

Warm-Bodied Fish

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SYNOPSIS. Two groups of fishes, the tuna and the lamnid sharks, have evolved counter-current heat-exchange mechanisms for conserving metabolic heat and raising their body temperatures. Warm muscle can produce more power, and considering the other adaptations for fast swimming in these fish, it seems likely that the selective advantages of greater speed made possible by the warm muscle were important in the evolution of this system. Some tunas such as the yellowfin and skipjack are at a fixed temperature difference above the water, but bluefin tuna can thermoregulate. Telemetry experiments show that the bluefin tuna can maintain a constant deep body temperature during marked changes in the temperature of its environment.

The ability to swim fast has been an important development in the evolution of the large predatory fish of the open ocean. There is an abundance of food in such fast swimming prey as squid, mackerel, and herring, which is available only to swift predators. Looking at these pelagic fish, one is struck by a marked similarity in their forms. The caudal fin, which works with short rapid strokes, is a hard, crescent-shaped hydrofoil. High-speed swimming requires ample power and the fish are heavy bodied with a large bulk of muscle. They are streamlined with fins folding back into slots or depressions, and with eyes and gill covers faired-in to present a smooth unbroken surface. Of these fish, tuna have the largest bulk of muscle and appear the most streamlined. Tuna are also very fast; yellow fin (*Thunnus albacares*) and wahoo (*Acanthocybium solanderi*) can swim 70 km/hr for 10 to 20 second sprints (Walters and Fierstine, 1964).

In addition to their streamlined shape and bulky muscle, tuna have high body temperatures and we believe that this development is also associated with the evolution of high-speed swimming. The power available from muscle increases markedly with temperature. In frog muscle the

contraction-relaxation cycle speeds up some three times with a 10°C rise in temperature (Hartree and Hill, 1921). Since there is no loss in contractile force, three times the power is available from the same muscle. The bluefin tuna (*Thunnus thynnus*) found off our coasts are commonly 10°C warmer than the water and can use the additional power this would make available for high speed. The lamnid or mackerel sharks, *Isurus oxyrinchus* (mako) and *Lamna nasus* (porbeagle), also are warm-bodied, and considering their streamlined form and active way of life, it is likely that their high body temperature is also a result of evolution for speed.

Despite the advantages of an elevated muscle temperature in gaining the extra power needed for speed, few fish have warm bodies. Our measurements of body temperature for a number of species show (Table 1) that most fish are at or within a degree or so of water temperature. Blood passing through the gills remains there long enough to saturate the hemoglobin with oxygen from the water. Since thermal diffusion is more than ten times as rapid as molecular diffusion, the blood temperature attains that of the water. As the blood returns to the tissues, the oxygen it contains is used in generating metabolic heat,

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and the blood and tissues are warmed. On the next passage through the gills, this heat is lost to the water; thus, body temperature is determined by the amount of heat which can be generated by oxygen removed from the blood during one pass

