HEAT EXCHANGE IN THE YELLOWFIN TUNA, *THUNNUS ALBACARES*, AND SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND THE ADAPTIVE SIGNIFICANCE OF ELEVATED BODY TEMPERATURES IN SCOMBRID FISHES

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ABSTRACT

Thunnus albacares and *Katsuwonus pelamis* are warm-bodied fish and use retia mirabilia as countercurrent heat exchangers. Both species have four sets of lateral exchangers, two epaxial and two hypaxial, each consisting of a large cutaneous artery and vein and rete. *Katsuwonus pelamis* has a central exchanger, located within the haemal arch, which consists of the dorsal aorta, the posterior cardinal vein, and a large vertical rete. The central heat exchanger in *T. albacares*, while also in the haemal arch, is simpler, consisting of two small "wing-shaped" retia on either side of the dorsal aorta and cardinal vein.

The adaptive significance of the specialization for heat conservation is discussed. Body temperatures, thermal profiles, and the natural histories of different warm-bodied species are compared, and warm fishes are contrasted with scombrids that do not conserve heat. The skipjack tunas, *Euthynnus* and *Katsuwonus*, have well-developed central heat exchangers and are much warmer than *T. albacares*. Higher body temperatures in skipjacks seems related to their requirement for a higher basal swimming speed and their faster burst speed.

Comparisons on the basis of existing knowledge about the two phyletic groups of *Thunnus* reveal few differences in swimming ability or factors related to locomotion. The bluefin group, consisting of *T. thynnus*, *T. maccoyii*, and *T. alalunga*, however does contrast with the yellowfin group (*T. albacares*, *T. atlanticus*, and *T. tonggol*) by maintaining generally higher body temperature differentials, having incomplete vertebral circulation through the absence of a posterior cardinal vein, and occurring at higher latitudes.

Scombrids (mackerels, bonitos, and tunas) are pelagic, oceanic fishes that are highly adapted for continuous swimming. Some of the more advanced scombrids (principally frigate mackerels, *Auxis*; skipjack tunas, *Euthynnus* and *Katsuwonus*; and tunas, *Thunnus*) have evolved the capacity to conserve heat generated by the continuous metabolic activity of their swimming muscle and thus maintain body temperatures that are warmer than ambient seawater (Carey et al. 1971; Carey 1973). There has been convergent evolution for this specialization in mackerel sharks (Isuridae) a highly active, continually swimming group (Carey and Teal 1969a).

Warm-bodied fish retain heat by using retia mirabilia (= wonderful network) as countercurrent vascular heat exchangers. The principal advantage of a high and fairly constant body temperature is facilitation of continuous swimming by increasing the frequency of muscular contractions, thus increasing available swimming power (Carey et al. 1971). Also, warm-bodied fish probably achieve a marked independence from environmental temperature permitting them to make rapid vertical and latitudinal migrations without the necessity of thermal acclimation.

In their extensive review of warm-bodied fish, Carey et al. (1971) described two types of heat exchanger, lateral and central. Lateral heat exchangers (Figure 1) are present in many warm-bodied species but are best developed in the genus *Thunnus* where they consist of four sets of longitudinal subcutaneous arteries and veins (two epaxial and two hypaxial), each with adjoining layers of retial vessels that penetrate the red muscle near the midplane (Gibbs and Collette 1967; Carey et al. 1971). Large, highly developed central heat exchangers (Figure 1) are found in *Euthynnus*, *Katsuwonus*, and *Auxis*. These are located below the vertebral column, in the haemal arch, and consist of a large vertical rete formed from branches of the dorsal aorta and the posterior

