

ENERGETICS OF LOCOMOTION IN WARM-BODIED FISH

E. Don Stevens

Department of Zoology, University of Guelph, Guelph, Ontario
N1G 2W1, Canada

Andrew E. Dizon

National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96822

INTRODUCTION

Most fishes are poikilothermic—i.e. their body temperature is within a few degrees of ambient unless ambient is changing rapidly. The exceptions are certain sharks and true tunas. Little is known about the locomotion and energetics of warm-bodied sharks. Our review focuses on a few species of tunas but draws on information from other fish (especially salmonids) to fill in the gaps in our understanding.

Of interest here is a measure of the metabolic cost of producing known amounts of work per unit time; but there are problems with both sides of this equation, especially in the aquatic environment. Webb (30) has used a scheme similar to that in Figure 1 to show how total metabolic costs are partitioned. Since this approach is appropriate for sustained swimming in steady-state (i.e. oxygen supply keeping up with demand), especially when experiments are performed for short periods (hours), it is used here.

Energy input or metabolic cost has been successfully estimated by measuring oxygen uptake and calories ingested. We focus our discussion on estimates based on these measurements.

Other techniques for measuring metabolic costs have either been tried unsuccessfully or are yet to be tried. For example, few measurements have been made of CO₂ production in fish (15, 16) and none for tuna. Knowledge of heat exchange rates and excess temperature has permitted some specula-

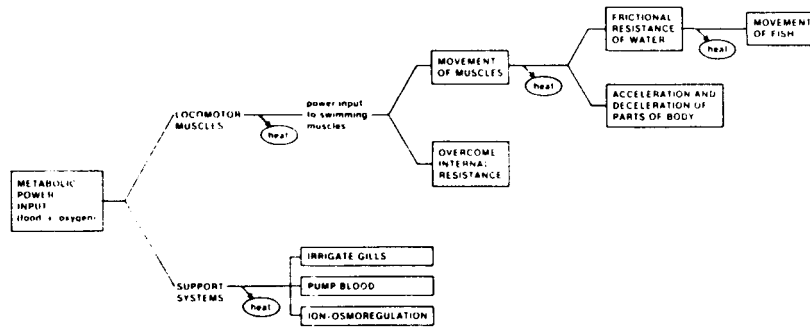


Figure 1 Schematic of energy distribution to components involved in propulsion at sustained swim speeds.

tion about energetics (19), but little is known about how heat exchange rates change during swimming. Guppy and co-workers have studied biochemical adaptations of burst swimming but not of sustained swimming (11).

Known amounts of work per unit time have never been measured for water breathers. Metabolic costs are usually related to swimming velocity. Some workers have used arbitrary estimates—e.g. measured oxygen uptake or temperature after “feeding frenzy.” Others have measured time to swim a specific distance when the tuna is controlling its own speed. Still other estimates are based on hydrodynamic theory, which is used to estimate the work to overcome drag or produce the thrust necessary to swim at a particular speed.

We review recent contributions on tuna energetics based on measurements of oxygen uptake, bioenergetic calculations from feeding and growth rates, and hydrodynamic calculations. We discuss the partitioning of this energy in tunas. Finally, we compare the cost of locomotion in tunas to that in birds and mammals and comment on the adaptive advantage of being warm-bodied.

We stress the two main differences between locomotion on land and in water. First, water as a medium offers much resistance (i.e. it has high viscosity and high density) so that almost all locomotive work goes to overcome drag. Second, water supports the fish’s weight, so that almost no work goes to overcome gravity. Warm-bodied fishes swim continuously; thus inertial losses are small when they swim at constant velocity.

TOTAL COST OF LOCOMOTION

Estimates of the total cost of locomotion are based on measurements of the gross cost. There have been many attempts to calculate net cost by estimating maintenance costs (i.e. of ion-osmoregulation, of obtaining oxygen from the medium, and of delivering oxygen to cells that need it). We first discuss total and then net costs.