TABLE 1. Measured body temperatures of a number of species of fishes.*

Species	No.	Muscle Temp. °C	Surface Water Temp. °C	Difference °C
<i>Lampris regius</i> , Opah	1	22.6	21.6	1.0
<i>Scieana regina</i> (?), Corvina (from Spain)	1	19.0	19.2	—2
<i>Caranx pampus</i> , Blue runner	1	31.5	30.5	1.0
<i>Elaqatis bipinnulata</i> , Rainbow runner	1	33.6	32.1	1.5
<i>Seriota</i> sp. Amberjack	1	29.8	28.4	1.4
<i>Coryphaena hippurus</i> , Dolphin	4	27.8	26.8	1.0
<i>Epinephelus</i> sp. Grouper	1	28.3	28.0	0.3
<i>Lepidocybium flavobrunneum</i> , Escolar	1	23.0	23.2	—2
<i>Scomber scombrus</i> , Mackerel	40	23.8	22.5	1.3
<i>Scomberomorus regalis</i> , Cero	7	30.4	29.8	0.6
<i>Sarda sarda</i> , Bonito	3	21.0, 20.5, 20.5	19.2	1.8, 1.3, 1.3
<i>Auxis thazard</i> , Frigate mackerel	6	29.5	19.2	10.3
<i>Katsuwonus pelamis</i> , Skipjack	3	30.2, 37.8, 37.3	18.5, 30.0, 29.0	11.7, 7.8, 8.3
<i>Euthynnus alletteratus</i> , Little tuna	1	31.2	19.9	11.3
<i>Thunnus alalunga</i> , Albacore	2	31.0, 32.0	17.8, 20.0	13.2, 12.0
<i>Thunnus obesus</i> , Bigeye tuna	13	28.9	21.0	7.9
<i>Thunnus thynnus</i> , Bluefin tuna	200	29.5	19.0	10.5
<i>Thunnus albacares</i> , Yellowfin tuna	23	27.5	22.5	5.0
<i>Thunnus atlanticus</i> , Blackfin tuna	1	30.3	28.4	1.9
<i>Tetrapterus albidus</i> , White marlin	4	22.2	20.4	1.8
<i>Tetrapterus audax</i> , Striped marlin	2	24.4, 28.4	22.2, 27.2	2.2, 1.2
<i>Makaira nigricans</i> , Blue marlin	2	22.2, 28.8	22.2, 26.1	0, 2.7
<i>Xiphias gladius</i> , Swordfish	5	20.1	19.2	0.9
<i>Sphyrna barracuda</i> , Great barracuda	4	28.8	27.9	0.9
<i>Remora</i> sp.	1	28.3	28.0	0.3
<i>Lamna nasus</i> , Porbeagle	7	19.3	11.5	7.8
<i>Isurus oxyrinchus</i> , Mako	26	24.9	20.4	4.5
<i>Cetorhinus maximus</i> , Basking shark	5	19.1	18.0	1.1
<i>Alopias superciliosus</i> , Bigeye thresher shark	2	20.3, 23.0	(16.0), (21.2)	4.3, 1.8
<i>Galeocerdo cuvieri</i> , Tiger shark	1	24.6	24.0	0.6
<i>Prionace glauca</i> , Blue shark	6	21.9	21.9	0
<i>Carcharhinus limbatus</i> , Black tip shark	51	28.2	26.8	1.4
<i>Carcharhinus leucas</i> , Bull shark	1	26.3	26.7	—4
<i>Carcharhinus floridanus</i> , Silky shark	4	24.9	24.3	0.6
<i>Carcharhinus milberti</i> , Sandbar shark	1	22.6	22.3	0.3
<i>Carcharhinus obscurus</i> , Dusky shark	6	22.3	22.5	—2
<i>Sphyrna lewini</i> , Scalloped hammerhead	4	24.3	23.5	0.8
<i>Sphyrna mokarran</i> , Great hammerhead	1	23.0	23.0	0
<i>Manta birostris</i> , Manta ray	1	24.0	24.5	—5

* Muscle temperature measurements were made by probing around in the fish with a long thermistor needle and recording the maximum value. Determination of water temperature was complicated by the fact that good fishing areas typically have an intricate thermal structure of thermocline and thermal inversions and it was often difficult to tell what temperature the fish had been at before being brought on deck. As a result we have listed few bottom fish which are almost always in a colder environment than the surface water. This is responsible for the few negative temperature differentials listed. The bigeye thresher sharks were caught in an area with a surface temperature of 12.7°C and 22.0°C at 30 meters. We do not know where the sharks had been swimming and the "water temperature" listed in the table is actually that of the heart and coldest muscle. Bigeye thresher sharks have a simple system of *retia* in their muscle and may well be warm.

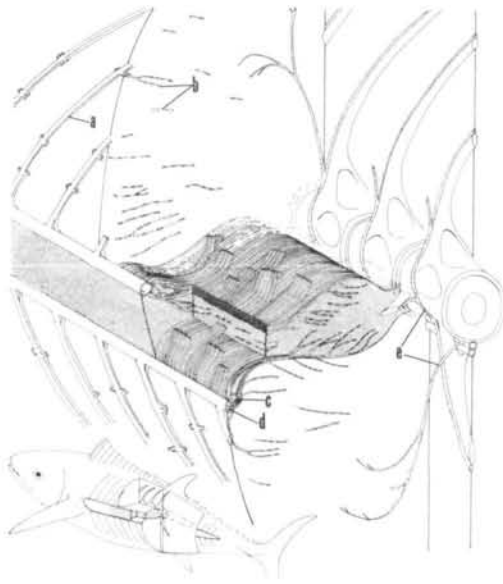


FIG. 1. Circulation in the muscles of a bigeye tuna. a, segmental artery and vein; b, vascular bands; c, cutaneous artery; d, cutaneous vein; e, arterial branches from dorsal aorta. (From Carey and Teal, 1966).