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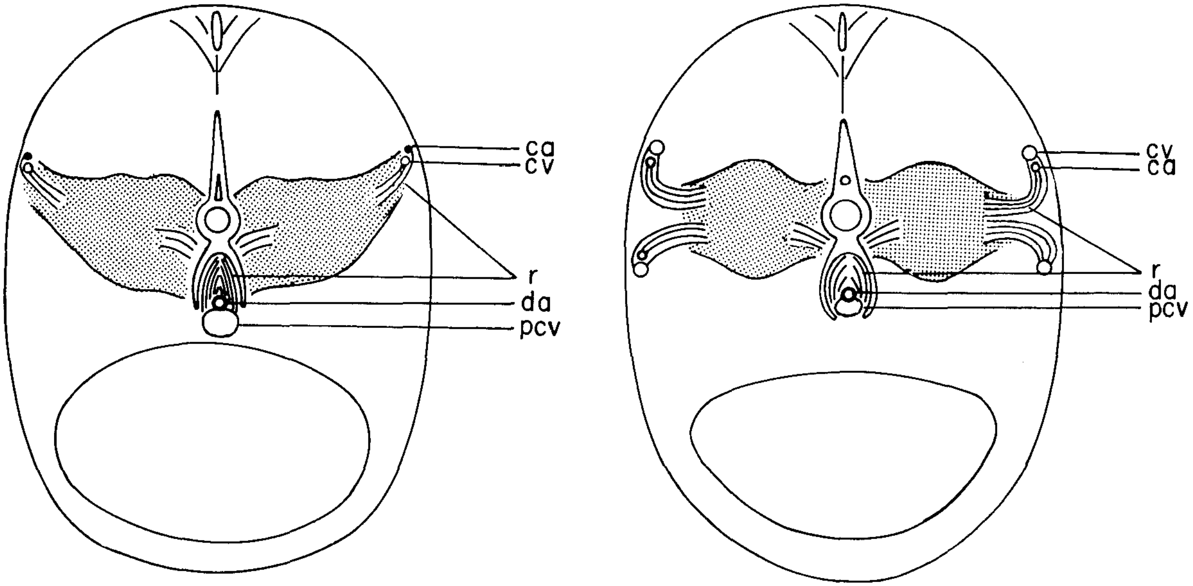
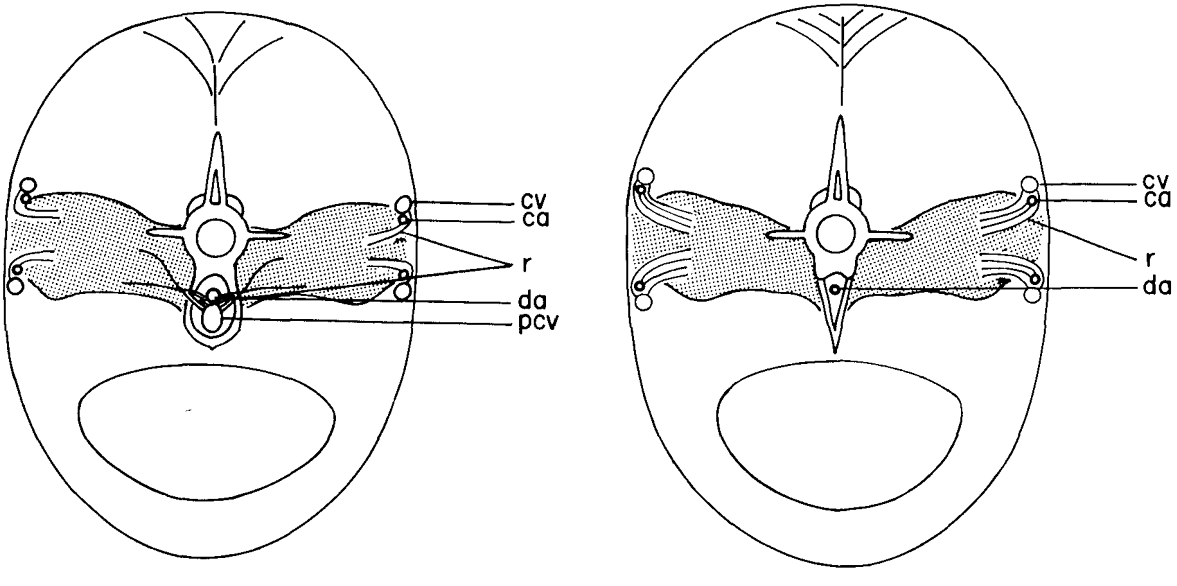


E. lineatus

K. pelamis



T. albacares

T. thynnus

FIGURE 1.–Transverse sections of four warm-bodied species showing the position of central and lateral retia mirabilia (r) that function as vascular heat exchangers. The major blood vessels supplying retia are: dorsal aorta (da), posterior cardinal vein (pcv), cutaneous arteries (ca), and veins (cv). Veins are shown with larger diameters and thinner walls. Red muscle distribution (shaded areas) is also depicted. Noted that the position of cutaneous arteries and veins in *Euthynnus lineatus* is reversed compared to that in other species and that only an epaxial pair is present. Also, *Thunnus thynnus* does not have a posterior cardinal vein. Frigate mackerels (*Auxis*) are not shown but are very similar to *Euthynnus*. Data contained in this figure are from various sources cited in the text.

cardinal vein (Kishinouye 1923; Godsil 1954; Carey et al. 1971; Carey 1973; Graham 1973).

Kishinouye (1923: 377; see discussion of *Neothunnus*, a synonym of *T. albacares*) described a special subspinal vascular plexus or "kurochiai" in the yellowfin tuna, *T. albacares* (Bonnaterre), and recent studies have indicated that this structure is a central heat exchanger (Carey et al. 1971; Carey 1973). The kurochiai has not been fully described, nor has the relationship between it and *T. albacares'* well-developed lateral heat exchangers been considered. Body temperatures of fresh-caught and swimming yellowfin tuna are known to be less than those of skipjack tunas and some other tuna when measured under similar conditions (Barrett and Hester 1964; Carey and Teal 1969b; Stevens and Fry 1971; Carey 1973), but where heat is distributed in the body (thermal profiles) has not been determined for either *T. albacares* or the skipjack tuna *K. pelamis* (Linnaeus).

The purpose of this study is to investigate the relationship between body temperature and the types of heat exchanger in *T. albacares*. The patterns observed for this species and *K. pelamis* are compared with those of other warm-bodied fish. Body temperatures and thermal profiles of fresh-caught *T. albacares* and *K. pelamis* are reported, and their central heat exchangers are described. The general structure and circulation pattern of these species' heat exchangers are compared with those of the bluefin tuna *T. thynnus*, and other skipjack tunas, *Euthynnus*, and are discussed in terms of their relation to differences in body temperature, morphology, swimming capability, and the natural history of these species. Studies of this type may enable us to understand why there are different kinds of heat exchangers and how these evolved.