Oxygen Uptake Used to Estimate Total Cost of Locomotion

The only measurements of oxygen uptake in free-swimming tunas at known swim speeds are those of Gooding et al (10). In their experiments, groups of two to six skipjack tuna (*Katsuwonus pelamis*) were placed in large respirometers (4.6 m diameter, 1 m deep; or 2.4 m diameter, 0.6 m deep) where oxygen depletion and swim speed were measured. Thus over the long term the experiment provided a measure of total oxygen uptake at known swim speeds (i. e. in cases for which the fish maintained the same velocity for hours). Swim speed was controlled by the fish and not the experimenters. The data appear in Figure 2. Three aspects of their results are unique. First, there was no statistically demonstrable effect of body weight among oxygen uptake rates for skipjack tunas over a weight range of 0.60–4.0 kg. Second, the metabolic rate at any speed over the range studied (i.e. 0.9–2.2 $l\text{-sec}^{-1}$) (l =body lengths) was higher than that of any other fish species studied. For example, at 1 $l\text{-sec}^{-1}$, oxygen uptake in the skipjack is 469 $\text{mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ whereas in eight other species it ranged from 90–300 (1). At 2 $l\text{-sec}^{-1}$ oxygen uptake in skipjack is 603 $\text{mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ whereas in the eight other species it ranged from 200–440 (1). These data show that tuna are less efficient than other fish species when swimming at these speeds and that the obvious streamlining of tunas does not lead to an obvious saving of total metabolic costs at swim speeds about 1–2 $l\text{-sec}^{-1}$. “Presumably, the evolution of skipjack tuna (like that of fast cars) has involved sacrifice of energetic efficiency at low speeds in favour of increased efficiency at high speeds, permitting a dramatic increase in maximum attainable speed” (10).

Unfortunately, there are no oxygen uptake measurements of tunas swimming at higher speeds. However, in skipjack tuna immediately after capture at sea the median rate of 15 measurements was 1300 $\text{mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ (range 900–2500) (10). Swim speed ranged from 2–5 $l\text{-sec}^{-1}$. These measurements are important because they suggest the tuna’s maximum aerobic scope. They are higher than any values for any other fish (or amphibian or reptile) under any exercise, temperature, or other experimental condition.

The third unique aspect of Gooding et al’s data is the fact that the slope of the line relating log metabolic cost to swim speed is less than that for other fish. When the logarithm of metabolic rate is plotted versus swim speed, a straight line can usually be fitted to the data. The slope of this line for skipjack tuna is 0.21 (Figure 2) (10), less than that for the other eight species tabulated by Beamish (1). “The rate of increase in the logarithm of oxygen uptake with relative swimming speed is surprisingly similar among species despite obvious variation in methodology, size, and temperature and is reasonably well represented by a coefficient of 0.36. Thus for each increase in relative swimming speed of $l\text{-sec}^{-2}$ there is a corresponding 2.3-fold eleva-

