Commentary

Tuna comparative physiology

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Summary

Thunniform swimming, the capacity to conserve metabolic heat in red muscle and other body regions (regional endothermy), an elevated metabolic rate and other physiological rate functions, and a frequency-modulated cardiac output distinguish tunas from most other fishes. These specializations support continuous, relatively fast swimming by tunas and minimize thermal barriers to habitat exploitation, permitting niche expansion into high latitudes and to ocean depths heretofore regarded as beyond their range.

Key words: fish, evolution, phylogeny, metabolism, thunniform locomotion, regional endothermy.

Introduction

Tunas capture the imagination of comparative physiologists because of the functional differences distinguishing them from other fishes. Relative to most other species, tunas have a fundamentally different swimming mode, a radically different thermal biology, increased rate functions [e.g. standard metabolic rate (SMR), aerobic capacity, heart rate and gut clearance] and a markedly different cardiac physiology. Lamnid sharks, which are remarkably convergent with tunas (Bernal et al., 2001, 2003; Donley et al., 2004), are the only other group with a similar ensemble of specializations.
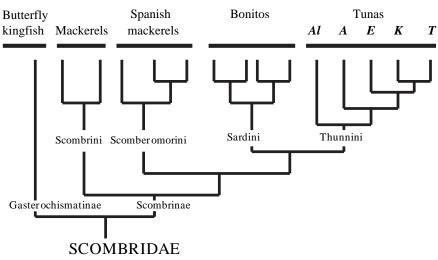
Tuna evolution and radiation

Comparative physiologists seek to understand the mechanism and biological significance of physiological adaptation, and tunas satisfy all criteria essential for this. Considerable data relate tuna natural history and behavior to functional morphology and ecology (Sharp and Dizon, 1978; Block and Stevens, 2001). Tuna taxonomy is known; there are 15 species in five genera comprising a monophyletic clade (Tribe Thunnini) of the family Scombridae (Fig. 1). The evolutionary relationships of tunas to other scombrids have also been characterized; their sister group is the bonitos (Tribe Sardini), which differ both morphologically and physiologically (Altringham and Block, 1997; Collette et al., 2001; Westneat and Wainwright, 2001; Dowis et al., 2003; Sepulveda et al., 2003).

Morphological evidence has been used to define tuna evolutionary relationships (Fig. 1). Molecular phylogenetic analyses based on different mitochondrial genes (Finnerty and Block, 1995; Chow and Kishino, 1995; Alvarado Bremer et al., 1997) have not yielded consistent results with respect to relationships among closely related species but do support a long separation of the four derived tuna genera into at least two clades: (1) *Thunnus* and (2) *Katsuwonus + Euthynnus + Auxis*. This relationship is also supported by some morphological evidence and by the fossil record (Graham and Dickson, 2000; Collette et al., 2001; K. A. Monsch, personal communication; Fig. 2).

Extant tuna and bonito genera appear in the early Tertiary period [~60 million years ago (mya); Carroll, 1988; Monsch, 2000; Fig. 2]. The earliest tunas lived in the Tethys Sea, a large circumtropical waterway that encircled Earth for about 50 million years [Mid-Cretaceous to the late Oligocene (~25 mya)]. Tuna and bonito radiations were influenced by tectonically induced changes in paleoceanography, including progressive cooling [beginning in the Eocene (~50 mya)], development of the modern ocean's thermohaline and gyre circulations, an accentuated vertical thermal stratification, and greater high-latitude upwelling, which increased productivity, expanded food webs and opened potential niches (Dickson and Graham, 2004). Most physical and biological features of recent ocean ecosystems have been in place since the Miocene (~20 mya; Macdougall, 1996; Fordyce and Muizon, 2001).

Swimming is fundamental to the natural history of most pelagic fishes, including tunas. We suggest that changes in Tertiary oceanography, in particular the appearance of more

Fig. 1. Morphological phylogeny of the Family Scombridae showing its two subfamilies, Gasterochismatinae and Scombrinae, the latter composed of four Tribes. The bonitos (Tribe Sardini) and tunas (Thunnini) are sister groups. Letter abbreviations for the five tuna genera: *Al*, *Allothunnus*; *A*, *Auxis*; *E*, *Euthynnus*; *K*, *Katsuwonus*; *T*, *Thunnus*. Modified from Collette et al. (2001); Graham and Dickson (2000).

extensive ocean areas with high productivity and diversified food webs, selected for tuna physiological adaptations that enhanced locomotor performance, favored migratory behavior and thus contributed to tuna radiation (Dickson and Graham, 2004). Tunas acquired a unique swimming mode and a level of integration between swimming and physiological performance not matched by other teleosts. Each of the three specializations featured in this commentary – thunniform swimming, the capacity for regional endothermy and an elevated aerobic capacity – are rooted in continuous swimming and are integral to expanded latitudinal and vertical habitat exploitation by tunas.

