yellowfin tunas versus 18 ml min^{-1} kg^{-1} for resting rainbow trout (19,32)]. Admittedly, these other adaptations for achieving high maximum oxygen extraction rates from the ventilatory water stream and high rates of ATP production may also contribute to high SMR.

There is one aspect of swimming where tunas may be unique. That is the rate of increase in oxygen demand with increasing swimming speed. Data from Gooding et al. (51), Graham et al. (58), and Dewar and Graham (41) show that the rate of increase of oxygen demand with speed appears less in yellowfin tuna and albacore (*Thunnus alalunga*) than in sockeye salmon (14) (Fig. 3). If the rate of increase in metabolic rate with swimming speed is used as the definition of "swimming efficiency," than these tunas appear more "efficient" than other teleosts. Measurement of energy demands in skipjack and yellowfin tunas made by Boggs (11), however, imply that the rates of increase in metabolic oxygen demand with speed are the same in tunas and salmon (Fig. 3). The reasons for the disparity in the tuna metabolic rate data sets were explained by Boggs and Kitchell (12) as an artifact due to differences in measurement techniques. Boggs' (11) and
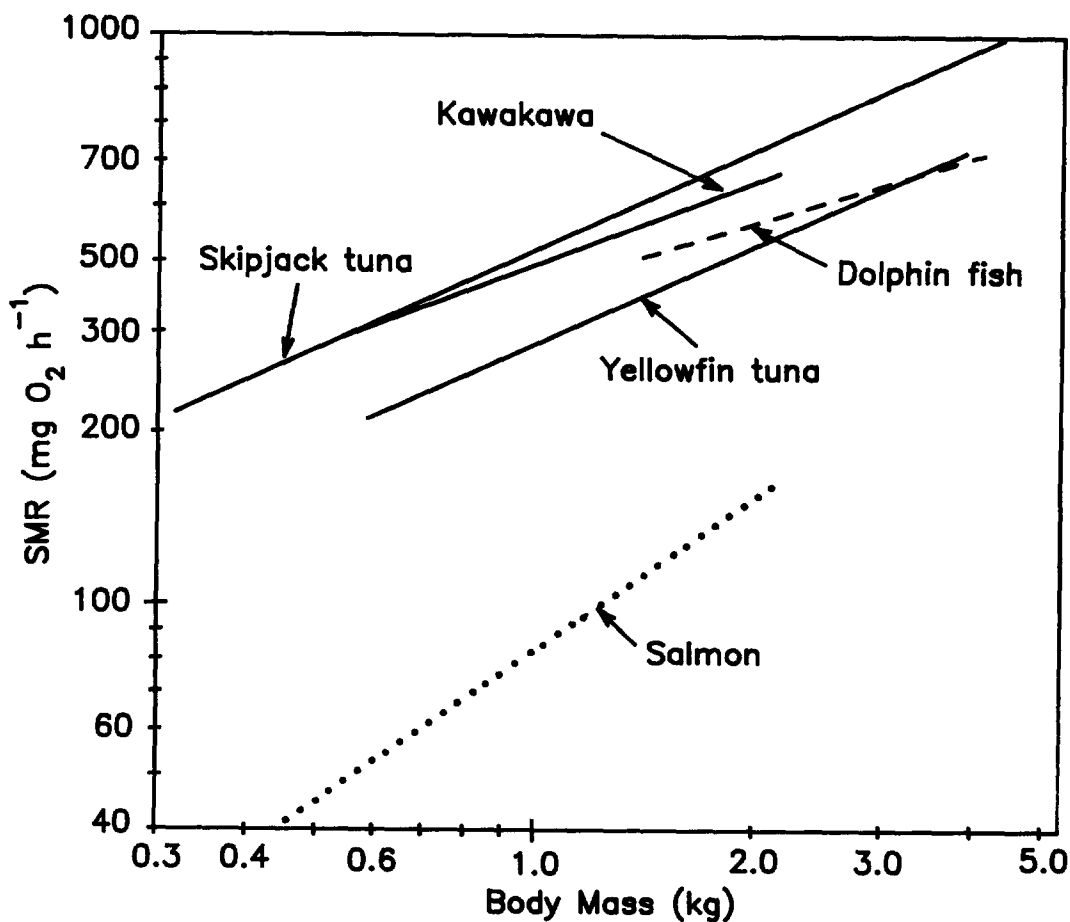
FIG. 5. The standard metabolic rates of skipjack tuna, yellowfin tuna, kawakawa, dolphin fish, (all measured at 25°C) and salmon (measured at 15°C). Data are from Brett (14), Brill (16), Brill (17), and Benetti *et al.* (7).

