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by

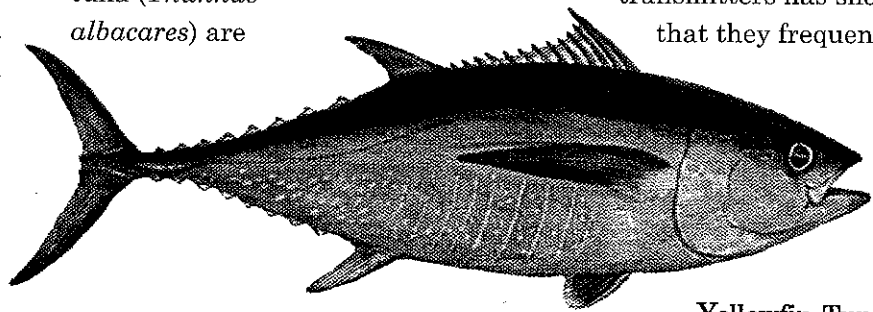
Peter G. Bushnell and Kim N. Holland

Tunas are the master swimmers of the oceans. They swim constantly, never stopping to rest on the bottom or to bask at the ocean's surface. In some species, such as the skipjack tuna (*Katsuwonus pelamis*), their movements around the oceans seem to be dictated solely by the availability of their food. With others, such as the giant bluefin tuna (*Thunnus thynnus*) of the Atlantic and Pacific oceans, their movements seem to be influenced both by the distribution of prey and the need to return to their tropical ancestral spawning grounds in time for the breeding season.

Evidence from seasonal abundances and recapture of tagged Atlantic bluefin tuna suggests that in midsummer these animals leave their spawning grounds in the Gulf of Mexico and travel north along the U.S. east coast, following the Gulf Stream to the shores of Massachusetts and Nova Scotia. There they feed on the seasonal blooms of pollock, herring, and mackerel. As summer ends, they may travel completely across the Atlantic to the shores of Europe and North Africa before returning to the Gulf of Mexico to participate in the next year's breeding season. In the Pacific,

bluefin tuna that spawn near Japan have been captured thousands of miles away, off the equatorial coast of Central America.

To humans, the pelagic environment seems devoid of signposts or maps. Nevertheless, even on a daily basis, tuna move large distances and display an uncanny ability to navigate skillfully in the open ocean. For instance, in the Pacific, yellowfin tuna (*Thunnus albacares*) are



Yellowfin Tuna
Thunnus albacares

frequently found patrolling their daytime haunts along the island edges where the coral reefs drop precipitously to the depths of the ocean floor. At night, however, these tuna make long excursions offshore, only to return the next morning to the same precise area they left the previous day. These nightly forays often cover up to 15 kilometers (9 miles). In human terms that represents, for a person two meters tall, a nighttime walk of 60 kilometers (37 miles)! Yellowfin tuna do it every night, possibly to feed on

organisms such as squid that swim up from the much deeper levels they occupy in the daytime.

Drawn to Floating Objects

A related phenomenon is the tendency of tunas and other pelagic fish to aggregate around floating objects such as logs or manmade debris or buoys. When evening comes, pelagic tunas move away from these objects just as coastal tunas move away from the reef at night. Tracking tunas with attached radio transmitters has shown that they frequently

return to the exact same log or buoy the next day.

The benefits of aggregating around floating objects, the function of these nighttime excursions, and the methods tunas use to make such precise movements around the trackless, deep oceans are still largely mysterious. The floating log or buoy may provide these oceanic nomads with a navigational reference point in their vast, three-dimensional realm. These

reference points may somehow assist them in their daily wanderings and help them conserve their precious supplies of energy. Making use of these habits, entire fishing industries in many parts of the Pacific are dependent on finding logs around which to set huge seine nets to capture fish milling around underneath.

The world of the tunas is truly three dimensional because, unlike terrestrial animals which are bound by gravity to the two-dimensional surface of the land, tunas are free to travel up and down in the ocean, as well as from side to side. Again, these fish display remarkable swimming abilities in their vertical movements. A small bigeye tuna (*Thunnus obesus*), equipped with a transmitter to relay its movements to scientists, was observed to dive over 250 meters (274 yards) in less than one minute. This is a spectacular behavior which, in addition to the superb locomotor ability it demonstrates, also reveals the tremendous temperature and pressure changes that tunas can withstand.

Built for Speed

These feats of long-distance and incessant swimming, and the ability to orient in the vastness of the ocean, are reflected in the anatomy and physiology of these highly specialized fish. Many of the anatomical adaptations found in tunas serve to reduce drag during high-speed swimming. In terms of energy costs,

high-speed swimming is expensive. It takes a 100-fold increase in energy expenditure to produce an eight-fold increase in swimming velocity. This is true even though fish such as tunas are specifically evolved for sustained high-speed swimming.

