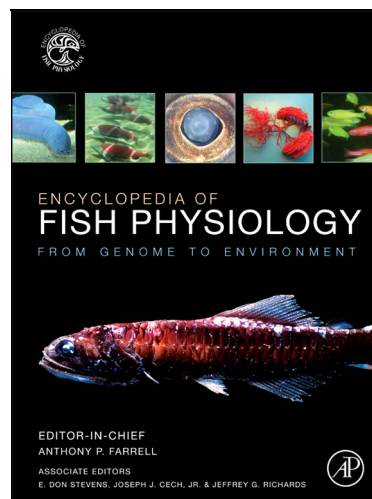


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## Endothermy in Tunas, Billfishes, and Sharks

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### Glossary

**Ectotherm** (adj. ectothermic) An organism whose body temperature is largely determined by heat exchange with its surroundings. It does not produce and retain enough metabolic heat to elevate its body temperature above ambient temperature, but may use behavioral mechanisms to regulate body temperature.

**Endotherm** An animal that uses its own metabolism as the major source of heat to maintain its body

temperature greater than that of the surrounding environment.

**Rete mirabile (pl. retia mirabilia)** A vascular network, usually consisting of a parallel array of both arterial and venous vessels with countercurrent flow. Retia facilitate transfer of heat or oxygen between the arterial and venous vessels. Rete is Latin for net or network, mirabile for 'wonderful' or 'miracle' (plural, retia mirabilia).

**Thermogenic tissue** A specialized heat-producing tissue.

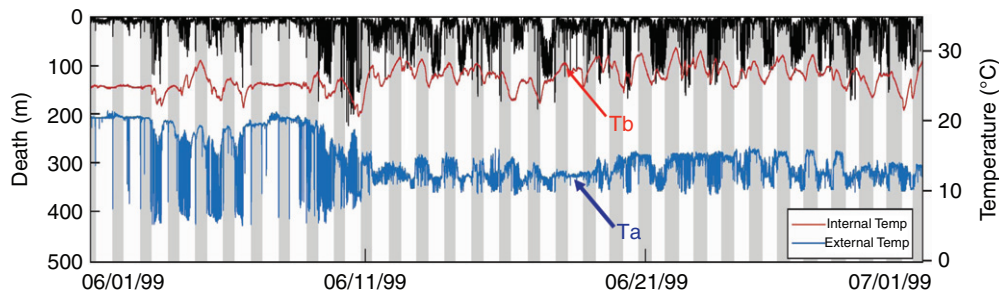
### Introduction

Powerful ocean predators such as swordfish, marlins, tunas, and some pelagic sharks are unique among fish for their capacity to maintain elevated temperatures of certain tissues even when swimming in cooler waters. Most fish are ectotherms, that is, their entire body temperature is the same temperature as the water in which they swim, primarily because they breathe with a gill. Body heat loss occurs as blood passes through the gills due to their large surface area optimized for gas exchange. Fish are surrounded by cooler ambient water, which has a much higher heat capacity than air. Thus, the core tissue temperatures of ectothermic fish are governed by the surrounding environment, not by metabolically derived heat production. Heat is rapidly and efficiently drawn out of the fish into the surrounding water, the gills acting as a convective cooling system.

Endothermy, the ability to maintain elevated body temperature by metabolic means, has been documented only within about 30 of the over 25 000 species of fishes. These remarkable examples illustrate the challenges of overcoming the physical constraints and are restricted to large, predatory, open ocean fishes – one assemblage among the teleosts the Scombroidei, which includes mackerels, tunas, and billfishes, and the other assemblage among the sharks of the family Lamnidae.