Tuna distribution

Allothunnus fallai occurs exclusively in the temperate Southern Ocean. Species of the other tuna genera (*Auxis*, *Euthynnus*, *Katsuwonus* and *Thunnus*) have widespread geographic distributions throughout tropical and subtropical oceanic and coastal ecosystems as far as 45° North and South latitudes. They also occur in every tropical ocean, and skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) are circumtropical. The genus *Thunnus* has two subgenera: *Thunnus* and *Neothunnus*. The four *T. neothunnus* species (*T. n. albacares*, *T. n. obesus*, *T. n. atlanticus* and *T. n. tonggol*) are mainly tropical. With
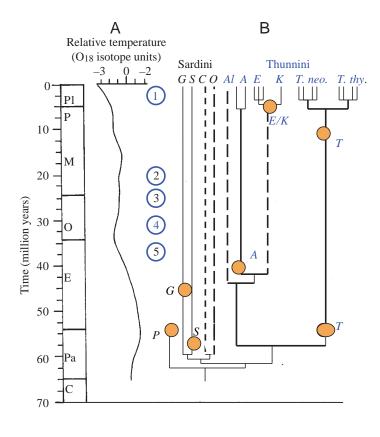

Fig. 2. (A) Cretaceous–Pleistocene (C–Pl) time scale showing relative cooling in benthic ocean temperature based on stable oxygen isotope ratios. Warmest times were late Paleocene (Pa), while coolest were Pleistocene. Numbers in circles mark the approximate timing of five major paleoceanographic events: (1) Central American land bridge formation (3 mya); (2) beginning of thermohaline circulation (22 mya); (3) closure of the Tethys seaway (25 mya); (4) Antarctic glaciation and polar cooling (30 mya); (5) Northward tectonic drift of Australia (36 mya). Data summarized from Macdougall (1996); Fordyce and de Muizon (2001); Graham and Dickson (2004). Other Tertiary epochs abbreviated on the left axis are: Eocene, E; Oligocene, O; Miocene, M; Pliocene, P. (B) Phylogeny for the Sardini and Thunnini based on the earliest known occurrences of fossil remains (orange circles) of two extant Sardini genera (G, *Gymnosarda*; S, *Sarda*) and extant tuna genera (A, *Auxis*; E/K, *Euthynnus* or *Katsuwonus*; T, *Thunnus*). (Note that *Thunnus* fossils extend from the late Paleocene to the Pliocene.) The extinct *Paleothunnus* (P) is considered to be closely related to the tuna–bonito common ancestor. Data from Bannikov (1985); Carroll (1988); Monsch (2000; personal communication). Bonito genera abbreviations: *S* and *G*, as above; *C*, *Cybiosarda*; *O*, *Orcynopsis*. Tuna abbreviations as in Fig. 1; the two *Thunnus* subgenera (*Neothunnus* and *Thunnus*), each with four species, are indicated. (Note: terminal lines indicate number of extant species in each tuna genus.)

apparently more effective heat conservation mechanisms, the four species of subgenus *Thunnus* (*T. t. thynnus*, *T. t. orientalis*, *T. t. maccoyii* and *T. t. alalunga*) frequent highly productive coastal and open ocean areas in high latitudes (Graham, 1975; Collette et al., 2001). All tunas, with the exception of *Allothunnus*, spawn in warm waters. The cool-water-occurring *Thunnus* migrate and spawn seasonally, whereas the tropical tunas spawn throughout the year. Species of both subgenera can exploit prey within the deep scattering layer (DSL; the diurnally migrating micronekton assemblage of fishes, crustaceans, cephalopods and other organisms; Gunn and Block, 2001; Schaefer and Fuller, 2002; Kitagawa et al., 2004).

Fisheries' catch statistics, acoustic and archival tag data, and laboratory studies of thermal and respiratory physiology identify factors affecting tuna vertical distributions (Fig. 3). In the eastern tropical Pacific, *Katsuwonus* up to 4 kg mass occur throughout the upper 200 m but do not enter waters cooler than 18°C or having less than 3.5 ml O_2 l^{-1} (~64% saturation at 18°C). With higher total O_2 requirements, larger skipjack are more spatially confined; 4–9 kg skipjack require water cooler

than 26°C (saturated O_2 ~4.9 ml O_2 l^{-1}), while >9 kg skipjack remain below 22°C (~5.2 ml O_2 l^{-1}) (Barkley et al., 1978).

Resource partitioning is suggested by the distributions of the tropical Pacific yellowfin and bigeye. Yellowfin range from 50 to 350 m (~15°C) but are also limited by the 3.5 ml l^{-1} oxygen barrier. By contrast, bigeye repeatedly dive from 100 m to deeper than 500 m (≤7°C) and may enter water with a lower oxygen content (1.0 ml O_2 l^{-1}; ~18% saturation at 18°C) (Brill, 1994; Schaefer and Fuller, 2002). On the other hand, both yellowfin and bigeye will aggregate under floating objects and remain at the surface for long periods (Schaefer and Fuller, 2002).