Brett's (14) models reflect the lower end of a range of possible metabolic rates at any speed whereas Gooding *et al.* (51), Graham *et al.* (58), and Dewar and Graham (41) all use the full range of metabolic rates measured at each speed. These discrepancies clearly need further scrutiny.

What Characteristics of Tunas, Billfishes, and Dolphin Fishes Are "High Performance"?

The three things that I feel are demonstratively "high speed" or "high performance" about tunas, billfishes, and dolphin fishes are:

1. rates of somatic and gonadal growth,
2. rates of digestion,
3. rates of recovery from exhaustive exercise (i.e., rates clearance of muscle lactate and the concomitant acid load).

I will examine each separately. There are, however, less data on these abilities of pelagic fishes than on those just discussed.

Rates of Somatic and Gonadal Growth

As clearly shown in Fig. 7, absolute rates of growth of skipjack tuna, yellowfin tuna, dolphin fish, and Pacific blue marlin (*Makaira nigricans*) are different, but all still clearly exceed those of other teleosts. (Chinook salmon, *Oncorhynchus tshwytscha*, was arbitrarily chosen as an example, other salmonids show similar growth rates [15].) Skipjack tuna grow more slowly than yellowfin tuna or Pacific blue marlin, and reach much smaller maximum sizes (≈ 22 kg, ≈ 150 kg, and >700 kg, respectively), apparently because of energetic constraints (60,76).