MATERIALS AND METHODS

Eleven *T. albacares* (360 to 700 mm fork length; weight, 1 to 5 kg) and four *K. pelamis* (500 to 600 mm, 3 to 4 kg) were caught by surface trolling in the Gulf of Panama and brought on board within 30 to 90 s of being hooked. Red and white muscle temperatures of these specimens were immediately taken with a fast-reading hypodermic thermistor probe (Yellow Springs Instrument No. 513)[2] that had been calibrated against a mercury thermometer. Measurements were made deep (near the vertebrae), midway from the vertebrae to the skin, and subcutaneously at several positions along the fishes' lateral midplane, from the operculum to the tail, in order to determine the relative contribution of the lateral and central heat exchangers to heat distribution. All temperatures were rounded to the nearest 0.5°C. Body temperatures of shaded fish remained fairly constant during the first 10 min after capture, and all measurements were made within this time.

A criticism that has been directed against the measurement and interpretation of temperature data from fresh-caught fish is that burst swimming to catch a troll lure, or frenzied swimming, together with struggling once hooked may increase body temperatures above typical values. This probably has some validity, but the effects of struggling and handling seem generally overrated. With telemetry, Carey (1973) has shown that free-swimming *T. thynnus* have body temperatures very similar to captured fish. Also, Barrett and Hester (1964) found that immediately captured yellowfin tuna and those that had been tethered for a few minutes had similar temperatures.

Large frozen *T. albacares* (800 to 1,400 mm, 8 to 42 kg) were obtained from a commercial fishing vessel, and a range of sizes was dissected to determine red muscle distribution, the position, size, and structure of the heat exchangers, and the dimensions of retial vessels. Specimens of *K. pelamis* were also dissected, and measurements were made.

RESULTS

Body Temperatures

Average deep, intermediate, and subcutaneous red muscle temperatures of eight *T. albacares* (caught in surface water of 28.5°C) were 30.5°, 30.5°, and 29.5°C. Three specimens caught in 30°C water had average deep body temperatures of 32.5°C. Elevated temperatures in *T. albacares* occur along the body from the pectoral fins to as far as the third or fourth finlet. The warm region also extends laterally through a large portion of the red muscle. Highest body temperatures were always found in the red and white muscle along and near the lateral midplane of the body. *Katsuwonus pelamis* is warmer than *T. albacares*, and its warm

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

region extends laterally to just below the skin. The average deep, intermediate, and subcutaneous red muscle temperatures of four *K. pelamis* (caught in 28.5°C surface water) were 35°, 35°, and 33°C. Deep white muscle temperatures in these fish averaged 34°C; brain temperatures were 33°C. The temperatures reported here for *T. albacares* and *K. pelamis* are in good agreement with those found for these species by other investigators (Barrett and Hester 1964; Stevens and Fry 1971).

Heat-Exchanger Structure and Red-Muscle Distribution

Thunnus albacares

The distribution and structure of the lateral heat exchangers found for *T. albacares* in this study agree fully with those described by Gibbs and Collette (1967) and are summarized here with new notes on variations related to size. Epaxial and hypaxial arteries and veins subdivide from their respective trunks at about vertebrae no. 10 and extend along the body to about two-thirds of the way from the second dorsal fin to the tail (vertebrae no. 29 or 30) where they are rejoined by a commissure. One row of retial vessels originates from the lateral edge of each artery and vein, and this is consistent with the observations of Kishinouye (1923, as *Neothunnus*). *Thunnus albacares'* lateral retia are long and strongly curved towards the center of the body. Retial curvature was not observed in specimens smaller than 3 kg. Cutaneous vessel diameters increase dramatically with increased size, ranging from 0.5 to 1.0 mm (artery and vein) in a 1.1-kg specimen to 6.0 to 8.0 mm in a 42-kg fish. Retial vessels ranged from 0.05 to 0.1 mm in diameter.

The central heat exchanger in *T. albacares* extends from the first to the second dorsal fins (vertebrae no. 8 or 9 to 20) and is situated immediately below the vertebrae in the haemal arch. This structure is composed of the dorsal aorta, the posterior cardinal vein, and their small vessels that form two "wing-shaped" retia (Figure 2). Diameters of the dorsal aorta and posterior cardinal vein only increase slightly with increasing size, ranging from 1.5 to 3.0 mm in a 2.7-kg fish to 3.5 to 4.0 mm in a 42-kg specimen. This contrasts markedly with the large weight-related change in the diameters of the lateral blood vessels. The central retia originate as thick bundles in the haemal arch, then extend supralaterally and pass through vertebral foramina into the red muscle. In the muscle these vessels flatten into broad continuous sheets of alternating veins and arteries (0.1 to 0.2 mm in diameter) that are only one layer thick (Figure 2). This layer penetrates far into the muscle, from 18 mm in a 2.7-kg fish to 40 mm in a 42-kg fish.

Red muscle in *T. albacares* appears in thin bands along each side of the fish at the level of the vertebrae (Figure 2). Only red fibers from the hypaxial muscles actually reach the vertebrae, but epaxial and hypaxial muscle both extend well toward the fishes' side. Longitudinally, red muscle extends from behind the transverse septum (vertebrae no. 6 or 7) to as far as the fifth finlet (vertebrae no. 28 or 29) and is fairly uniform in thickness and shape (cf. Kishinouye 1923, Plate XVII, as *Neothunnus*). As was found for *E. lineatus* (Graham 1973) and, as would be expected, there is good agreement in the lineal distribution of red muscle and the lateral and central heat exchangers of *T. albacares.*

Katsuwonus pelamis

Except for its higher position in the body, the central exchanger of *K. pelamis* (Figure 3) is very similar to that of *Euthynnus* and *Auxis*, consisting of the closely associated dorsal aorta and posterior cardinal vein and a thick vertical rete, all in the haemal arch (Kishinouye 1923; Godsil 1954; Graham 1973). Just posterior to the pectoral fins in a 580-mm (about 4 kg) specimen, the following vessel diameters were measured: dorsal aorta, 2.0 mm; posterior cardinal vein, 4.0 mm; retial vessels, 0.05 to 0.1 mm. At its center (Figure 3), vessels in the central rete of this fish were 8.0 mm long.