Acoustic telemetry and archival tags (recording microprocessors affixed to the fish and recovered at capture) show that yellowfin and bigeye routinely dive deeper than indicated by longline data, and this has dramatically altered concepts about the importance of vertical niche expansion (Holland and Sibert, 1994; Brill and Bushnell, 2001; Lowe et al., 2000). Schaefer and Fuller (2002) report that bigeye occasionally dive to 1000 m (~3°C), and a recently recovered
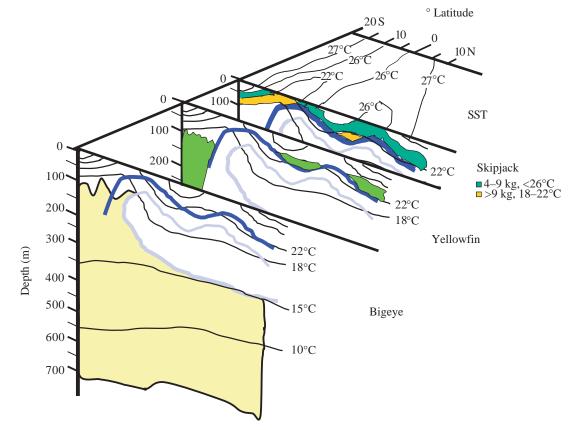

Fig. 3. Data from Barkley et al. (1978); Brill (1994); Dagorn et al. (2000); Schaefer and Fuller (2002) rendered into a three-dimensional depiction of the vertical distribution of three tuna species in relation to ocean temperature (black isotherms) and O_2 depth profiles (thick blue lines) in the vicinity of 160° W longitude of the equatorial Pacific Ocean. The back panel shows sea surface temperature (SST) isotherms in relation to latitude. Vertical panels show temperature and O_2 at depth and the occurrence of each species (shaded areas). Skipjack of <4 kg move freely between the surface and 200 m but do not enter water at <18°C or with less than 3.5 ml O_2 l^{-1} (dark blue line). Larger skipjack have the same low temperature and O_2 limits but are also restricted by warm temperatures: 4–9 kg skipjack are restricted to <26°C whereas >9 kg skipjack are confined to 18–22°C. Yellowfin extend from the surface to depths greater than 400 m but have the same O_2 limit as skipjack. Bigeye are found at greater depths than the other two species and have an O_2 limit of 1.0 ml O_2 l^{-1} (light blue line).

tag indicates a maximum bigeye depth of 1839 m (~2.5°C) (K. M. Schaefer, personal communication).
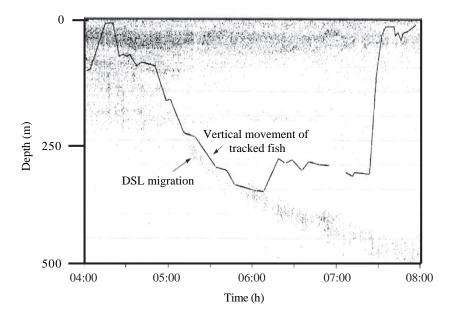
Deep-diving tunas appear to be foraging in the DSL. Stomach contents and behavioral observations show that tunas do not exploit the DSL at night when it is near the surface (Dragovich and Potthoff, 1972; Kitagawa et al., 2004). However, as daylight approaches, yellowfin and bigeye begin feeding on the DSL and pursue it to depth (Fig. 4). Acoustic and archival records show repeated (10–15 day^{-1}) foraging dives by bigeye; these fish swam relatively fast [≥2 fork lengths per second (FL s^{-1}; FL is body length from snout to caudal fork)] both up and down and spent considerable time in 3–7°C water (Holland and Sibert, 1994; Schaefer and Fuller, 2002). Atlantic northern bluefin at 1000 m are reportedly feeding on the DSL (Gunn and Block, 2001). Observations by Kitagawa et al. (2004) indicate that young Pacific bluefin do not dive this deep and opt for food near the surface when available.

Integrated tuna physiology

The preceding sections provide an evolutionary and ecological framework for a synthesis of tuna comparative physiology emphasizing the role of continuous swimming, both in this group's unique physiology and its ecological radiation.

Thunniform swimming

Thunniform swimming is a lift-based propulsion mode characterized by minimal lateral body undulation and the concentration of thrust production at the rapidly oscillating, lunate caudal fin (Altringham and Shadwick, 2001; Katz et al., 2001; Syme and Shadwick, 2002). Among teleosts, only tunas use this swimming mode, and comparisons with other scombrids show that (1) thunniform swimming is a derived tuna characteristic resulting from modification of ancestral features including body and caudal-fin shape, myotomal architecture, red muscle (RM) position, and its connections with the skin and skeleton (Graham and Dickson, 2000; Westneat and Wainwright, 2001; Dowis et al., 2003) and (2) the shift in RM position favored a reduction in its thermal conductance and may have preceded or co-evolved with endothermy (Graham and Dickson, 2000).