The evolutionary transition from ectothermy to endothermy required both an increase in heat production by elevating metabolic capacity plus the evolution of mechanisms to reduce the rate of heat loss. Among these endothermic fish, two distinct strategies for elevating tissue temperatures have evolved: systemic and cranial endothermy. Examples of systemic endothermy occur in the sharks of the family Lamnidae (white shark, makos, salmon shark, and porbeagle) and tunas (bluefins, albacore, and skipjack). Both groups have species that have expanded their range into northern waters, often swimming in frigid seas but can have regions of their body at temperatures 20 °C or more above ambient water temperature (**Figure 1**). An example of cranial endothermy is the monotypic swordfish (*Xipbias gladius*), where highly specialized extraocular muscles are modified into a thermogenic organ that warms just the brain and eyes up to 15 °C above ambient water temperatures.

Some of the literature refers to these fish as heterotherms rather than endotherms. Their point is that the entire body temperature is not constant (some tissues may be warm while others are cold) or temporally (the stomach may be warm only after a large meal). The use of endothermy herein stresses that the source of the heat is metabolic heat produced by the fish rather than from the environment.



**Figure 1** An archival tag record demonstrating endothermy over a 3-week period in an Atlantic bluefin tuna swimming in the North Atlantic. Modified from Walli A, Teo SLH, Boustany A, et al. (2010) Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. *PLoS ONE* 4(7): e6151 (doi:10.1371/journal.pone.0006151).

## Systemic Endothermy

Endothermy in fish evolved in groups that attain large body size. A requirement of endothermy is an internal heat source, which occurs in some species as an increase in metabolic rate, or evolution of high aerobic capacity within a tissue. Countercurrent heat exchangers or retia mirabilia are required to conserve the metabolic heat (see also **Design and Physiology of Arteries and Veins: The Retia**). Tunas (Scombridae, Tribe Thunnini (*Katsuwonus*, *Euthynnus* and *Auxis*)) and sharks (Lamnidae) are unique among fishes because of their unique ability to maintain elevated tissue temperatures above ambient water temperatures in their locomotory muscle, viscera, brain, and eye muscles. Dr. Frank Carey of Woods Hole Oceanographic Institution was the first scientist to measure tissue temperatures in free-swimming tuna, and subsequently made major contributions to our understanding of endothermy in fishes. Some tuna species, similar to birds and mammals, have an elevated standard metabolic rate and numerous specializations associated with increased oxygen delivery to the tissues. The heat generated by this elevated metabolic rate is retained within these tissues with vascular countercurrent heat exchangers embedded in the systemic circulation.

Cranial endothermy in the tunas and lamnid sharks occurs through a heat exchanger retia located in the circulation to the eyes and brain. To date, there has not been a heater organ-like tissue for thermogenesis identified in tunas or sharks; the heat sources are the highly aerobic extraocular muscles as well as the brain, which thus far have been shown to occur in the bluefin tuna group only. Heat conservation mechanisms involving vascular retia are found in the lamnid sharks as well as closely related thresher sharks of the family Alopidae.

In tunas and lamnid sharks, endothermy in locomotory muscle is associated with two distinct anatomical changes: (1) the movement of the red slow-twitch aerobic swimming musculature internally and forward in the body plan and (2) the insertion of a complex countercurrent heat exchanger in the circulation to the oxidative muscle mass



**Figure 2** A cross section through a tuna that illustrates the internal location of the aerobic muscle that powers endurance swimming. This location differs from most teleosts that have the aerobic red muscle located laterally near the surface of the fish, just beneath the skin. 1, aerobic red muscle; 2, white muscle.

to reduce conductive and convective heat loss. Strong convergence in structure and function is seen in these two lineages. Both have a very streamlined shape and a shift in the body plan such that the red muscles that power endurance swimming have a central position near the vertebral column (**Figure 2**). This differs from most teleosts that have the aerobic red muscle located laterally near the surface of the fish, just beneath the skin. The central position of the aerobic muscle source facilitates heat retention as the red muscle fibers are continuously recruited, contracting and generating heat during the sustained locomotion characteristic of these lineages. The central positioning of the red muscle in tunas and lamnid sharks has received considerable attention as a result of its role in endothermy; however, it primarily reflects the evolution of a unique locomotor style. This stiff-bodied thunniform and lamniform swimming is more efficient for drag reduction (see also **Buoyancy, Locomotion, and Movement in Fishes: Functional**

Properties of Skeletal Muscle: Work Loops and Undulatory Swimming). These fish generate thrust exclusively via the tail and restrict their propulsive movements to the caudal region rather than bending the whole body. Evolution of this locomotory form may be tightly coupled with the movement of the central aerobic muscle mass internally in addition to the use of this metabolic source of heat for endothermy.