through the tissues. The heating process, metabolism, is locked to the cooling that occurs when the blood passes through the gills; therefore, the fish cannot accumulate heat to raise its body temperature. A high rate of metabolism, such as occurs during exercise, demands more oxygen, and thus more cooling, and does not cause an increase in body temperature.

From Table 1, however, it is clear that tuna and lamnid sharks do have high body temperatures. These fish conserve metabolic heat by a system of counter-current heat-exchangers located in the circulation between the gills and the tissues. The heat-exchangers act as a thermal barrier, blocking the flow of heat but permitting blood to pass and carry out its function of molecular transport.

ANATOMY OF THE HEAT EXCHANGE SYSTEM

The presence of vascular heat-exchangers changes the plan of the circulatory system. Normally, fish have a central distribution system with the dorsal aorta and post cardinal vein running just beneath the vertebrae as the main supply and with seg-

mental arteries and veins leading out to the periphery. In the tuna and lamnid sharks, the system is reversed; the main blood supply is found just beneath the skin, and small branches from it are directed inward toward the vertebrae. In Figure 1, the circulation to the muscle of a bigeye tuna (*Thunnus obesus*) is diagrammed showing the main features peculiar to warm-bodied fish. The main blood supply is through a double set of cutaneous arteries and veins running along the side of the fish and segmental vessels which run dorsally and ventrally between the skin and the muscle (Cuvier and Valenciennes, 1831). The entire system is composed of parallel arteries and veins in close contact. When swimming at cruising speed, the fish is propelled mainly by the contractions of a broad band of dark muscle located in the horizontal mid-plane (Bone, 1966; Rayner and Keenan, 1967). The blood supply to the dark muscle is the second remarkable feature of the tuna circulatory system. This vascular tissue is composed of small (0.1 mm diameter) arteries and veins which arise at right angles to the cutaneous vessels and are directed inward along the surface of the dark muscle. It is a *rete mirabile* serving as an efficient, large-capacity counter-current heat-exchanger (Carey and Teal, 1966). The mass of the *rete* is thickest and the vessels finest near its origin from the cutaneous vessels, where in a large bluefin it may be 1 cm thick. The *rete* gives off broad branches into the dark muscle as it passes inward and the numerous small vessels anastomose into a few large ones, some of which connect with the small centrally located dorsal aorta.

The blood supply to the light muscle is also unusual. The light-colored muscle is apparently used intermittently for fast swimming and may become anoxic during intense activity. The blood supply to this tissue, while ample, does not have the large capacity of that found in the dark muscle. Blood for the light muscle is supplied through segmental vessels which run over the surface of the muscle and which send numerous branches down into it. These branches are in the form of vascular

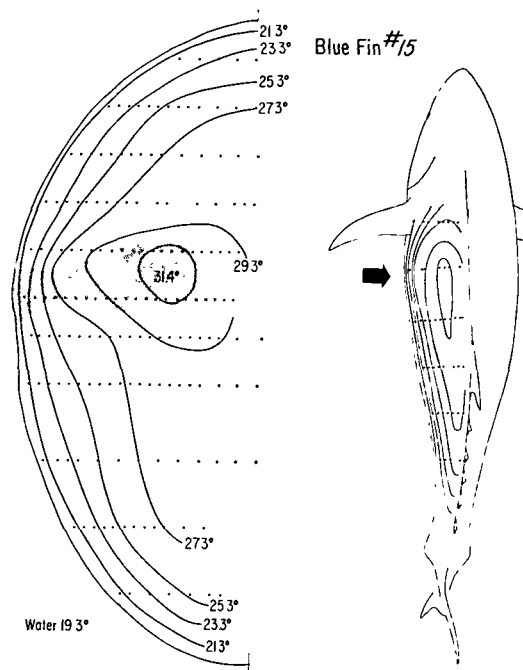


FIG. 2. Temperature distribution in a bluefin tuna, *Thunnus thynnus*. Shortly after death, temperatures were measured with long thermistor needles at points indicated by dots. Isotherms are drawn on 2.0°C contours. (From Carey and Teal, 1969b).