Structural modifications for thunniform swimming include a more anterior point of maximum body thickness and accentuation of posterior body tapering, peduncular narrow-necking, development of the dense anterior corselet scale layer, accentuation of grooves for paired and median fins and increases in lateral keel area and caudal-fin aspect ratio (Fig. 5A). These body shape modifications increase streamlining and minimize anterior body undulation and are accompanied by alterations in myotomal architecture that affect swimming biomechanics and kinematics (Graham and Dickson, 2000; Westneat and Wainwright, 2001). Tuna myotomes have longer cones, and the RM is in the anterior-medial body position (Fig. 5B) unique to tunas and lamnid sharks (Bernal et al., 2001; Westneat and Wainwright, 2001; Donley et al., 2004). Regional connections of tuna RM to the skin are reduced, supplanted by robust tendinous connections within the horizontal septum and longer lateral tendons connecting to the caudal fin (Figs 5, 6). The ratio of output motion at the tail to input motion due to RM shortening (the velocity ratio) is greater in tunas than in other scombrids (Graham and Dickson, 2000; Westneat and Wainwright, 2001). This is reflected in the higher tailbeat frequency and reduced lateral displacement along the body in tunas relative to comparably sized bonitos and mackerels swimming at similar speeds (Donley and Dickson, 2000; Altringham and Shadwick, 2001; Dowis et al., 2003; Fig. 6B).

Scombrid myotomal differences extend to RM activation and strain development patterns. In both chub mackerel and bonito, with lateral-posterior RM tightly connected to the overlying skin, shortening results in local body bending. By contrast, activation of yellowfin and skipjack RM, with reduced connection locally to skin, results in greater RM strain than predicted by the bending beam theory (Shadwick et al., 1999; Altringham and Shadwick, 2001; Katz et al., 2001). This requires that RM contracts independently of the fast-glycolytic white muscle (WM) within the same myotome, and this is possible because RM and WM are separated by connective tissue sheets. This separation was demonstrated with simultaneous sonomicrometry (SMC) and electromyography

Fig. 4. Pre-dawn to daylight acoustic track record of a South Pacific (Polynesia) bigeye tuna, showing its deep diving in pursuit of the downward migrating deep scattering layer (DSL). Reproduced with permission from Dagorn et al. (2000).

(EMG), which indicated a higher RM shear and a greater extent of shortening than would be possible if it were bound to WM (Katz et al., 2001; Syme and Shadwick, 2002). Work-loop studies yielded maximum performance for yellowfin and skipjack RM fibers when they were actuated using *in vivo* RM activation and strain parameters. This result, together with the SMC findings and EMG 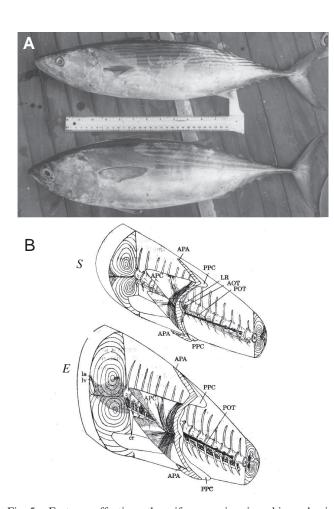data showing sequential onset of RM activation down one side of the body and then the simultaneous cessation of RM contraction at all positions, suggests that during sustained swimming maximal RM power production along one side of a tuna's body occurs at nearly the same instant (Altringham and Shadwick, 2001; Katz et al., 2001).

Although the reduced lateral displacement characteristic of thunniform swimming should reduce drag, Korsmeyer and

Fig. 5. Factors affecting thunniform swimming biomechanics. (A) Contrasts of the more fusiform body shape of the striped bonito, *Sarda orientalis* (top), with the black skipjack's (*Euthynnus lineatus*) increased anterior vertical thickness (from Graham, 1975). (B) Three-dimensional perspective for *Sarda* (*S*) and *Euthynnus* (*E*) of similar size showing structural features of a single myotome. The hatched area is the only aspect of the myotome that would be visible in a skinned fish. Myotomes have anterior pointing arms (APA) and cones (APC) and posterior pointing cones (PPC) and connect to the vertebral column *via* the anterior (AOT) and posterior oblique tendons (POT) within the horizontal septum. Lines on the surface of APCs show how AOTs wrap around the APCs for force transfer. The tuna has thicker, longer APCs and an anterior-medial red muscle (RM) mass (stippling). In the bonito, with laterally placed RM, the AOT is longer than in the tuna. As the bonito POT extends posteriorly to insert on vertebrae, it makes a greater angle of incidence with the vertebrae than in tuna. Also illustrated for *Euthynnus* are its left-side lateral artery (la) and vein (lv) and its central rete (cr). Reproduced from Graham and Dickson (2000).
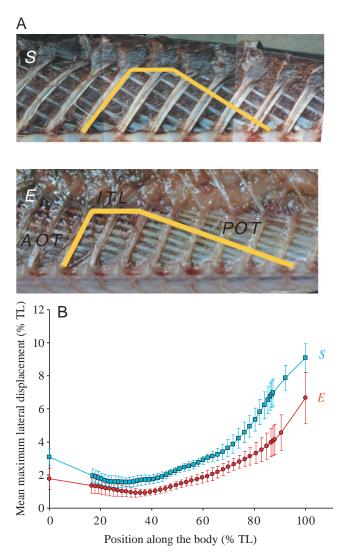