Lateral heat exchangers are better developed in *K. pelamis* than in either *Euthynnus* or *Auxis* (Figure 1). Both epaxial and hypaxial sets of cutaneous vessels, with retia, are present, but they are further apart than in *T. albacares* (Figure 1), reflecting the laterally thicker wedge of red muscle in *K. pelamis* (see below). The cutaneous vessels are smaller than in *Thunnus.* The most developed retial vessels occur anteriorally but are variable in their position, length, and the direction they penetrate red muscle (cf. Godsil and Byers 1944, Figure 15).

Red muscle in *K. pelamis* is thicker than in *T. albacares* but does not appear to extend as far into the tail. In a transverse section (Figure 3), both

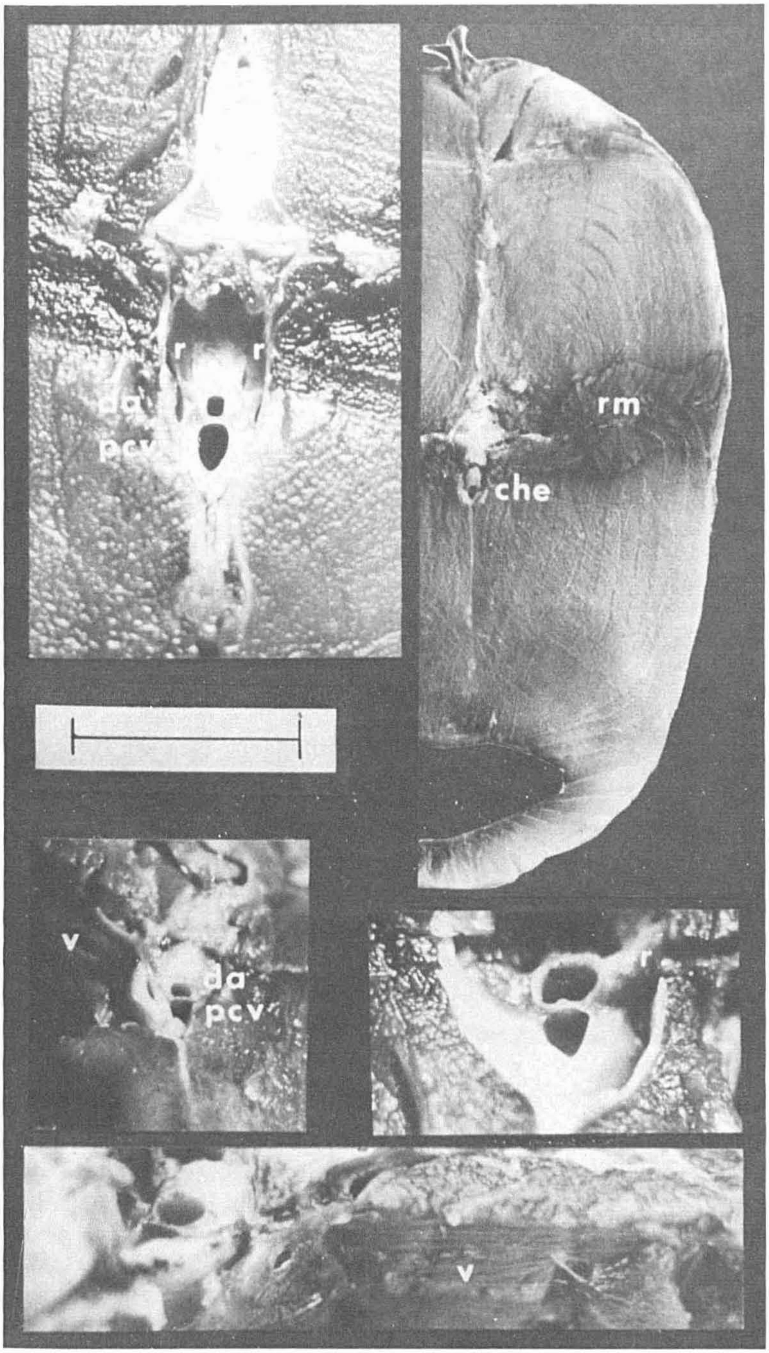

FIGURE 2.—Central heat exchanger of *Thunnus albacares*. (Top right, scale = 6.5 cm): Transverse sections showing the position of red muscle (rm) and the central heat exchanger (che). (Top left, scale = 1.5 cm): Transverse section of the che showing the dorsal aorta (da), posterior cardinal vein (pcv), and retia (r). (Middle right, scale = 2 cm): A close view of the che showing the da, pcv, and two wing-shaped retia that proceed supralaterally from the vessels. (Middle left, scale = 1.2 cm): A ventrolateral view of the da, pcv, and the sheet of vessels (v) outside the haemal arch that penetrate red muscle. (Bottom, scale = 2.0 cm): Ventrolateral view showing the che on the left and the thin sheet of vessels in red muscle.

hypaxial and epaxial red muscle reach the vertebrae. Longitudinally, shape as well as thickness of red muscle varies at different points (cf. Kishinouye 1923, Plate XVII). Generally, red muscle in *K. pelamis* appears to have more ligaments than *T. albacares*. In both species the myomeres are continuous through red and white muscle (Figures 2, 3), but red and white muscle are easily distinguished and separate with slight teasing.