There are some data that imply rates of gonadal synthesis are high in tunas, although comparing rates of gonadal synthesis is more difficult than comparing rates of somatic growth. Yellowfin tuna, skipjack tuna and black skipjack tuna (*Euthynnus lineatus*) spawn a volume of eggs equivalent to up to $\approx 1-3\%$ of the body mass every one to two days during a three-month spawning season (65,105,106). For yellowfin tuna, this represents an annual energetic investment in reproduction of approximately 16% of total energy income (106)
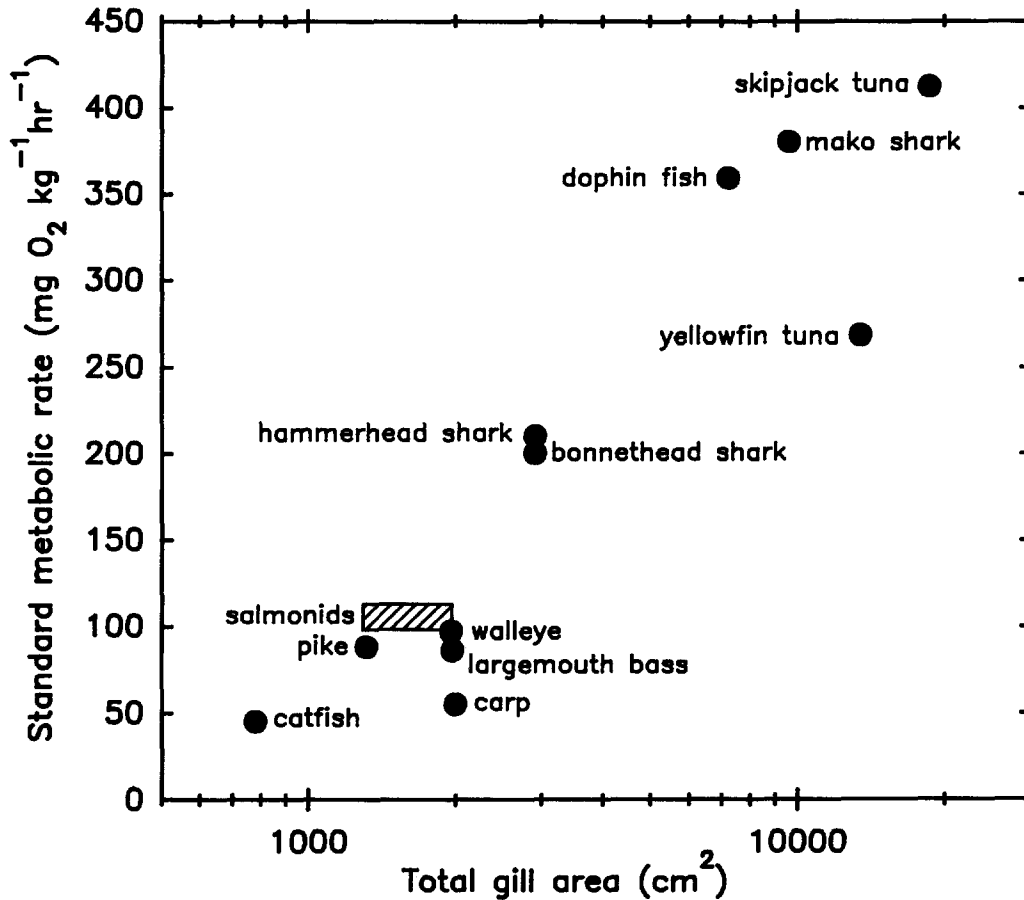
FIG. 6. SMR (at 1 kg body weight and 25°C) and gill surface area for various fish species. When necessary, SMR data were scaled to 1 kg body weight using the allometric equation and weight exponent of 0.89 (4), and to 25°C assuming a Q_{10} of 2. Data for SMR were taken from Beamish (4), Beamish and Mookherjii (6), Brett (14), Beamish (5), Brill (16), Tarby (114), Brill (17), Graham et al. (54), Parsons (96), Brown and Cameron (26), Armstrong et al. (1), Benetti et al. (7), except for hammerhead sharks. Those data were provided by Chris Lowe (Hawaii Institute of Marine Biology, unpublished observations). Data for gill surface area were taken from Emery and Szczepanski (48) and Palzenberger and Pohla (95). Gill surface areas for hammerhead and bonnethead sharks were assumed equal. Species names are as follows: bonnethead shark = Sphyrna tiburo, carp = Cyprinus carpio, catfish = Ictalurus punctatus, dolphin fish = Coryphaena hippurus, hammerhead shark = phyrna lewini, largemouth bass = Micropterus salmoides, mako shark = Isurus oxyrinchus, salmonids = Oncorhynchus spp, pike = Exox lucius, skipjack tuna = Katsuwonus pelamis, walleye = Stizostedion vitreum vitreum, yellowfin tuna = Thunnus albacares.

which is roughly equivalent to that seen other teleosts (130). The energy income of tunas is, however, well above those of other teleosts (92). Expressed another way, Schaefer (106) estimates that yellowfin tuna spawn an equivalent of 3.5 times their body weight per year, which represents 2.5 times the energy allocated to somatic growth.

Rates of Digestion

Yellowfin, skipjack and black skipjack tunas have rates of digestion (i.e., inverse of the time required for gastric evacuation) from two to five times higher than those of other piscivorous species when comparisons are made to other fishes of equal body size held at equivalent water temperatures (81,104,92). For example, 1.6–3.0 kg tunas held at 24–29°C reach 100% gastric evacuation (following being fed to sat-

iation) in approximately 5–12 hr. Other similarly sized teleosts (held at 18–25°C) require 25–40 hr (81).