Fig. 6. (A) Dorsal view photograph of the horizontal septum (i.e. vertebrae level) of a 62.7 cm fork length (FL) *Sarda orientalis* (*S*) and a 75.4 cm FL *Euthynnus affinis* (*E*). Yellow lines mark an anterior oblique tendon (AOT) extending from a vertebra out to the inter-tendon length (ITL), the segment of the posterior oblique tendon (POT) that parallels the backbone and spans one or two adjacent AOTs. The AOTs act as slings to support the POT (see Westneat and Wainwright, 2001), and the POT segment that inserts onto posterior vertebrae. The greater POT angles in *Sarda* reflect its lateral red muscle (RM) position. (B) Maximum lateral displacement (as percentage of fish total length, % TL) at each vertebral joint as a function of relative position along the body for *Sarda chiliensis* (turquoise squares) and kawakawa tuna (*Euthynnus affinis*; red circles). Modified from Dowis et al. (2003); tuna data from Donley and Dickson (2000).

Dewar (2001) note minimal evidence that cost of transport is reduced for tunas relative to other species. In fact, tunas have greater total metabolic swimming costs relative to bonitos and mackerels (Sepulveda and Dickson, 2000; Sepulveda et al., 2003). Further investigations of the biological advantage of thunniform swimming are therefore needed.

Regional endothermy

The evolutionary and ecological significance of endothermy is the expanded thermal niche it opens for tunas, whether in deep water, at high latitudes or both (Block et al., 1993). Counter-current vascular heat exchangers (retia mirabilia) conserve metabolic heat, allowing the warming of RM, WM, viscera, brain and eyes above ambient water temperature (T_a; Carey et al., 1971; Graham and Dickson, 2001). Because of water's high heat capacity and the in-series circulation of fishes, elevated temperatures could not be maintained without circulatory adaptations to regulate both heat loss and gain (Dewar et al., 1994). Moreover, a tuna's capacity to maintain body temperature (T_b) in the face of changing T_a stabilizes muscular, metabolic, sensory and digestive functions. A tuna that swims from near the surface to 1000 m benefits from the thermal conservation of RM power production, of visual perception and of other processes as it undergoes a $\geqslant 10°C$ T_a reduction and severe light attenuation.

Elevation of tuna RM temperature combines the requirement to swim continuously with the inefficiency of muscle in chemical-to-kinetic energy conversion, providing a steady source of heat. Retia are essential for RM heat conservation, but the anterior-medial RM position also favors heat retention. The developmental processes affecting the differential development and growth patterns of RM in tunas and other scombrids are unknown. Juvenile tuna form their anterior-medial RM before the RM retia develop (Graham and Dickson, 2001), but comparative studies are needed to determine if this reflects selective forces underlying thunniform swimming or endothermy.

RM retia are arrays of intimately positioned, oppositely flowing arterioles and venules located adjacent to the muscle (Carey et al., 1971; Graham and Dickson, 2001; Fig. 7). Retial connections to major arteries and veins show a phylogenetic trend for the elaboration of lateral heat exchangers in more derived tunas; the pattern also suggests the possible independent origin of lateral retia in the *Thunnus* and the *Katsuwonus* + *Euthynnus* + *Auxis* clades (Figs 2, 7). In most fishes, including most scombrids, the routing of myotomal blood is *via* the central circulation [dorsal aorta (DA) and post cardinal vein (PCV)]. Tunas are an exception. *Allothunnus*, the most basal tuna, has a small DA and PCV-connected central rete within its expanded hemal arch. In addition to a large central rete, *Katsuwonus* + *Euthynnus* + *Auxis* perfuse RM *via* retia branching from the lateral arteries (branched anteriorly from the DA) and veins (draining to the PCV or the duct of Cuvier); *Auxis* and *Euthynnus* have only epaxial lateral vessels and retia whereas *Katsuwonus* has both epaxial and hypaxial vessels and retia (Fig. 7). Each of the *Thunnus* (*neothunnus*)
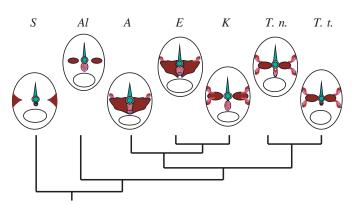