In addition to the muscle heat, in some species of tunas and lamnid sharks the metabolic heat of digestive processes is conserved as well. Energy is expended (and heat is produced) during ingestion, digestion, absorption, and assimilation of a meal. When bluefin tunas digest a meal, they have a metabolic response that includes elevation of oxygen uptake called specific dynamic action (SDA) and the associated post-feeding thermogenesis (**Figure 6**; see also **Food Acquisition and Digestion: Cost of Digestion and Assimilation**). By having visceral retia mirabilia, the tunas and sharks retain the heat and warm the tissues involved in digestion of the meal. The entire muscle mass buffers visceral tissue from the surrounding aquatic heat sink to reduce conductive heat loss. Often, the muscle below the gut contains a very high fat content that probably adds to its insulative value.

An unusual aspect of endothermy in fishes is the requirement for a robust cardiac physiology as the hearts of all tunas operate at ambient water temperatures because they are not protected by retia mirabilia. The unusual physiological arrangement of endothermy in some tissues is unique among vertebrates and can result in a cold heart supplying the metabolic demands of warm tissues. In response to this, bluefin tunas and lamnid sharks have a higher capacity to cycle calcium ions in the heart cells that helps maintain beat-to-beat contraction at reduced temperatures. Results from molecular, structural, and physiological data indicate a significant role of mammalian-like calcium-induced calcium release in the cardiac myocytes of tunas and sharks. Thus, endothermic fish can protect their cardiac function in frigid seas using mechanisms that increase the capacity of the heart to function, ensuring delivery of oxygen to the metabolically active tissues required for warming the muscles, visceral, and cranial tissues.

### Cranial Endothermy

The elevation of cranial tissue temperatures has the same two main requirements: (1) a heat source based on aerobic metabolism plus (2) vascular countercurrent heat exchangers to retain the heat. The main source of metabolic heat in the cranium is the extraocular muscles, the muscles that move the large eyes of these visual predators.

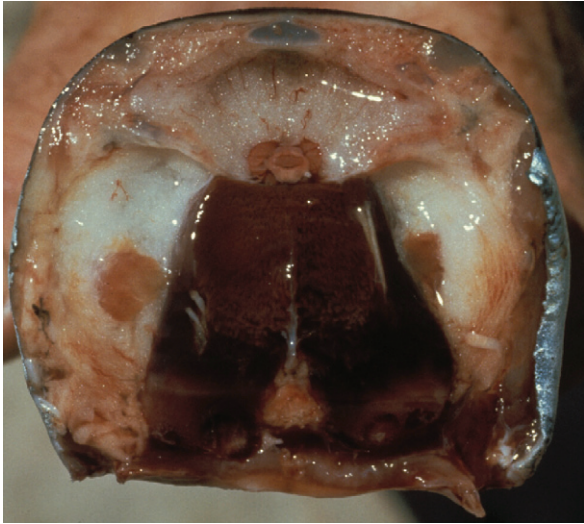
Cranial endothermy in tunas and sharks is not associated with a specific thermogenic tissue but with