bands that appear as ribbons of alternating arteries and veins containing few or many vessels. The vascular bands form a two-dimensional heat-exchanger, and although this arrangement allows less thermal contact between the vessels than in the thick dark-muscle *rete*, the blood flow to this usually inactive tissue is probably slow and metabolic heat is retained efficiently.

The distribution of body temperatures follow the arrangement of the vascular heat-exchangers. The thermal distribution in a 500 lb bluefin tuna is shown in Figure 2. The isotherms are generally perpendicular to the course of the dark muscle *retia* and the vascular bands; the steepest thermal gradients occur along the finely divided region of the dark muscle *retia*. The highest temperatures are located in a relatively small region of dark muscle, but a large volume of dark and light muscle is also considerably warmer than the water. The deepest muscle is not the warmest;

tissues near the vertebral column are partially supplied by cold blood from the dorsal aorta, and usually have a somewhat lower temperature than the more lateral muscle.

This description of the muscle circulation applies to the bluefin, bigeye, albacore (*Thunnus alalunga*), and partially to the yellowfin. In addition, the yellowfin and particularly the skipjack (*Katsuwonus pelamis*) have another important heat exchanger for the muscle. The hemal canal of the yellowfin is large, and that of the skipjack may be even larger than the diameter of the centra of the vertebrae. A large dorsal aorta and a post cardinal vein run along floor of this space and give rise to numerous small parallel vessels which pass vertically and intermingle to form a massive *rete* filling the canal (Kishinouye, 1923). Dorsally, the small vessels in the hemal canal of each vertebra anastomose to form segmental arteries and veins which run out along the vertebral spines. We have plotted the distribution of temperature in one skipjack. These are small fish and the surface temperatures may change rapidly, so our map is not exact. However, the results are consistent with the importance of the central heat-exchanger; the warmest temperatures are found deep in the fish, near the vertebrae.

Lamnid or mackerel sharks, very different animals from the tunas, have a strikingly similar system of vascular heat-exchangers (Carey and Teal, 1969a). These sharks have the same reduced dorsal aorta and large cutaneous vessels to supply blood to the muscles. There is one main set of cutaneous vessels on each side, rather than two sets as found in tuna, and these give rise to a single massive *rete* serving the dark muscle. In *Isurus* (mako) this *rete* is a slab of vascular tissue as it is in the tuna, but in *Lamna* (porbeagle) and *Carcharodon* (white shark), the *rete* is diffuse, having many groups of small vessels running between the muscle fibers to the centrally located dark muscle. The segmental vessels of these sharks, as those of tuna, run over the surface of the muscle and send vascular bands down into it.

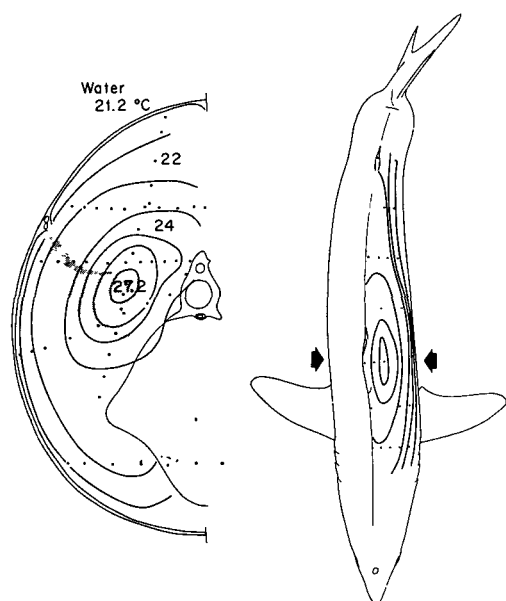


FIG. 3. Temperature distribution in a mako shark, *Isurus oxyrinchus*. 1.0°C isotherms. (From Carey and Teal, 1969a).