Fig. 7. Cladogram for *Sarda* and the five tuna genera (abbreviations as above) reflecting differences in the position and the relative quantity (as illustrated in near mid-body transverse sections) of RM (deep red), and the phyletic trend for greater emphasis on lateral vascular supply [arteries (red), veins (blue)] and *retia* (red and blue lines) for RM. See text for detail.

species has two expaxial and hypaxial vessel pairs with retia, and three species [*T. n. albacares*, *T. n. atlanticus* and *T. n. tonggol*] also have a small central rete (absent in *T. n. obesus*). The four *Thunnus* (*thunnus*) species have the four vessel-set lateral circulation each with an extensive rete but lack a complete central circulation (reduced DA, no PCV; Fig. 7). Both central rete size and central circulation completeness are reflected in the interspecific differences in hemal arch structure among the tunas (Graham and Dickson, 2000).

Recent works document tuna capacity to alter whole-body thermal conductance to minimize or maximize rates of T_b change. Archival data for Atlantic northern bluefin indicate that T_b is conserved (20–24°C) over a range of depths and T_a (Gunn and Block, 2001). Acoustic telemetry records suggest that bigeye 'bounce dive' behavior allows heat gain in shallower, warmer water to lengthen forays into deeper, cooler water where, despite heat conservation, RM (and other warm regions) gradually cools (Holland and Sibert, 1994). At shallower depths, the bigeye is in thermal equilibrium and has a T_{RM} that is warmer than T_a. After a time in deeper water it is cooler and as it ascends and enters water warmer than its end-dive T_{RM}, heating occurs 100–1000 times faster than diving heat loss. Although increased RM work during upward swimming and a faster heart rate in warmer water augment post-dive heating, a much higher heat gain rate suggests that the ascending bigeye may bypass its lateral heat exchangers, allowing blood warmed and oxygenated in the gills to enter RM directly *via* the DA (no central rete in *T. obesus*). Dewar et al. (1994) quantified changes in thermal conductance by rapidly imposing dive-depth equivalent T_a changes on yellowfin swimming steadily in a large water tunnel. Korsmeyer and Brill (2002) showed that blockade of adrenergic vascular control with bretylium in yellowfin eliminates these conductance changes.

Future studies need to detail the control of and structural bases for blood-flow alteration through and around retia. Questions also persist about visceral and cranial endothermy.

Heat production during prey digestion, absorption and assimilation is used to elevate tuna $T_{viscera}$ in the species of the subgenus *Thunnus*, all of which have visceral retia to conserve this heat (Carey et al., 1984; Gunn and Block, 2001). A warm viscera would speed digestion and gut evacuation for the next feeding opportunity because of the thermal enhancement of digestive enzyme activity, as shown for Atlantic northern bluefin trypsin and chymotrypsin (Stevens and McLeese, 1984).

Some tunas are similar to billfish, lamnids and the butterfly kingfish (*Gasterochisma melampus*; Fig. 1) in elevating their brain and eye (retinal or optic nerve) temperatures (Korsmeyer and Brill, 2002; Dickson and Graham, 2004). While the brain-heating mechanisms of billfishes are well characterized (Block, 1991), the cranial heat source of tunas is unknown.

Metabolic scope and related specializations
SMR and aerobic scope

The high aerobic capacity of tunas is reflected in both standard and active metabolic rates. Tuna SMR (i.e. metabolic rate at zero velocity, an index of maintenance metabolic costs) is 2–3 times greater than that of other scombrids (Korsmeyer and Dewar, 2001; Sepulveda et al., 2003). [As tunas never stop swimming, SMR is estimated by extrapolating swimming velocity–metabolic rate regressions to zero velocity or by direct measurement (stasis metabolism) in spinally blocked tunas; Brill and Bushnell, 2001.] However, the estimated costs of factors contributing to SMR [i.e. endothermy and greater aerobic maintenance requirements for osmoregulation, WM and organs (gills, heart) having a larger mass] total less than the twofold SMR elevation, implying the importance of other factors.

Fishes with a high SMR often have a large aerobic scope (Priede, 1985), which appears true for tunas (Korsmeyer and Dewar, 2001; Brill and Bushnell, 2001; Sepulveda et al., 2003). Compared with other fishes, tunas have a 2–10-fold greater swimming rate of oxygen uptake ($\dot{V}_{O_2}$) at comparable speeds and temperatures; they also have a much higher maximum $\dot{V}_{O_2}$ (estimated at ~2500 mg O_2 kg^{-1} h^{-1}). Greater locomotion costs reflect higher SMR as well as swimming power. Tunas have a larger gill area than other fishes and, while tunas are not unique in requiring ram ventilation, a larger gill area should increase drag and swimming costs and require more energy for osmoregulation. Tunas have either a small (*Thunnus*) or no (skipjacks) gas bladder, making them denser than seawater and requiring relatively rapid swimming to generate hydrodynamic lift. Considering only the minimum speed needed to ventilate and maintain hydrostatic equilibrium, a 1 m-long tuna must swim 0.5 FL s^{-1} or ~43 km day^{-1} (Magnuson, 1978).