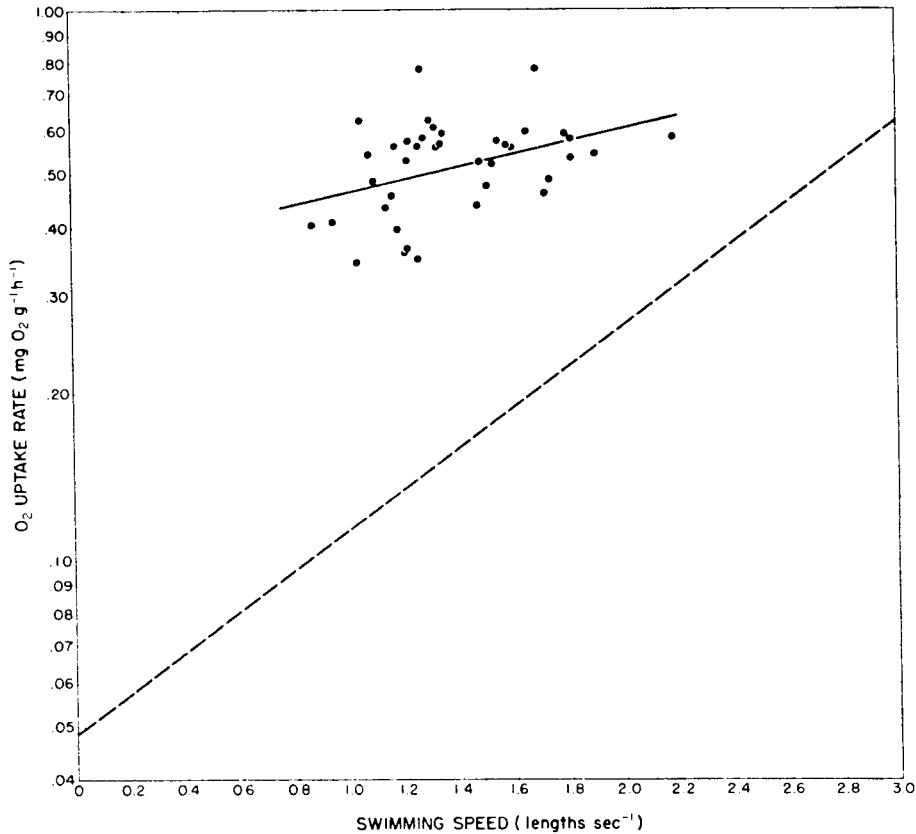


Figure 2 Relation between oxygen uptake and swim speed of skipjack tuna. The dashed line is for 1.8 kg sockeye salmon (2). Figure adapted from (10).

tion in metabolic rate" (1). But this coefficient is 0.21 for skipjack, involving only a 1.6-fold elevation in metabolic rate. The tuna becomes more efficient than the salmon at a speed of less than $5 \text{ l}\cdot\text{sec}^{-1}$, and tuna can sustain speeds greater than $5 \text{ l}\cdot\text{sec}^{-1}$, whereas salmon cannot (7).

NET COST OF LOCOMOTION

Calculation of the net cost of locomotion requires an estimate of basal metabolic rate (or at least the rate at zero activity). The major fraction of these costs is usually attributed to irrigation of the gills with water, circulation of the blood, and ion-osmoregulation.

Stevens (24) measured respiration in skipjack tuna restrained in a chamber. The average oxygen uptake was $692 \text{ mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ and the mean of the lowest value recorded for each of five skipjack was $457 \text{ mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$. Clearly these values are not resting or basal and thus cannot be used to

estimate net cost of locomotion. Brill (3) attempted to overcome the problem of obtaining resting values by measuring "stasis" metabolism (metabolism of restrained skipjack injected with a muscle relaxant, gallamine triethiodide, and then spinalectomized to stop all overt muscular movement). Smaller animals had higher mass-specific stasis metabolic rates. For a mass range of 0.32–4.7 kg, the relation was $M = 8431 W^{-0.437}$, where M = oxygen uptake ($\text{mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$) and W = mass (g). Thus stasis metabolic rate for a 2 kg skipjack is $304 \text{ mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ or about one half the value reported for a nonspinalectomized fish and about one half the value from the swimming fish when extrapolated to zero activity ($529 \text{ mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$). We assume that this measurement is a reasonable estimate of the metabolic cost of the support systems in tuna at zero activity. Most evidence shows that these costs increase in proportion to swim speed.

Cost of Irrigating The Gills

The typical pattern of rhythmic movements of respiratory muscles to force water over the gills is not seen in tunas. Tunas, swimming with an open mouth, irrigate the gills by ram pressure. The literature on irrigation of the gills by open-mouth swimming has been reviewed (23).

Thus the metabolic cost of irrigating the gills is a small fraction (of the order of 1%) of total metabolic cost of swimming in tunas (i.e. it is about one order of magnitude less than that in fish irrigating their gills with buccal and opercular pumps).