conservation of heat from continuously active red aerobic swimming muscle (lamnid sharks) or large extraocular muscles (tunas). In the case of the sharks, an unusual arrangement occurs whereby the vein coursing from the aerobic swimming muscle travels to the orbital sinus behind the eyes to bathe an orbital retia mirabilia with warm venous blood, the heat from which can be retained in the cranial region. That is, metabolic heat produced in the swimming muscle is used to warm the brain. Less complex is the situation in tunas, where the aerobic eye muscles are disproportionately large relative to eye size for ectothermic species. These extraocular muscles are among the fastest contracting muscles in vertebrates, and fiber populations are enriched with the cellular machinery for superfast contraction: the sarcoplasmic reticulum (SR) and proteins that cycle calcium. The presence of aerobic muscle fibers within the extraocular muscles, already specialized for superfast contraction, provides this muscle with relatively high thermogenic capacity and underlies the evolution of heat retention mechanisms in the circulation to the brain and eyes. The extraocular muscle of billfishes is similarly large and fast contracting, but has an additional feature, a heater organ.

### Heater Organ Tissue

Some fish have evolved a heater organ for cranial endothermy. This thermogenic (heat producing) tissue, which warms only the brain and eyes, is found beneath the brain of all billfishes: swordfish, *X. gladius* (family Xiphiidae), marlins (*Makaira* sp.), spearfish (*Tetrapturus* sp.), and sailfish (*Istiophorous* sp.) (family Istiophoridae) and in one species of Scombrid fish, the butterfly mackerel (*Gastrophysa melampus*). It has also been reported in a monotypic genus, the slender tuna (*Allothunnus fallai*). The moonfish or opahs (Lamprididae) have also been reported to have a countercurrent heat exchanger behind the eye, but it remains unresolved as to whether thermogenic cells are involved. Cranial endothermy in these species involves the presence of a specialized thermogenic heater organ tissue that develops from extraocular muscle and is located beneath the brain and near the eyes. The thermogenic capacity has been shown by direct telemetry in the swordfish to warm the cranial cavity up to 15°C above ambient water temperature. The appearance of cranial endothermy independently of warming any other portion of the body indicates that there is a strong selective pressure for warming the brain and eyes.

The billfish heater organ is comprised of a mass of thermogenic tissue that is deep red in color with the appearance and texture of liver (**Figure 3**). It is associated with the superior rectus eye muscle in billfishes and with the lateral eye muscles in the butterfly



**Figure 3** Transverse section through the head of a swordfish showing the position of the heater tissue beneath the brain and within the orbit. The head is packed with fat to reduce conductive heat loss.

mackerel, where modified muscles from both sides of the orbital cavity converge at the base of the braincase. In the swordfish, the brain is embedded in the dorsal surface of the heater, at the basisphenoid bone that forms the base of the braincase, which has been reduced to a membranous sheath. Large amounts of adipose tissue surround and insulate the brain, eyes, and heater organ. The major difference between heater organs in the billfishes is that of size; the heater organ is largest in the swordfish – the total mass of heater organ tissue exceeds the mass of the heart. The eyes of the swordfish are equivalent in size to small grapefruits. Both the eyes and the heater organ are surrounded by insulating fat.