The enigma of tuna energetics is that their apparently larger aerobic scope does not translate into swimming performance; water tunnel studies indicate tuna maximum sustainable swimming velocities in the range of other fishes (~3 FL s^{-1}). It may be that tunas require a larger scope to accommodate multiple aerobic costs simultaneously (Brill and Bushnell,

2001; Korsmeyer and Dewar, 2001). Because tunas are required to swim continually, they cannot suspend RM activity to meet other aerobic demands such as growth, gonadal production, replenishment of a post-feeding O_2 debt, lactate processing, and breakdown and assimilation of prey (Korsmeyer and Dewar, 2001). Instead, these costs must be added to swimming $\dot{V}_{O_2}$.

O_2 transport and utilization

Brill and Bushnell (2001) document numerous tuna specializations for tissue O_2 delivery, and the biochemical poising of tunas for high aerobic energy production is detailed by Dickson (1996) and Korsmeyer and Dewar (2001). The high tuna $\dot{V}_{O_2}$ requires 5–10 times greater branchial water flow than other fishes. Tuna gill structure maximizes contact between water and the respiratory epithelium and minimizes anatomical and physiological dead space, enabling over 50% O_2-extraction efficiencies (compared with 25–33% in other fishes). Tunas have 7–9 times more gill surface area than rainbow trout and a much smaller water to branchial capillary diffusion distance (Brill and Bushnell, 2001; Olson et al., 2003).

With a high hematocrit and mean corpuscular hemoglobin (Hb) concentration, tuna blood O_2-carrying capacities exceed those of other fishes. Specific differences in the shapes of Hb–O_2 dissociation curves and P_{50} values correlate with habitat and behavior (Cech et al., 1984; Lowe et al., 2000). The bigeye, which penetrates hypoxic water (Fig. 3), has a higher Hb–O_2 affinity (P_{50}=1.6–2.0 kPa; 15–25°C) than other tunas (skipjack and yellowfin – 2.8–3.1 kPa; 15–25°C; albacore – 3.5 kPa; 25°C). While bigeye, skipjack and yellowfin have sigmoidal O_2-dissociation curves, that of the albacore is hyperbolic.

The thermally independent Hb–O_2 binding shown for Atlantic northern bluefin (Rossi-Fanelli and Antonini, 1960) has now been documented for several tuna species and appears to be adaptive in compensating for rapid thermal changes during vertical migration. Closed-system temperature changes that simulate arterial blood warming during transit from gills through the heat exchanger to RM capillaries reveal interspecific differences in thermal effects on Hb–O_2 affinity. Closed-system warming increases Hb–O_2 affinity in albacore and bluefin but decreases that of bigeye and yellowfin and has no effect on skipjack (Cech et al., 1984; Lowe et al., 2000). Tuna Hb has a large Bohr effect (O_2 dissociation caused by elevated CO_2 and reduced pH). The Root effect (reduction of Hb–O_2-carrying capacity at low pH) has been demonstrated for skipjack, yellowfin and bigeye but not albacore (Lowe et al., 2000). For tunas, a high concentration of Hb, with differential Bohr and Root effects and with a pronounced Haldane effect (greater CO_2 content of deoxygenated blood), has implications for respiratory gas binding and transport, particularly in light of regional thermal differences.

Heart function

Most tunas have large hearts, a large ventricular stroke volume (1 ml kg^{-1}), a greater rate of ventricular pressure

development (dP/dt>700 kPa s^{-1}) and a higher ventral aortic pressure (10–12 kPa) than other fishes (Brill and Bushnell, 2001; Braun et al., 2003). The striking pyramidal tuna ventricle, with its thick walls, a high percentage of compact myocardium and extensive coronary circulation, allows high cardiac output ($\dot{Q}$).

Both *in vitro* experiments and *in vivo* measurements of heart rate and blood flow in swimming tunas show that $\dot{Q}$ is modulated by changes in heart rate and not stroke volume (Korsmeyer et al., 1997a; Brill and Bushnell, 2001; Blank et al., 2004). This differs markedly from most other fishes, in which ~30–70% of $\dot{Q}$ adjustment occurs through stroke volume change. It may be that space limitations imposed by body streamlining, a large heart, a thick ventricular wall and high heart rate limit stroke volume range. Tuna heart rate is affected by temperature and regulated by adrenergic stimulation and cholinergic (vagal) inhibition. The extent of heart-rate increase elicited by vagal blockade (atropine) indicates a greater level of cholinergic inhibition for tunas than for other fishes (Keen et al., 1995). At normal temperatures and activity levels, a tuna's heart rate can approach 200 beats min^{-1} (Brill and Bushnell, 2001).