Rates of Recovery From Exhaustive Exercise

Skipjack tuna chased to exhaustion achieve some of the highest white muscle lactate levels found in vertebrates (up to 100–150 μmoles · g^{-1}, 59,2). Other teleosts (e.g., rainbow trout, winter flounder (Pseudopleuronectes americanus), plaice (Pleuronectes platessa)) reach maximum white muscle lactate levels of only $\approx$15–40 μmoles · g^{-1} (125,93). Yet, tunas show rates of lactate clearance and recovery of blood acid-base status much faster than other teleosts. In skipjack and yellowfin tunas, recovery to pre-exercise white muscle lactate and glycogen levels and blood acid-base balance may be completed in two hours (3,100,2). In other teleosts, recovery from
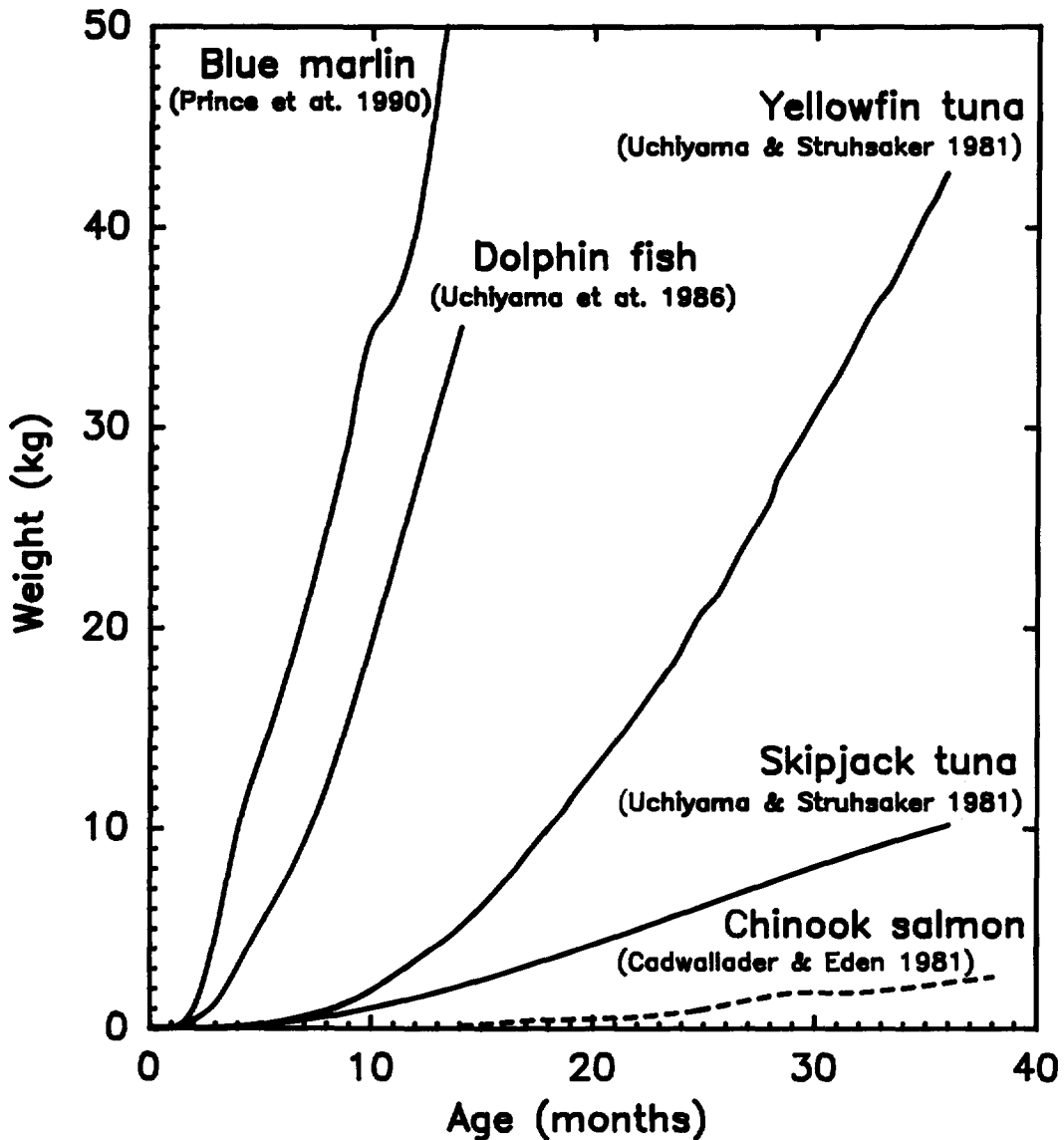
FIG. 7. Size at age for yellowfin tuna, skipjack tuna, dolphin fish, Pacific blue marlin, and a landlocked population of chinook salmon. Data were taken from Uchiyama and Struhsaker (117), Uchiyama et al. (116), Prince et al. (101) and Cadwallader and Eden (33).

lower muscle lactate levels and lesser proton load takes two to twelve times longer (125,93).