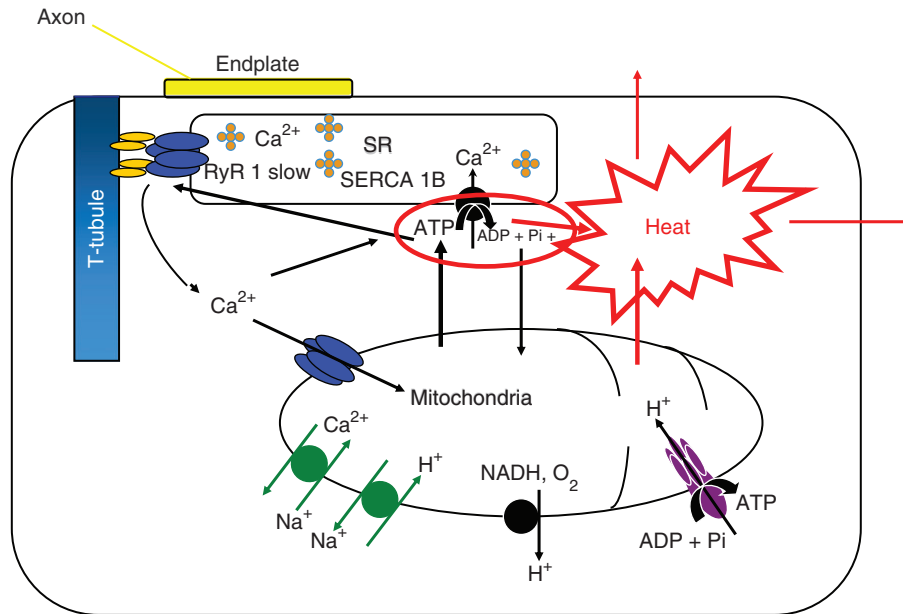
In addition to the adaptation of the eye muscle to generate heat, these fish also have well-developed retia to reduce heat loss. At its base, a countercurrent heat exchanger is formed from the carotid artery and the venous return from the heater to retain the heat produced by the heater organ. Billfishes have two separate blood supplies to the brain and eyes: one supplying oxygen and the other retaining heat. The carotid circulation divides into numerous capillaries that bathe the oxidative heater cells with blood. In addition to this warm blood supply to the retina, the billfishes, like most teleost fishes, have a separate oxygenated source of blood to the retina by way of the choroid retia mirabilia. The choroid retia is extraordinarily enlarged in the marlins and other Istiophorid billfishes, and is supplied with blood via a pathway separate from the heater organ insuring a well-oxygenated blood supply to the eye. These fish have a separate circulation to the retina because the blood coursing through the heater organ is depleted in oxygen by the time the warm blood gets to the retina.

## How Fish Have Built a Furnace Out of Muscle

The cells that make up the heater organ are modified skeletal muscle cells that are often called muscle fibers because they are multinucleate. They lack myofibrillar contractile proteins and are no longer involved in force generation but have an extremely high content of mitochondria and SR. In vertebrate skeletal muscle, contraction and relaxation are regulated by the concentration of calcium in the cytosol, which, in turn, is controlled by the SR and transverse tubule membranes. The SR of skeletal muscle cells is a highly organized intracellular membrane system that stores and releases  $\text{Ca}^{2+}$  in a highly regulated fashion. The SR has release channels (termed ryanodine receptors) that, when opened, allow  $\text{Ca}^{2+}$  to flow from the SR down its concentration gradient into the cytosol.  $\text{Ca}^{2+}$  is pumped back into the SR by the calcium ATPase (calcium pump protein), the major protein constituent of the SR bilayer. The calcium pumping consumes adenosine triphosphate (ATP) and heat is produced as a by-product of ATP production. If  $\text{Ca}^{2+}$  is cycled more than normal between the cytosol and the SR, then more ATP is consumed and more heat is produced. This is a key feature of the heater organ. In heater tissue and lacking extensive contractile protein, a thermogenic process is associated with  $\text{Ca}^{2+}$  cycling involving excitation–thermogenic coupling unlike the excitation–contraction coupling that normally occurs between the T-tubule, SR, and protein components of regular skeletal muscle.

Consistent with this role, certain morphological features stand out in all high power microscope pictures (electron micrographs) of heater tissue. The mitochondria of the heater cell are among the most densely packed in any cells in any animal, with as much as 63% of the cell volume being mitochondria. Also, located throughout the cytoplasm and in between the mitochondria is an extensive smooth membrane system comprised of tubules and membranous stacks. The tubules and membranous stacks are components of the two internal membrane components of muscle usually involved in excitation–contraction coupling, the SR. The very high oxidative capacity of the heater tissue also is reflected in high myoglobin concentration ( $400 \mu\text{mol kg}^{-1}$  wet weight) and in very high aerobic metabolic enzyme profiles.