These bands are generally in groups of three vessels, vein—artery—vein, rather than many vessels arranged artery—vein—artery, as in the tuna. The circulatory system of *Lamna* was described by Burne (1923) in a paper aptly titled, "Some peculiarities in the blood vascular system of the porbeagle shark." The distribution of temperature in the muscle of these sharks is similar to that of the tuna, with the highest temperatures confined to a small region of dark muscle, rather lower temperatures near the center line region served by the dorsal aorta, and a sharp thermal gradient near the surface (Fig. 3).

The viscera of some of these fishes are also served by a heat exchange system. In the albacore, bluefin, and bigeye tuna, *retia* are conspicuously located on the dorsal surface of the liver. Branches of the coelomesenteric artery break up into masses of small arteries which mingle with small veins to form discrete organs of tightly packed parallel vessels. In a large bluefin some of these bundles are five cm in diameter. On the distal side of the *rete*, the small vessels coalesce into a few large ones

which connect to the organs they serve. This system was described by Eschricht and Müller (1835). An illustration from this paper is shown in Figure 4. They also mentioned an analogous organ in *Lamna* which is well described in Burne's (1923) paper. Among lamnid sharks, the coelomesenteric artery is absent from *Isurus*, is very small in *Lamna*, and is small in *Carcharodon*. The main arterial supply to the viscera is through the pericardial arteries, normally insignificant vessels which are greatly enlarged in these sharks. These arteries penetrate the hepatic sinuses just before the latter empty into the sinus venosus. Within the hepatic sinus the artery breaks up into a mass of anastomosing vessels of increasingly smaller dimensions until the lumen is filled by a sponge-like mass. On the distal side, the arteries coalesce and form single, large collecting trunks which supply the various visceral organs. This arterial "sponge" in the venous sinus forms the hepatic *rete*. It is clearly a counter-current heat-exchanger, but one of different structure from the usual mass of parallel arteries and veins.

We have many measurements of visceral temperatures from tuna and lamnid sharks. There is large variation; temperatures range from as warm as the warmest muscle to slightly above that of the ambient water. Apparently the visceral temperatures vary with time and circumstance, perhaps correlating with the activity of the digestive system. The visceral heat-exchangers probably act to speed digestion and absorption. These warm fish, particularly the tuna, have a remarkably small mass of visceral organs. Higher temperatures may make up for the small sized viscera by aiding the rapid processing of food (Magnuson, 1969).

We feel that the advantages of high-speed swimming provide an explanation for the similarities between tuna and the lamnid sharks. Their bulky, muscular bodies with highly streamlined shapes, the detailed streamlining of fins and body openings, and the hard, narrow crescent-shaped tails are remarkably similar and seem well adapted for the speed needed in

the pursuit of their small, swift prey. The high body temperatures which would make additional power available from the muscle could be viewed as further evolution in this direction. The counter-current heat-exchangers which make this possible have

evolved on two separate occasions to produce remarkably similar forms. Multiple, parallel arteries and veins in close contact rather than single, separate vessels are found in all organs. Cutaneous vessels of small size in most fish have enlarged to