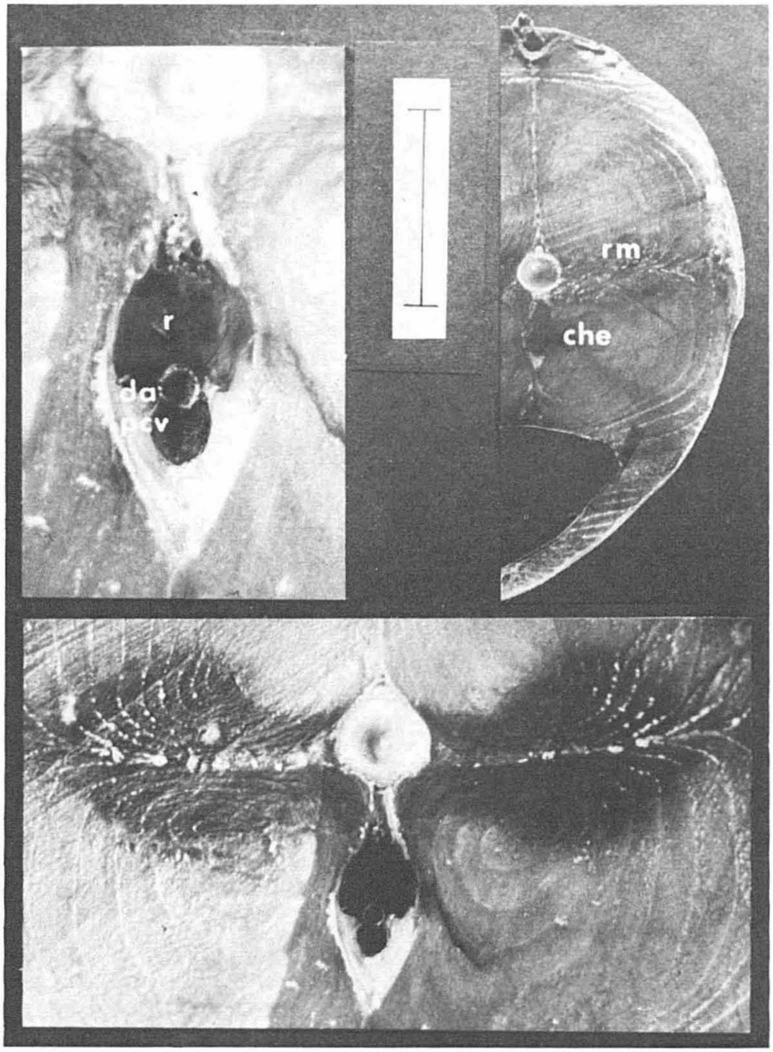

FIGURE 3.–Central heat exchanger of *Katsuwonus pelamis*. (Top right, scale = 5.6 cm): Transverse section showing the position of the central heat exchanger (che) and red muscle (rm). (Top left, scale = 1.1 cm): Close view of the rete (r), the dorsal aorta (da), and the posterior cardinal vein (pcv) in the haemal arch. (Bottom, scale = 1.9 cm): Red muscle and the central heat exchanger.

COMPARISON OF *KATSUWONUS*, *EUTHYNNUS*, *AUXIS*, AND *T. ALBACARES*

Differences in Heat Exchangers

Central heat-exchanger differences can be summarized as follows: *Katsuwonus*, *Euthynnus*, and *Auxis* have only a single vertical rete whereas *T. albacares* has two much smaller retia. *Thunnus albacares'* central exchanger is immediately below the vertebral centrum (Figures 1 and 2) while in *K. pelamis* it is lower, about midway between the vertebrae and the coelomic cavity, and in *Euthynnus* and *Auxis* it is quite low, occurring just above the coelom (Kishinouye 1923; Godsil 1954; Graham 1973). In *E. lineatus* and *E. alletteratus*, and *K. pelamis* that I have examined, and in *Auxis* (Godsil 1954), the dorsal aorta is actually embedded in the dorsal side of the posterior cardinal vein and is surrounded by a vast network of retial vessels which in effect bathes the aorta in venous blood. This structure has been interpreted as allowing the rete to occupy a full arc over the vessels, thus maximizing its heat-exchanging area (Graham 1973).

Both *K. pelamis* and *T. albacares* have two pairs of lateral exchangers. *Katsuwonus* has two somewhat variable rows of retial vessels in each lateral exchanger while *T. albacares* only has one. *Euthynnus* and *Auxis* (Figure 1) have only a small pair of epaxial heat exchangers.

Thermal Profiles of Fish with Central Exchangers

Lateral midplane thermal profiles of *T. albacares* and *K. pelamis*, taken in the red muscle just posterior to the pectoral fins, illustrate general differences in thermal profiles and body temperatures between these species, *E. lineatus*, and *T. thynnus* (Figure 4). *Katsuwonus* and *Euthynnus* have much warmer core temperatures than *T. albacares*, but warmest temperatures in *Euthynnus* are restricted to a fairly narrow zone around the vertebral column. *Euthynnus'* profile therefore seems related to its poorly developed lateral exchangers (also red muscle is very thick in the center and thinner laterally, Figure 1) and, based on structural similarities, this type of thermal profile would be predicted for *Auxis*. *Katsuwonus* on the other hand, with its lateral exchangers has heat widely distributed across its body.