Heater cells are innervated by a branch of the oculomotor nerve, and large clusters of acetylcholine receptors on the plasma membrane indicate that the cells are under nervous control similar to that in skeletal muscle. It is hypothesized that upon entering cooler water, nerve impulses to the heater cells result in depolarization of their cell membrane and that depolarization leads to  $\text{Ca}^{2+}$  release from the SR internal heater cell membrane



**Figure 4** A model of excitation–thermogenic coupling in heater cells. Thermogenesis in heater cells is proposed to occur via depolarization-induced Ca<sup>2+</sup>-release pathways. Nervous stimulation mediated by acetylcholine receptors at the endplate results in heater cell depolarization and DHPR–RyR1-mediated Ca<sup>2+</sup> release from the SR. Increased cytoplasmic Ca<sup>2+</sup> stimulates Ca<sup>2+</sup> transport and ATP turnover by SERCA 1B and mitochondrial influx and efflux pathways. The physiological properties of the RyR1-slow isoform expressed in heater cells may facilitate prolonged channel openings under these conditions (high Ca<sup>2+</sup> and the presence of adenine nucleotides) and promote further release of Ca<sup>2+</sup> in a futile cycle that results in thermogenesis. Abbreviations: T-tubule, transverse-tubule; SR, sarcoplasmic reticulum; SERCA, sarco/endoplasmic reticulum Ca<sup>2+</sup>-ATPase; RyR, ryanodine receptor. Modified from Morrisette JM, Franck JPG, and Block BA (2003) Characterization of ryanodine receptor and Ca<sup>2+</sup>-ATPase isoforms in the thermogenic heater organ of blue marlin (*Makaira nigricans*). *Journal of Experimental Biology* 206: 805–812.

system in much the same manner as occurs in a typical skeletal muscle through the Ca<sup>2+</sup> release pathway (Figure 4). That is, depolarization leads to a conformational change in the voltage-sensitive dihydropyridine receptors (DHPRs) or L-type Ca<sup>2+</sup> channels, which in turn induces the opening of SR Ca<sup>2+</sup> channels and release of Ca<sup>2+</sup> into the cytosol. Ca<sup>2+</sup> release initiates a cycle of calcium-induced Ca<sup>2+</sup> release. Similar to skeletal muscle, uptake of Ca<sup>2+</sup> back into the SR requires energy in the form of ATP produced by the numerous mitochondria. The majority of energy used in generating ATP (and consumed by the Ca<sup>2+</sup> pump) is released as heat – it is this heat that is used to heat the brain and eyes.