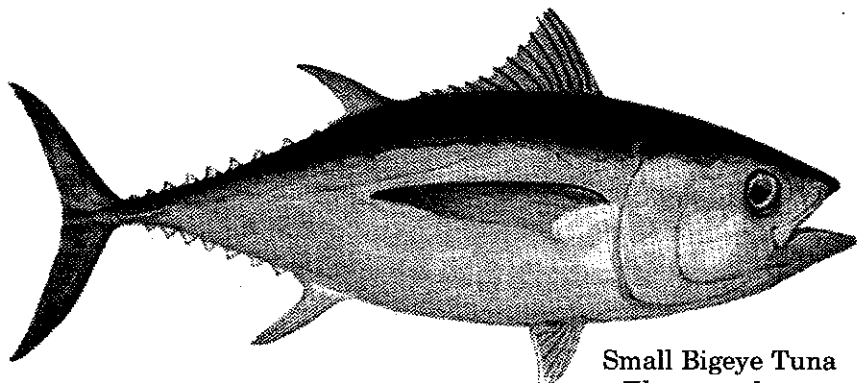
One structure that has evolved to reduce drag is the caudal peduncle keel located on each side of the anterior base of the caudal fin. These keels tend to reduce the turbulence at the tips of the tail fin and lower the drag created by that part of the body. Also, behind the dorsal and anal fins, there is a series of one to 11 nondepressible sail-like finlets. These are thought to act as movable slots that eliminate vortices of water that spin off the trunk and tail, thus allowing the caudal fin to work more efficiently in undisturbed water. The spinous, first dorsal fin folds down into a groove, making it flush with the body surface; this reduces drag when the fish is not maneuvering but swimming in a straight line. All these adaptations allow the tuna to move at extremely high velocities (up to 45 kilometers per hour/28 mph) and for long periods of time.

Clearly, some physiological modifications are required to

support the tuna's active, nomadic, and energetically expensive life style. Tunas are similar to trained athletes in that they are capable of taking in very large amounts of oxygen and burning them metabolically. In these fishes, the active oxygen-consumption rate is on the same scale as that of mammals and is the highest recorded in any fish group. In order to consume oxygen at such a tremendous rate, fish must first extract it from the water and then move it to the tissues, where it can be used to burn the metabolic fuels that power the muscles. At each stage of this process, tunas have evolved to make these systems work as effectively as possible.

Swim or Suffocate

The first step in providing oxygen to the respiratory system is to provide water to the organ that extracts oxygen—the gill. Most fish accomplish this by contracting jaw and opercular muscles in a coordinated and rhythmic fashion, enabling them to pump water over their gills. When more oxygen is needed, the pumps are sped up.



Small Bigeye Tuna
Thunnus obesus

Tunas, as well as billfishes and some species of sharks, use a different system to move water over their gills; they ram ventilate. These fish swim through the water with their mouth open, using their forward motion to drive water over the gills. Tunas are obligate ram ventilators, meaning they have lost the ability to simply pump sufficient water over their gills to meet oxygen demand. The consequence of this adaptation is enormous—tunas cannot stop swimming, or they will suffocate! In fact, they must swim at a speed of at least 65 centimeters (26 inches) per second in order to provide sufficient water flow.

What are the advantages? The first is efficiency. Ram ventilation transfers the work of breathing from the head musculature to the swimming muscles, which are mechanically more efficient. Second, hydrodynamic drag is reduced because the fish's swimming is not disturbed by the opening and closing of gill covers (opercals) during pumping. Third, ventilation volume can be increased to some extent, quite cheaply, by opening the mouth wider. As a result, ram ventilators spend only one to three percent of their total energy expenditure obtaining water for respiration. This contrasts to estimates of up to 15 percent for non-ram-ventilating fish such as goldfish or trout.

The ability to provide large amounts of water to the gill at a low price is a great advantage, but it is not too useful if the gill

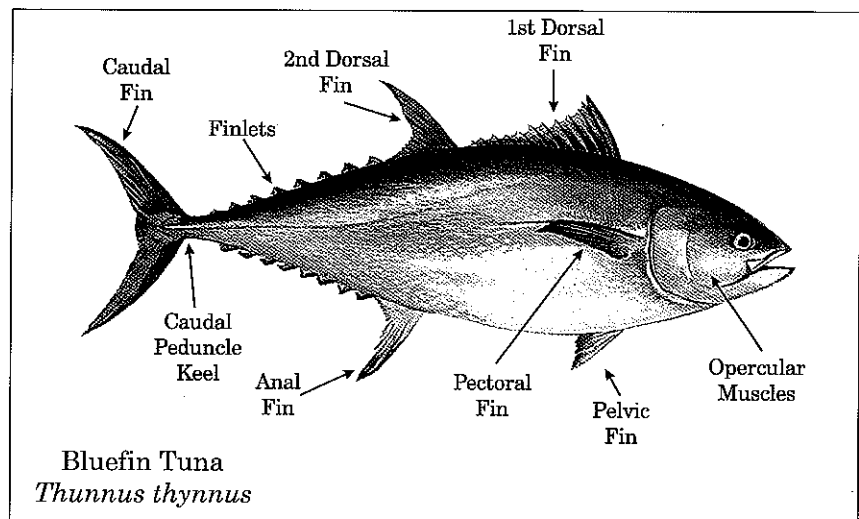
cannot use the water effectively. To this end, tunas have evolved gills that are up to 30 times larger in surface area than those of other fish. The increased surface area allows tunas to extract a high percentage of oxygen (approximately 50 percent) from the water stream flowing over their gills, as compared to the usual 10 to 30 percent extraction rate of other fish.