Thunnus albacares, with a small central exchanger and well-developed lateral exchangers has a widely distributed warm region although it is much cooler than *K. pelamis* and *E. lineatus* (Figure 4). The dimensions of *T. albacares'* cutaneous vessels increase at a much faster rate with increased body weight than do the dorsal aorta and posterior cardinal vein, and in larger fish a greater proportion of blood flow would occur through lateral vessels which might change the thermal profile.

COMPARISONS WITHIN THE GENUS *THUNNUS*

Heat Exchangers and Thermal Profiles in *T. albacares* and *T. thynnus*

Comparative studies of the vascular anatomy of *Thunnus* show different levels of structural complexity in the heat-exchanging systems (Kishinouye 1923; Godsil and Byers 1944; Gibbs and Collette 1967) which relate to thermal profiles and body temperatures. In *T. thynnus*, lateral heat exchangers are used solely (Carey and Teal 1966). Two rows of retial vessels emanate from each cutaneous artery and vein (only one row occurs in *T. albacares*), and these extend axially for a long distance (Carey et al. 1971). Reliance upon cutaneous circulation is so extensive in *T. thynnus* that the dorsal aorta is reduced in diameter and the posterior cardinal vein is absent. In warm water *T. thynnus* is about the same temperature as *T. albacares*, but its thermal profile (Figure 4) reflects the exclusive presence of lateral heat exchangers in that warmest temperatures are found in the middle of the muscle, while the center of the fish is cooler (Carey et al. 1971). (Again, thermal profiles probably change with body size.)

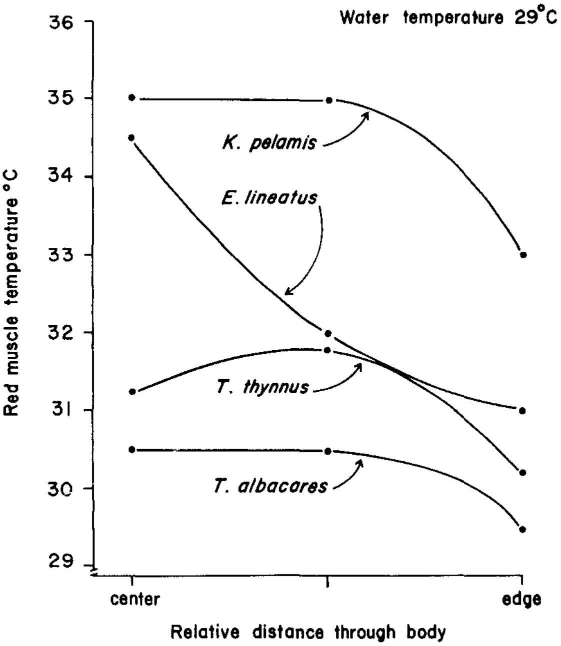

FIGURE 4.–Lateral midplane thermal profiles from the center (near the vertebrae) to the edge (subcutaneous) of red muscle in four species of warm-bodied fish. (Data for *Thunnus thynnus* were provided by F. G. Carey, that for *Euthynnus lineatus* are from Graham 1973).

Anatomical Features and Phyletic Groupings Related to the Presence or Absence of Complete Vertebral Circulation

In their comprehensive study of the genus *Thunnus*, Gibbs and Collette (1967) recognized seven species which, on the basis of 18 characters, were separated into two phyletic groups: the bluefin tuna group, *T. thynnus*, *T. alalunga*, and *T.*

maccoyii; and the yellowfin tuna group, *T. albacares, T. atlanticus,* and *T. tonggol.* (The seventh species, *T. obesus,* has traits in common with both groups and will be discussed later.) Several of the characters used (Gibbs and Collette 1967, Table 4) to distinguish these groups are related to the presence or absence of complete vertebral circulation (both a dorsal aorta and posterior cardinal vein present). The yellowfin tuna group has a posterior cardinal vein, the bluefin tuna group does not. Another striking difference is the presence of large striations and vascular cones on the livers of fish in the bluefin tuna group. The importance of this is discussed below.

There are several structural modifications in the vertebrae of the yellowfin tuna group which permit the passage of more or larger blood vessels through the haemal arch. Prezygapophyses arise far more ventrad on the haemal arch, postzygapophyses are longer, and the inferior foramina are larger (Gibbs and Collette 1967, Figures 10-13). In describing these vertebrae, Gibbs and Collette (1967:80) remarked that the development of the vertebral openings and processes in the yellowfin tuna group is almost as complex as that in *Auxis, Euthynnus,* and *Katsuwonus.* The presence of complete vertebral circulation and appropriate modifications in the vertebral column suggested to me that other species in the yellowfin tuna group, in addition to *T. albacares,* may have central heat exchangers. I have examined a preserved section of vertebral column from *T. atlanticus* (collected in the Gulf of Mexico and sent to me by F. G. Carey) and *T. tonggol* (obtained by G. Sharp) both of which have a central exchanger like that of *T. albacares.*

ADAPTIVE SIGNIFICANCE OF DIFFERENT HEAT EXCHANGERS, BODY TEMPERATURES, AND THERMAL PROFILES

Heat exchangers in *T. albacares* differ from those of *K. pelamis* and *E. lineatus,* and among these three species, there are marked differences in body temperatures and thermal profiles (Figure 4). *Thunnus albacares* and *T. thynnus* also have different heat exchangers, different body temperatures, as well as different thermal profiles depending on body size. Are there morphological features related to locomotion, or ecological factors, such as geographical distribution patterns or feeding behavior, that would explain thermal and anatomical differences between *K. pelamis* or *E. lineatus* and *T. albacares* or between species of *Thunnus*?