Heart enzyme profiles indicate a high aerobic capacity and are consistent with the utilization of fatty acids and lactate as metabolic fuels (Dickson, 1996; Korsmeyer and Dewar, 2001). There is limited information about tuna cardiac myocytes (Brill and Bushnell, 2001); their diameters are more similar to those of other fishes (2–10 μm) than mammals (10–25 μm). The sarcoplasmic reticulum (SR) of the tuna heart does not appear to have more structural complexity than that of other fish hearts, but studies with the SR Ca^{2+} cycling blocker ryanodine suggest a greater dependence on SR Ca^{2+} for tuna heart contraction compared with other species (Keen et al., 1995).

Because lowered temperature and hypoxia both reduce tuna heart rate, forays into deep, cool and potentially hypoxic water (Fig. 3) may be limited by that organ's diminished capacity to supply the O$_2$ requirements of the endothermic tissues (Brill and Bushnell, 2001; Blank et al., 2004). On the other hand, a tuna's high venous O$_2$ reserve (Korsmeyer et al., 1997b) allows a margin for sustaining RM oxidative requirements at a reduced $\dot{Q}$ that, by increasing blood residence time in the warm tissues and retia, would also conserve heat (Graham and Dickson, 2001).

RM and WM biochemistry

RM specializations for a high O$_2$ flux include small-diameter fibers, with a high myoglobin (Mb) content and capillary density, and capillary manifolds that increase surface area and red-cell residence time (Mathieu-Costello et al., 1996; Dickson, 1996; Bernal et al., 2003). Metabolic enzyme assays at a common temperature show tuna and other scombrid RM to have comparable activities of citrate synthase (CS; which catalyzes the first Krebs' cycle reaction and correlates with mitochondrial density). However, when adjusted to *in vivo* temperatures, tuna RM CS activity is ~70% greater than in ectothermic scombrids (Dickson, 1996). Tuna WM has a much

greater CS activity and a greater anaerobic capacity (lactate dehydrogenase and creatine phosphokinase activities) than the WM of other scombrids (Dickson, 1996; K.A.D., unpublished data). Although bouts of intense exercise, such as a feeding frenzy, result in high lactate concentrations in tuna blood (50 mmol l^{-1}) and WM (100 mmol l^{-1}), lactate clearance by the skipjack is much faster than in other fishes and approaches the rate in mammals (Arthur et al., 1992).

Conclusions

Paleontology, paleoceanography, morphology, taxonomy, fisheries oceanography and laboratory and field studies of physiology and behavior have all contributed to knowledge about tuna comparative physiology. Not only does tuna physiology differ markedly from that of other fishes, tunas enrich the comparative perspective by their close approach to the functional limits imposed by physical and biological principles. Tunas offer a heuristic exception to general principles linking the high heat capacity and low O$_2$ content of water and the imposition of ectothermy on aquatically respiring animals. Temperatures in some ocean habitats increase tuna O$_2$ requirements to above the quantity available because of water's low O$_2$ solubility. Tunas derive physiological and ecological advantage by coupling counter-current heat exchange to the intrinsic inefficiency of muscle energy conversion. A temperature-insensitive Hb, endothermy and the capacity to modulate heat transfer enable tunas to gain partial independence from cold-water effects on temperature-dependent rate functions.

The richness of tuna comparative physiology lies in unanswered questions about thermal effects on RM and digestive, brain and sensory physiology, about blood flow regulation, about Hb–O$_2$ transport and temperature interactions in open (gills) and closed (capillaries) exchange venues, and about scaling. New findings about tuna depth penetration renew interest in their barobiology. Differences between tunas and bonitos deepen the comparative perspective, as do the independent evolution of comparable specializations in lamnid sharks and the occurrence of cranial endothermy in other teleosts.

In several respects, tuna physiological ecology parallels that of marine mammals: both make a high metabolic energy investment to acquire energy capital needed to sustain activity and for growth and reproduction. Tunas swim steadily in search of food and, like some marine mammals, dive to feed at depth, and some make long annual migrations between fertile, high-latitude feeding grounds and warmer waters favorable for reproduction and offspring success.

Tunas are at risk of over-exploitation and are vulnerable to the effects of global climate change. As recently as three decades ago, it was thought that tuna fishing methods would never succeed to the point that populations would be threatened, as is now true for Atlantic northern bluefin (a staple seasonal food resource in Mediterranean civilizations for over 3000 years!). The Pacific bigeye, now fished intensively on

fish-aggregating devices, is declining in number. Just as regions of the tropical ocean may be too warm for large skipjacks, ocean warming has the potential of making the breeding areas of the Gulf of Mexico too warm for adult bluefin, and high-latitude warming (where global change effects will be pronounced) will reduce upwelling and diminish the prey biomass important to migrating tunas.

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