Cost of Circulating The Blood

The cost of circulating the blood must be higher in tunas than in other fishes. The absolute cost must be higher because the metabolic rates are so high—i.e. because more oxygen must be delivered to the tissues. The relative cost is probably also high because of the unusual circulatory system of tunas. Tunas have elaborate counter-current heat exchangers that keep their body temperatures substantially higher than that of the water. The imposition of the heat-exchanger vascular beds in series with the typical vascular beds must result in a greater work load on the heart. The cost of circulation is estimated at 3.5% of total oxygen uptake at rest and 4.5% of total oxygen uptake at maximum activity in salmon (13). In tuna it is probably greater than 5%.

Cost of Ion-Osmoregulation

There are two elaborate studies on the metabolic cost of ion-osmoregulation in fish (8, 22). Both used euryhaline species and estimated the cost by measuring oxygen uptake at a variety of salinities. Costs increased exponen-

tially with swimming speed, reaching 17% of total metabolism at maximum swim speed.

Thus the costs of maintaining the support systems during swimming as fractions of the total metabolic cost are probably about 1% to irrigate the gills, 5% to circulate the blood, and 15–20% for ion-osmoregulation.

METABOLIC COSTS BASED ON CALORIC INPUTS

Kitchell et al (14) constructed energy budgets for two species of tuna using the principles of bioenergetics in order to estimate the scope for growth.

Small Tropical Tuna

From (10), M (routine metabolic rate in $\text{mgO}_2\cdot\text{h}^{-1}\cdot\text{fish}^{-1}$) is $0.288\cdot W^{1.08}$, where mass is in g. Thus for a 2 kg skipjack routine metabolic rate is $1058\text{ mgO}_2\cdot\text{h}^{-1}$ or $86\text{ kcal}\cdot\text{day}^{-1}$. Given the caloric density of skipjack ($1.46\text{ kcal}\cdot\text{g}^{-1}$), this is about 3.7% of total energy content per day. Measured values show that actual losses of energy content during 10 days starvation are 3.6% per day. Because this calculation is based on Gooding's estimate of routine metabolic rate, the result depends on body mass. However, because the exponent is small (0.08), changes with mass are small. The decrease in energy content per day is $2.012\ W^{0.08}$ (where mass is in g) or 3.2% for the smallest skipjack used by Gooding (0.32 kg) and 4.0% for the largest (4.7 kg).

Kitchell et al extended their calculations to estimate the energy required to account for observed growth rates of skipjack in the field. The observed growth rate is 0.7% mass per day or $10\text{ kcal}\cdot\text{fish}^{-1}\cdot\text{day}^{-1}$ for a 1 kg skipjack. In the laboratory small skipjack can consume food equivalent to 28–35% of their body mass $\cdot\text{day}^{-1}$. Kitchell et al deduced that small skipjack (less than 7–10 kg) grow at rates substantially lower than maximal and thus appear limited by food availability and/or their efficiency as predators. Growth of large skipjack (greater than 7–10 kg) appears limited by the rate at which food can be consumed and physiologically processed. This upper limit appears to account for the upper size limit of skipjack observed in the field (25 kg). Observed growth rates in the field and maximum size in the field are concordant with a metabolic rate slightly more than twice the routine rate observed by Gooding (14), i.e. about $577\cdot W^{0.08}$. For a 0.32 kg fish this is $915\text{ mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$; for a 2 kg fish it is $1060\text{ mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$; and for a 4.7 kg fish it is $1134\text{ mgO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$. All of these values are higher than rates measured at maximum sustained swimming speeds for any other species at any temperature. We can calculate the approximate speed for a particular mass when oxygen uptake = $0.577\ W^{0.08}$ (i.e. when it is twice the

routine rate measured by Gooding) by substituting into the original relation (10).

$$S = (22.35 - 2.558 \log W) \cdot W^{0.2831},$$

where S is speed in $\text{km}\cdot\text{day}^{-1}$ and W is mass in g. To estimate fuel used we convert metabolic rate to grams of fat used per day. Fuel economy (FE) can now be calculated by dividing km travelled per day by fat used per day. $FE = (4511 - 516.4 \log W) \cdot W^{-0.7969}$, where FE is in $\text{km}\cdot\text{g fat}^{-1}$ when swimming at speeds equivalent to twice the routine rates.