Comparisons Within the Genus *Thunnus*

The morphologies and locomotion of *T. thynnus* and *T. albacares* have not been compared. There are some data; however it is diffuse and mostly anecdotal, and it does not suggest functional differences in these two species or in the bluefin and yellowfin tuna groups of *Thunnus.*

If species in the yellowfin and bluefin tuna groups are compared on the basis of existing body-temperature data (cf. Carey et al. 1971, Table 1), it is apparent that species in the yellowfin tuna group have lower relative temperatures than those in the bluefin tuna group. Ambient water temperatures are not the same for these different species, and only a general comparison is possible. Still, these differences agree with the known differences in *T. albacares* and *T. thynnus* (Carey and Teal 1969b; Carey 1973) and are suggestive of a general trend of body-temperature differences that might in turn reflect a significant functional difference between the two taxonomic groups.

A feature in the natural history of species in the yellowfin and bluefin tuna groups that clearly separates them, and relates to their anatomical and temperature differences as well, is the water temperature that they normally inhabit. *Thunnus maccoyii* and *T. alalunga* of the bluefin tuna group occur only in cool water while *T. thynnus,* because of its thermoregulatory ability, is wide ranging and may occur in waters from 6° to 30°C but seems most common in the range 16° to 22°C (Gibbs and Collette 1967; Carey and Teal 1969b). Of the yellowfin tuna group, *T. albacares* usually occurs from 20° to 28°C (Schaeffer et al. 1963), and both *T. tonggol* and *T. atlanticus* are strictly tropical species (Gibbs and Collette 1967).

Several facts suggest that incomplete vertebral circulation in the bluefin group is a specialization for living in cooler water and that central heat exchangers are a primitive character related to the occurrence of the yellowfin tuna group in tropical waters. First, central heat exchangers, being restricted to within the haemal arch, are, of necessity small and therefore have limited heat-exchanging capacity. Thus, in cool water, and, given that red muscle is large and located at varying distances away from the vertebrae, a small central heat exchanger may prove insufficient to maintain a warm temperature. Carey and Teal (1966, 1969b) pointed out the obvious insulative value of having a large lateral heat exchanger between the warm muscle and cool water. Also, in cool water it may not be efficient for heat conservation to pump a large volume of cool blood (from the gills) into the center of the body via the dorsal aorta, and this might explain why the dorsal aorta in *T. thynnus* is small. Indeed, the lower core temperature found in *T. thynnus* may result from the small volume of unheated blood that does flow through the dorsal aorta. Another vascular specialization that appears directly related to the cool-water distribution of the bluefin tuna group is the presence of vascular bundles on their livers which enables these fish to warm their viscera, thus facilitating digestion in cooler water.

A consideration of the bigeye tuna, *T. obesus*, substantiates the idea that central heat exchangers and ultimately complete vertebral circulation are lost as tuna species evolve into cooler habitats. Although *T. obesus* and *T. albacares* have practically the same latitudinal distributions (Gibbs and Collette 1967), the former occurs in deeper and therefore cooler water (Kishinouye 1923:390 as *Parathunnus mebachi*, a synonym for *T. obesus*). This aspect of the distribution of *T. obesus* thus makes it intermediate, in terms of its thermal habitat, to that of the bluefin and yellowfin tuna groups. *Thunnus obesus* is also morphologically intermediate to the bluefin and yellowfin tuna groups of *Thunnus*. It has complete vertebral circulation and vascular bundles on its liver (Gibbs and Collette 1967) yet, F. G. Carey (pers. commun.) who has extensively studied this species reports that it does not have a central heat exchanger. With respect to body temperatures, thermal profiles, and the structure of its lateral heat exchangers, *T. obesus* closely resembles *T. thynnus* (Carey and Teal 1966). Thus for the bigeye tuna, which in terms of adapting to cool water appears to be at an intermediate position between the yellowfin and bluefin tuna groups, a central heat exchanger is not present although complete vertebral circulation persists. With respect to the latter, however, and perhaps underscoring the de-emphasis of vertebral circulation, it is relevant to point out that although *T. obesus* does have a posterior cardinal vein, Godsil and Byers (1944:114) describe it as "relatively small" and note that it fuses anteriorly with the right cutaneous vein.

Elevated Body Temperatures and Locomotion in Skipjack Tunas and *T. albacares*

Studies of scombrid locomotion (Fierstine and Walters 1968; Magnuson 1970, 1973) suggest that elevated body temperature in skipjacks, while related to their requirement for a faster typical (basal) speed, primarily contributes to their higher burst swimming speed.

Magnuson (1970, 1973) pointed out that scombrids are negatively buoyant and that the skipjack tunas, which lack a gas bladder, are even more negatively buoyant than is *T. albacares*. To compensate for this, and to maintain hydrostatic equilibrium, skipjack tunas must swim more rapidly. Magnuson has argued that the need for a faster basal speed correlates well with a significantly higher amount of red muscle found in skipjack tunas (about 8% of body weight in *Katsuwonus* and *Euthynnus*, compared with 7.4% in *T. albacares* of the same size) and with their slightly greater amounts of blood hemoglobin (Magnuson 1973, Table 7).