The Common Denominator—Oxygen Delivery at Rates Above that Needed for Swimming and SMR

The common feature of somatic and gonadal growth, digestion, and recovery from exhaustive exercise is that all are energy-consuming processes and all require oxygen and metabolic substrate delivery to the tissues at rates above those needed by the swimming muscles and for other routine metabolic activities (i.e., the SMR).

There are no data on the increase in metabolic rate following feeding in tunas. Based on data from other species, how-

ever, it seems likely that feeding in tunas could cause a doubling or tripling (66,1,80,70). The increase in oxygen consumption is due to the burst of protein synthesis that follows feeding, more than the mechanical actions of the stomach or gut required for digestion, or amino acid transport (25,26). There are also no data on metabolic rates of tunas recovering from exhaustive exercise. The highest metabolic rates in skipjack tuna ever measured (2500 mg $O_2 \cdot kg^{-1}h^{-1}$) were, however, recorded from fish immediately after their capture from a feeding school (51). The fish were most likely recovering from oxygen debt (i.e., metabolizing lactate) (61) and/or showing increased metabolic rates due to recent feeding.

Bluefin tuna (Thunnus thynnus) have vascular counter-

current heat exchangers associated with their viscera and maintain significantly elevated visceral temperatures presumably to increase digestion rates (35). I hypothesize that high digestion rates must be paired with high rates of protein synthesis which, in turn, must be matched by high rates of oxygen delivery, because protein synthesis is an energy consuming process. Moreover, Pauly (97,98) has clearly demonstrated that growth rates of a large number of teleosts are positively correlated with gill surface areas, and that maximum growth rates are limited by maximum oxygen delivery rates. In other words, fishes like tunas with the largest gill surface areas (and high maximum metabolic rates) have the highest growth rates. The situation is not as described by Olson and Boggs (92) that ". . . many tropical pelagic predators [i.e., tunas, billfishes, and dolphin] . . . grow rapidly in spite of high metabolic rates . . ." but rather, as suggested by Boggs and Kitchell (12), tunas grow rapidly *because of* their ability to sustain high metabolic rates.

SUMMARY AND CONCLUSIONS

I hypothesize that the ability of tunas (and probably other pelagic species) to deliver oxygen and metabolic substrates to the tissues at high rates evolved to permit high rates of gonadal and somatic growth, rapid digestion, and rapid recovery from exhaustive exercise, not exceptionally high sustained cruising speeds. Indeed, the uniqueness of the anatomy (e.g., high capillarity) and biochemistry (e.g., level of substrate transporters, myoglobin levels, LDH activity) of the white muscle and gut of tunas appears to support this hypothesis (45). Future research on tunas should, therefore, probably not concentrate on "how" or "why" tunas are "high speed" or "efficient" swimmers, because the data summarized here clearly implies they are not. Rather, future investigations should concentrate on actually measuring the maximum aerobic metabolic rates of various tuna species. I suspect these will not necessarily be observed in fish swimming at their maximum sustainable speeds, but rather in tunas recovering from exhaustive exercise, or following feeding to satiation, or both. Future studies could also be fruitfully directed at determining which factors limit maximum rates of oxygen uptake in tunas as has been done for mammals (e.g., 46,47) and how tunas are able to reach their very high maximum metabolic rates (i.e., rapidly extract large quantities of oxygen from a high ventilation volume, deliver substrates and oxygen to the tissues at high rates, etc.) (e.g., 78,79).

Finally, there is some evidence that tunas' unique abilities may actually effect their movements and depth distribution. It appears tuna hearts may function in ways more similar to those of mammals than to those of other teleosts, and that tuna hearts have a more limited ability to increase stroke volume than those of other fishes (49,73,115). The limited ability to increase stroke volume may, in turn, limit tunas' ability to withstand reduced ambient oxygen, with its accom-

panying bradycardia, because the limited increase in stroke volume is not sufficient to offset reductions in heart rate, as it is in other teleost (e.g., 50,31,30). This inability to tolerate lowered ambient oxygen appears, in turn, to significantly influence tunas' depth distributions and may limit their vertical movements (18).

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