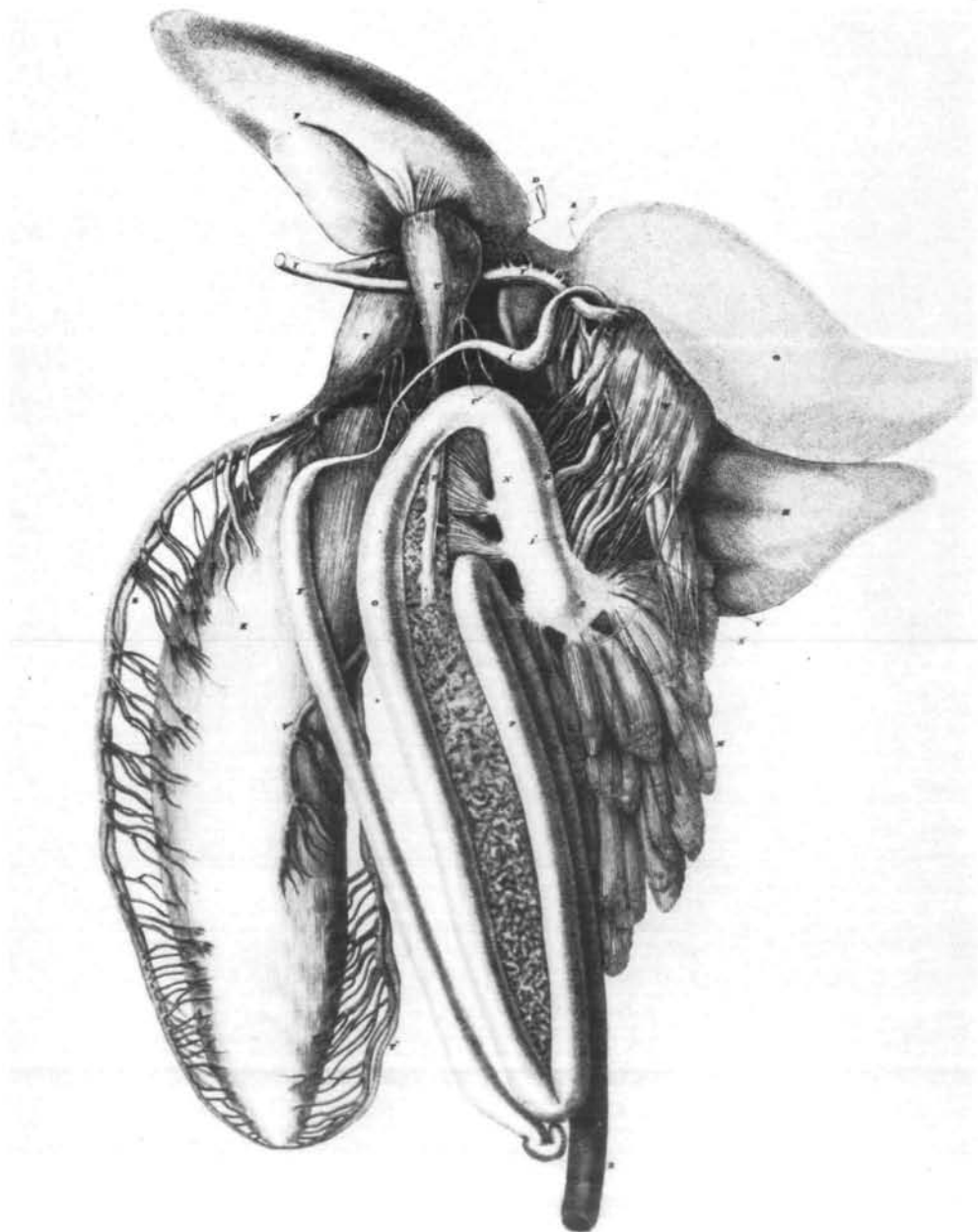


FIG. 4. Illustration from Eschricht and Müller (1835) showing the location of the visceral *retia* in a bluefin tuna. This is a ventral view of the

viscera with the liver lobes raised to show the large, fusiform retia on their dorsal surface, T, U, and V.

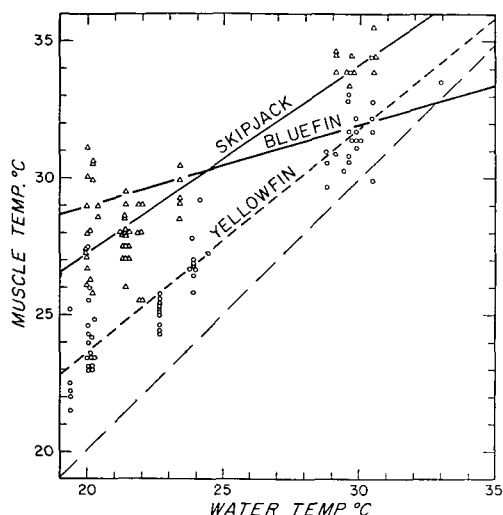


FIG. 5. Barrett and Hester's (1964) data showing the variation of muscle temperature with water temperature for skipjack and yellowfin tuna. These fish maintain fixed elevation above the water temperature. A line for bluefin, which thermoregulates, is included for comparison. (From Carey and Teal, 1966).