### Telemetry of Brain Temperature

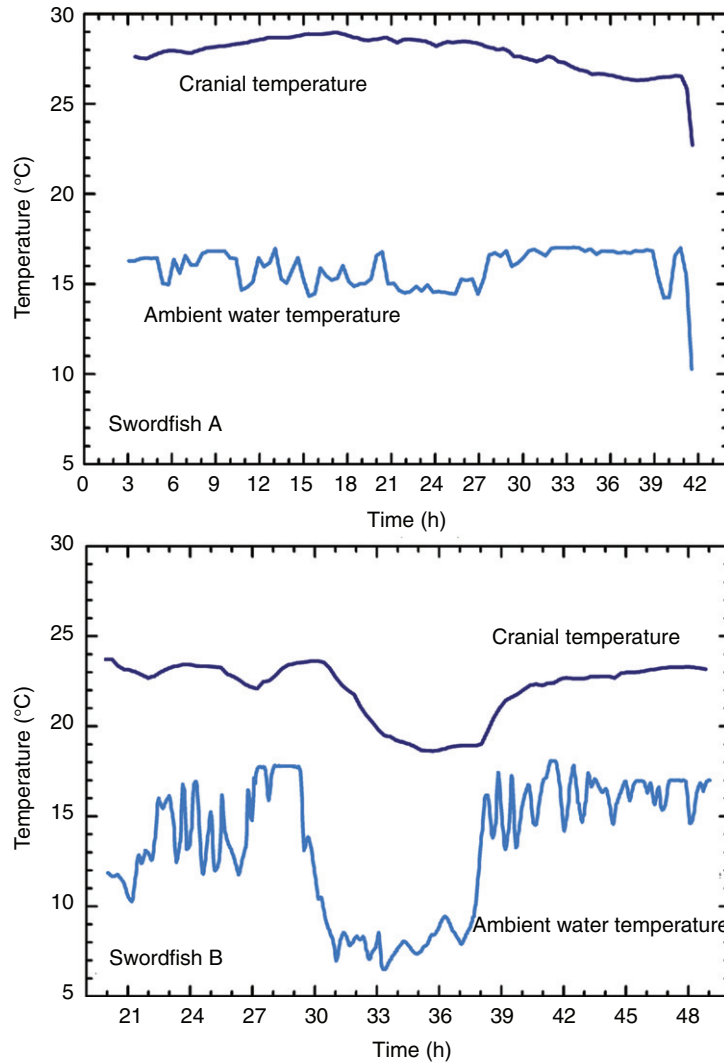
The best evidence for physiological regulation of brain temperatures comes from experiments with free-swimming swordfish conducted in the 1980s by Dr. Frank Carey. Swordfish have remarkable diel behavior, swimming to depths as deep as 600 m during the day in search of squid but spending most of the evening hours at the surface. During these vertical excursions, which primarily occur at dusk and dawn, the fish encounters rapid water temperature changes up to 19 °C in a short

period. Measurements of cranial temperature provide direct evidence that the fish are able to warm the cranial cavity. Temperature in the cranial cavity remained about 28 °C for 36 h while the fish encountered water temperatures that ranged from 13 °C to 17 °C (Figure 5).

### Why Be Warm?

The repeated evolution of endothermy in the scombroid fishes and lamnid sharks indicates that there is strong evolutionary selection for this energetically costly metabolic strategy. All endothermic lineages have species that have expanded their ranges into cool temperate waters and, in some cases, subpolar seas (Atlantic bluefin tunas and salmon sharks). This supports a niche expansion argument for the evolution of endothermy in fishes. There are several hypotheses on the advantages to warming of the brain, eyes, muscle, and visceral tissues.

In cranial endotherms such as swordfish, the warming of the brain and eye regions, the central nervous system and retina, is of key importance. Physiological processes such as synaptic transmission and the conduction of nerve impulses are temperature sensitive. Studies on the sensitivity of the retina indicate that vision and flicker frequency, as well as temporal resolution of a light flash,

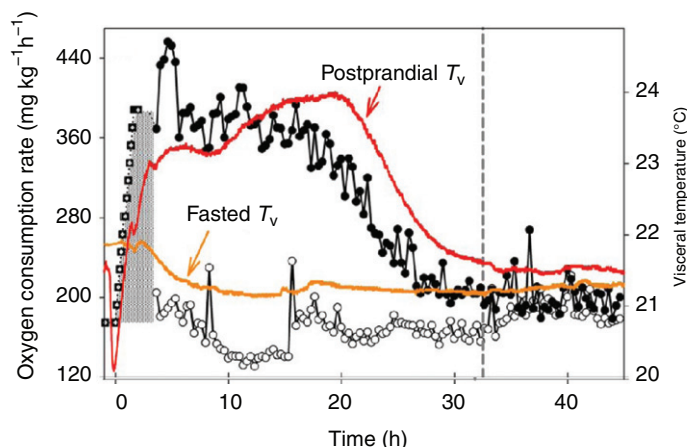


**Figure 5** Telemetry record of cranial temperature and ambient water temperature from a free-swimming swordfish. Zero on the x-axis is midnight, top line is cranial temperature, and bottom line is water temperature. Swordfish swim to depths as deep as 600 m, typically at dusk and dawn. Modified from Carey FG (1990) Further observations on the biology of the swordfish. In: Stroud RH (ed.) *Planning the Future of Billfishes*. Savannah, GA: National Coalition for Marine Conservation.