Not surprisingly, the circulatory system is also modified to take large amounts of oxygen from the gills and move it to the other tissues. Compared to other

containing a large number of oxygen-carrying red blood cells, adds up to a circulatory system designed to move high quantities of oxygen.

The majority of oxygen moved to the tissues is used by the swimming muscles. In all fish, these muscles can be divided into two types: white and red muscle. Red muscle contracts at a comparatively slow rate and is, therefore, used for slow, continuous swimming. White muscle, on the other hand, contracts quickly and is used for short periods of high-speed-burst swimming.

White muscle makes up over



less-active fish, tunas have hearts that are ten times larger on a heart-weight/body-weight scale, pump blood at a rate three times higher, and have blood pressure three times higher. The blood has a hematocrit (percent packed red blood cell volume) of 40 percent, an extremely high figure usually associated with diving mammals such as seals and porpoises. A very powerful heart, pumping a higher-than-average blood volume and

90 percent of the muscle mass and generates its energy by breaking down glucose without oxygen (anaerobic metabolism). This anaerobic pathway is not very efficient and yields lactic acid as a by-product. (The accumulation of lactic acid in the tissues is what makes you feel tired when you exercise vigorously for a prolonged time period and gives you muscle cramps if you exercise too fast.) The buildup of lactic acid in white

muscle ultimately inhibits its performance because the acid is not removed or metabolized very quickly. Red muscle generates energy by metabolizing glucose with oxygen (aerobic metabolism) to yield carbon dioxide and water. As long as it has oxygen and glucose, red muscle can keep contracting indefinitely.

Tunas have a much larger proportion of red muscle than is found in the average fish. This allows them to cruise at higher speeds while generating energy aerobically. As the tuna begins to swim faster, the white muscle is slowly graded in to provide additional thrust. At this point, another adaptation comes into play. Not only does tuna white muscle work anaerobically, but it also has all the necessary biochemical equipment to work aerobically. This allows the animal to move at an even faster rate without going anaerobic. When the tuna does have to shift to an even faster rate, for instance, to catch prey, it can move with blinding speed. The final burst speed is provided by the white muscles working anaerobically. The anaerobic energy-generating ability of tuna white muscle is unsurpassed by any animal in nature.

A Warm-Blooded Fish


The breakdown of glucose to provide energy for contracting muscles generates heat as a by-product. In most fish, this heat is lost to the surrounding water and, therefore, the fish's body

temperature is the same as the water it is swimming in. Not so with tunas—these fish, as well as some sharks, have evolved a specialized circulatory system that traps the heat before it escapes to the water. This particular adaptation consists of a heat exchanger comprised of small arteries and veins; it is called the rete mirabile or “wonderful net.” It is so effective that core temperatures of tunas are often 10°C (50°F) warmer than the water. Giant bluefin tuna have been reported to have core temperatures 21.5°C (71°F) warmer than the surrounding water.

There are several advantages to being “warm bodied.” Most biochemical reactions proceed at a more rapid rate at a warmer temperature. Therefore, all of the metabolic machinery used to generate energy, as well as use it, will operate faster. Specifically, a warmer temperature allows red muscle to contract more quickly, approaching the contraction rate of the white muscle. The more-energy-efficient red muscle can then be used at higher swimming speeds and, consequently, the white muscle does not have to simply carry around the “dead weight” of red muscle during high-speed swimming. Lactic acid breakdown is also enhanced at higher temperatures. Finally, the transfer of oxygen from blood to muscle cells is quicker at warmer temperatures.

Clearly, all of these interrelated factors enhance the tuna's ability to sustain its high-speed cruising ability. In this vein,

consider the tuna making rapid excursions up and down the water column. Water temperatures fall quickly with depth; for instance, the bigeye tuna that was observed to dive 250 meters in one minute went from water at 24°C (75°F) to water at 9°C (48°F). The heat exchanger gives tunas some “thermal inertia,” allowing them to swim for short periods in colder waters without suffering a radical drop in their core temperatures. Similarly, temperate-water tunas that live in cold water all their lives will be warmer than other sympatric fish species and will have the various swimming advantages discussed.

The rete mirabile's ability to conserve heat generated by the swimming muscles can also produce a problem: insufficient heat dissipation. Heavily exercising tunas may solve the problem of getting rid of excess heat by a combination of physiological and behavioral responses. Physiologically, they appear to be able to control the efficiency of the heat exchanger by closing down some of the small arteries and veins perfusing the rete. This allows them to “dump” heat as the need arises. Behaviorally, excursions into cooler water will help them control their overheating problem. This may be why some species of tunas are found only in certain geographical areas and at depths that provide optimum temperature ranges. 

This article is an adaptation of the one which first appeared, in German and French, in Documenta Maritima.