provide the major blood supply to the muscle, while the central dorsal aorta has been greatly reduced. The resulting pattern of circulation, with the blood supplied from the surface rather than from the center, locates the cool end of the counter-current heat-exchangers at the surface and the warm end deep in the muscle, thus reducing heat loss through the skin. Even those tuna, such as the yellowfin and skipjack, which have also evolved a major, central heat-exchanger, retain the peripheral system in a somewhat reduced form. It probably functions to reduce surface heat losses in these fishes also.

REGULATION OF BODY TEMPERATURE

If it is possible for a fish to attain an elevated body temperature, it would seem a simple matter to maintain it at a constant value. Any way of decreasing the efficiency of the heat exchangers with increasing water temperature would accomplish this. The possibility of thermoregulation has been studied in three species: skipjack, yellowfin, and bluefin. Barrett and Hester (1964) measured the muscle

temperatures of a large number of skipjack and yellowfin caught in the Pacific. It is quite clear from Figure 5 that these fish maintain a fixed temperature difference above the water. Our measurements of yellowfin temperatures from the Atlantic (Table 1) average somewhat higher than Barrett and Hester's, but show the same trend. Apparently, skipjack and yellowfin work at a constant efficiency to maintain the highest possible muscle temperature. (One skipjack we measured had a temperature as high as many mammals—37.8°C.) These fish do not occur in cold water, and are mainly found in water warmer than 20°C. The giant bluefin, on the other hand, may be found in water of 6° to 30°C. The muscle temperatures of giant bluefin from areas of different water temperature along the east coast show that these big fish control their temperatures quite well (Fig. 6, Carey and Teal, 1969*b*). The relationship of muscle temperature (T_m) to water temperature (T_w) for the bluefin is:

$$T_m = 0.25T_w + 25^\circ\text{C}$$

In 7°C water some of the fish were more than 20°C warmer than their environment and must have been conserving metabolic heat very efficiently.

It seemed possible that the apparent thermoregulation in the bluefin was the

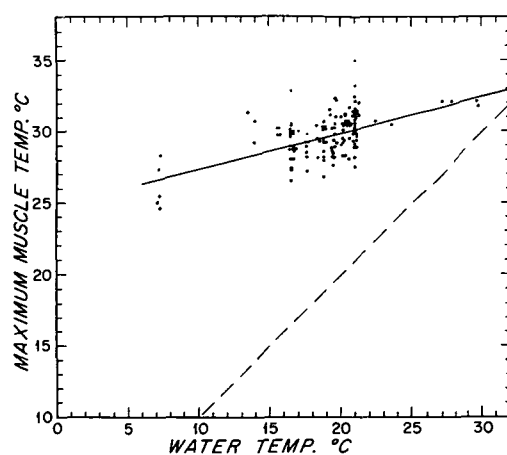


FIG. 6. Muscle temperature of bluefin tuna taken from areas of different water temperature. The muscle temperature changes only 5°C over a 20°C range. (From Carey and Teal, 1969*b*).