The amount of red muscle of course bears an important relationship to body temperature. In warm-bodied fish, retia supply blood to red muscle which is highly aerobic. Red muscle is the principal organ used for basal swimming (Rayner and Keenan 1967), and therefore it is the principal site of thermogenesis. (White muscle mainly functions in burst swimming.) Thus skipjack tunas, to maintain a high basal speed, have a large mass of red muscle, and it could be logically concluded that to augment power output, the capacity to conserve heat and keep swimming muscles warm has evolved in skipjack tunas. The difficulty with this idea however is that other scombrids such as the Pacific bonito, *Sarda chiliensis*, have minimum speed requirements as high as those of the skipjack tunas (Magnuson 1973), but are not warm-bodied, nor do they have high hemoglobin levels or large amounts of red muscle. This obviously indicates that elevated body temperatures and high amounts of hemoglobin and red muscle in the skipjack tunas, while contributing to the sustenance of a high basal speed, must have other functions as well.

Further comparison of *Sarda* with *Euthynnus* provides valuable insight to the significance of elevated body temperature to burst swimming. *Sarda velox* and *E. lineatus* (Figure 5) attain about the same size and are morphologically

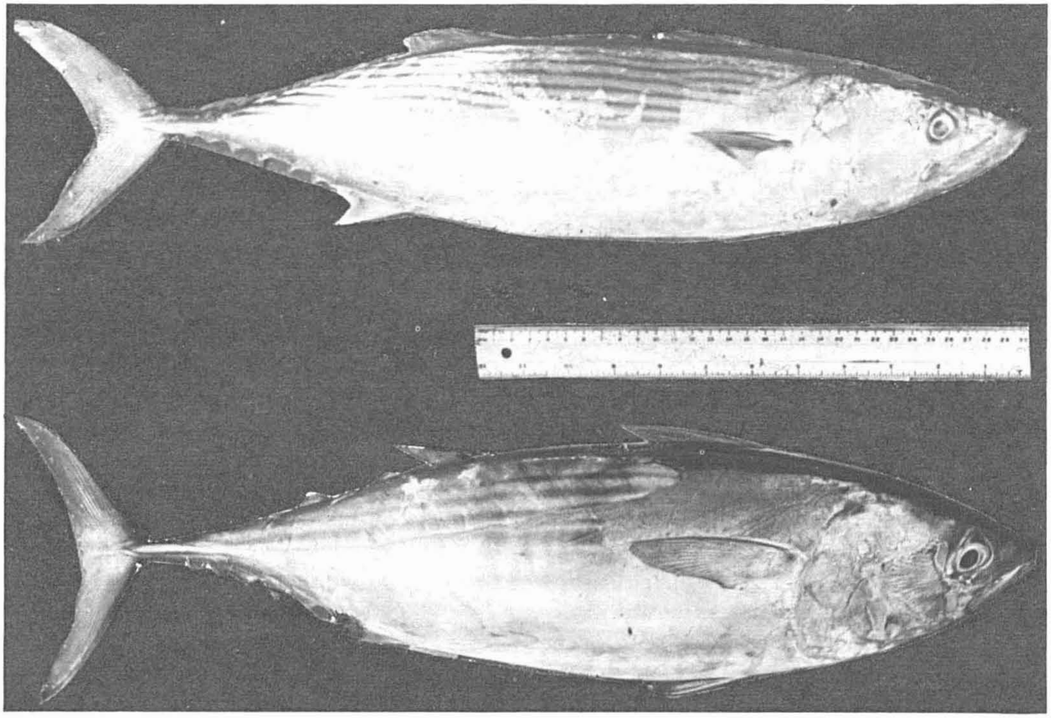

FIGURE 5.–The bonita, *Sarda velox*, (top) and the skipjack tuna, *Euthynnus lineatus* (bottom). Note differences in body shape and pectoral and caudal fin size and shape.

similar. These species also have similar distributions and, in the Gulf of Panama, they occur in the same areas and eat similar prey (crustaceans, squid, and small fishes; pers. obs.) although *Sarda* has a bigger mouth and large teeth. The different mouths and other differences suggest that the swimming capability of these species are also different. *Sarda* has a smaller pectoral fin (Magnuson 1973; Figure 5, this paper) and a lower caudal fin aspect ratio (Fierstine and Walters 1968, Table 7). Its red muscle is not as well developed as that in *Euthynnus* (Fierstine and Walters 1968:17), and *Sarda* has much less blood hemoglobin (Klawe et al. 1963). Finally, a very striking difference exists in the maximum burst speeds of *E. affinis* and *S. chiliensis* (Magnuson 1973, Table 6). In fact, the three warm-bodied species listed by Magnuson (Table 6), all have burst speeds nearly double those of *S. chiliensis*, suggesting that elevated body temperatures, coupled with morphological adaptations, greatly increase the maximum swimming speed. The principal contribution of high body temperature to burst swimming is probably the maintenance of a thermal profile that warms large portions of white muscle.

For *Katsuwonus*, *Euthynnus*, and *T. albacares*, which are all tropical species, there are differences in several structures related to locomotion such as caudal fin aspect ratio and the amount, distribution, and shape of red muscle (Fierstine and Walters 1968). It is reasonable to assume that these differences, combined with elevated body temperature, must confer different capabilities for acceleration, maneuverability, and sustained swimming on different species. One difficulty with the data presently available however is that *T. albacares* grows to be much larger than skipjack tunas, and allometric growth is known or thought to occur in several locomotion-related structures (see discussions by Gibbs and Collette 1967; Magnuson 1973). Without quantitative data on growth patterns of these features, their contribution to locomotion cannot be fully evaluated.

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