are thermally sensitive. The warming of the eye and specifically the retina has been shown experimentally to significantly improve visual acuity, specifically the temporal resolution of nervous signals by the retina. Warming of the retina may improve the ability to detect prey in the dimly lit mid-waters (light penetration ceases around 1000 m; (see also **Deep-Sea Fishes**). Thus, fish with warm eyes can detect the rapid motion of prey species better than fish with cold eyes. Because these fish are fast-swimming predatory fishes, improvements in the temporal resolution mean that the swordfish eyes are operating faster than prey at the same temperature as the surrounding water. The convergence of cranial endothermy in several species indicates that there is strong selection for warming of the eyes and brain. Cranial endothermy has evolved multiple times in large

predatory fish that experience cooler waters at high latitude distributions (temperate or subpolar seas) or at depth. Thus, warming of sensory structures in the cranium appears to be key to occupation of the colder (both at high latitude and at depth) as well as dimly lit environs.

Studies in tuna also indicate that warming of the swimming muscle permits them to generate more power that results in enhanced locomotory performance because power output of muscle is highly temperature dependent. A countercurrent heat exchanger that could maintain a 10°C temperature differential would typically double maximum muscle power output and the frequency at which maximum power is generated. The deep slow muscle of a tuna operates at higher temperatures than slow muscle from ectothermic sister taxa such as bonito and has been shown to generate more power. However,



**Figure 6** Traces of fasted and digesting oxygen uptake rate ( $MO_2$ ; open and closed circles, respectively) and visceral temperature ( $T_v$ ) from Pacific bluefin tuna (*Thunnus orientalis*) swimming at  $1 \text{ BL s}^{-1}$  at  $20^\circ\text{C}$ . Spikes in  $MO_2$  for the fasted trace resulted from short bursts of unsteady swimming. Modified from Clark TD, Brandt WT, Nogueira J, et al. (2010) Postprandial metabolism of Pacific bluefin tuna (*Thunnus orientalis*). *Journal of Experimental Biology* 213.

internal warm muscles are more thermally sensitive to temperature changes than more superficially located swimming muscles in tuna. This suggests evolutionary specialization for operation at higher, but also in relatively stable temperatures for function.

Digestion, like vision and muscle power, is temperature sensitive. An example of a tuna warming its viscera after a meal is shown in **Figure 6**. Food resources are ephemeral in the open ocean and often spread over large distances. Acquiring a meal quickly, digesting, and being able to take on more energy quickly is a matter of survival. Increasing the temperature of the viscera after a meal hastens digestion, largely because the action of enzymatic degradation of the meal is very temperature sensitive. Thus, when a tuna swimming in  $10^\circ\text{C}$  water warms its gut from 10 to  $30^\circ\text{C}$  after a meal, it decreases the time to digest the meal about threefold. Considered over a longer time period, for example, a week or a month, a tuna that warms its viscera can eat more if it can digest faster, and thus grow more rapidly than if it did not warm its gut. That is, the advantage of the warm cecum is that protein is digested in about one-third the time so that these tuna can process about three times as much food per day.

In summary, these large, fast, oceanic predators have a number of specializations that permit them to achieve tissue temperatures higher than ambient water temperatures. Most important are the retia to conserve the heat, and an increase in metabolic heat production. Unique to a few of them is the evolution of a tissue specialized for the generation of heat to achieve high brain and eye temperatures, the heater organ.

See also: **Buoyancy, Locomotion, and Movement in Fishes:** Functional Properties of Skeletal Muscle: Work Loops; Undulatory Swimming. **Deep-Sea Fishes.**

### Design and Physiology of Arteries and Veins: The Retia. Food Acquisition and Digestion: Cost of Digestion and Assimilation.

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