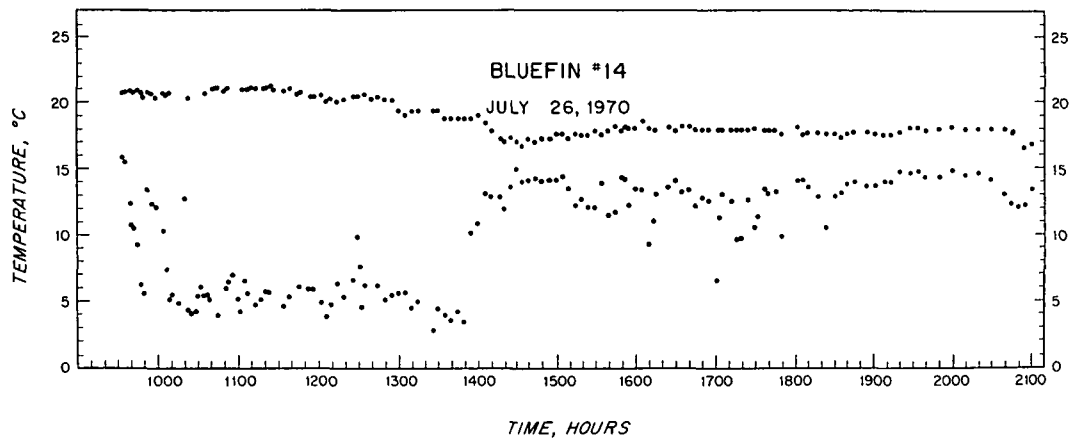


FIG. 7. Telemetry experiment on a free-swimming bluefin tuna showing the first 10 hours of a 56 hour record. The upper set of points are stomach temperature and the lower, water. Stom-

ach temperature remained constant during an 11°C drop in water temperature which lasted for 4 hours.

result of long term adaptation to local water conditions and involved tissue and cellular changes. This is in contrast to the rapid thermoregulation of which mammals are capable. We continued our investigations with a series of telemetry experiments on free-swimming fish to see if they could maintain a constant temperature when the water temperature changed rapidly. To do this we used an acoustic telemetry system which broadcast as a series of 21 KHz sound pulses, tissue and water temperatures for alternating one minute periods. The signal was received by a directional hydrophone and it proved to be a simple matter to follow the fish by steering our ship in the direction of the strongest signal. We hoped that the fish would pass through the thermocline so that we could follow his body temperature as the water temperature changed. As commercial seiners had told us, tuna do not like to change their water temperature and most of the fish we followed maintained a remarkably constant water temperature, usually staying near the surface or on the upper side of the thermocline. Some fish would dive through the thermocline, but only spent a few minutes in the cold water before coming up again. Toward the end of last summer's experiments, however, we were lucky enough to get a most satisfactory result. This fish was a 600 lb bluefin

with a transmitter in his stomach.* Water temperatures were sensed by a thermistor on a wire running up the esophagus and out the last gill slit. This particular fish had been handled quite roughly during the struggle to install the transmitter, and, possibly because of this, when released from the trap at 0930 hours he immediately went from the 16°C surface water down into deeper 5°C water and stayed there for four hours (Fig. 7). At 1400 hours he returned to 13 to 14°C water on the upper side of the thermocline and remained there for the rest of the day. While in the cold water, the stomach temperature gradually decreased from 21° to about 19°C, but remained at about 18°C after the fish returned to the warm water. Clearly this fish was maintaining a remarkably constant deep-body temperature despite an 11°C drop in water temperature for an extended period of time. Thus, large bluefin tuna can thermoregulate during rapid changes in ambient temperature.

In other experiments we followed muscle temperature and found that this is also

* The transmitter in the stomach may have sensed the temperature of the stomach and its contents or of the caecal mass which rests against the stomach and is quite warm. The stomach is separated from the muscle mass which extends deep below the vertebrae by the gas bladder and should not be directly influenced by muscle temperature.

well controlled during changes in water temperature. These experiments are less dramatic and less convincing, however, as we were not fortunate enough to get the marked and prolonged change in water temperature illustrated in Figure 7.

In the tuna there are no obvious shunts such as those that the surface veins provide for the brachial artery-venae comitantes heat-exchanger in the human arm. Presumably, control is achieved by degrading the efficiency of the heat-exchangers in warmer water, but though it is easy to speculate on mechanisms, we have no evidence as to how this is done.

The Atlantic bluefin tuna range from the tropics to the Arctic. They are the largest and most powerful of the tuna and undertake long seasonal migrations. They can travel over great distances rapidly, as indicated by tags returned from fish released in the Bahamas and caught less than 50 days later and 4200 miles away near Bergen, Norway (Mather, 1962). The movements of these fish do not appear to be restricted by water temperature, for their travels may take them from the near 30°C waters of the Bahamas to 6°C northern waters. The bluefin can maintain its body at a relatively constant value despite marked and rapid changes in the water temperature. We believe that this independence of water temperature gives the tuna its unsurpassed mobility. Unbounded by water temperature, it can seek favorable

areas in the north for feeding and in the tropics for spawning.

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