Thus the 0.32 kg tuna travels $82 \text{ km}\cdot\text{day}^{-1}$ using 2.52 g fat ($32 \text{ km}\cdot\text{g fat}^{-1}$) whereas the 4.7 kg tuna travels 142 km using 45.8 g fat ($3.10 \text{ km}\cdot\text{g fat}^{-1}$). Large tuna must consume and physiologically process ten times as much fuel to swim less than twice as far. For each doubling of mass, fuel economy is approximately halved, a relation analogous to that between the fuel consumption rates of small and large cars.

Pennycuik has made similar calculations for birds (20, 21). A 3 g hummingbird travels 880 km per g fat, whereas the larger bird, a 384 g pigeon, travels only 11.7 km per g fat. The 384 g pigeon and the 320 g skipjack get similar mileage. Similar calculations can be made for a 384 g white rat (29). At maximum speed ($2.25 \text{ km}\cdot\text{h}^{-1}$) it could travel 54 km at a total cost of $13.8 \text{ g fat}\cdot\text{day}^{-1}$. These relations are summarized in Table 1.

Giant Bluefin Tuna

The approach of Kitchell can be applied to the largest tuna, the giant bluefin. This animal's oxygen uptake has not been measured, but we do know something about its feeding and growth rates. Giant bluefin arrive in Nova Scotia in July weighing about 350 kg. They gain about 20% in body mass (all fat) in about 60 days when fed a rate of about 4% body mass per day. The caloric content of the food, mackerel, also a scombroid, is probably about the same as that of the tuna. Assuming a caloric density the same as skipjack, then mass-specific metabolic rate is:

$$\frac{0.0227 \text{ kg}}{\text{kg}\cdot\text{day}} \times \frac{1000 \text{ g}}{\text{kg}} \times \frac{1.46 \text{ kcal}}{\text{g}} \times \frac{1 \text{ mgO}_2}{0.0034 \text{ kcal}} \times \frac{1 \text{ day}}{24 \text{ h}} = 406 \text{ mgO}_2\cdot\text{h}^{-1}\cdot\text{kg}^{-1}.$$

This is surprisingly similar to the maximum active rate for salmon extrapolated over two orders of magnitude: Active salmon metabolism = $(1.772 \times 385000^{0.888}) / 385 = 420 \text{ mgO}_2\cdot\text{h}^{-1}\cdot\text{kg}^{-1}$. The speed at this metabolic rate extrapolated from the salmon equation is $1.53 \text{ l}\cdot\text{sec}^{-1}$. This is slightly more than the observed speed ($1 \text{ l}\cdot\text{sec}^{-1}$ or $3 \text{ m}\cdot\text{sec}^{-1}$) for which the bluefin metabolic estimate is made.

We can also compare the giant bluefin's net cost to that of a similar-sized mammal (28). Net mammal metabolism is: $M = 760 \cdot W^{-0.4} = 760 \cdot 385^{-0.4} = 70.3 \text{ mgO}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$. The net cost for bluefin is almost exactly half the value for a mammal of equivalent mass. Thus the fuel economy of the tuna is twice that of the mammal (Table 1).

NET COSTS BASED ON THRUST AND DRAG ESTIMATES

Independent estimates of net energy costs can be made in a straight-forward manner from the thrust/drag relationships of a swimming fish (6, 7). These estimates can then be compared with the laboratory values from the respirometers. The estimates are made as follows: In steady-state swimming, total thrust force (dynes) equals total drag force (dynes). By first principles (30), drag force is $D = 0.5 \cdot S \cdot \rho \cdot V^2 \cdot C_D$, where S = wetted surface area (cm^2), ρ = fluid density ($\text{g} \cdot \text{cm}^{-3}$), V = velocity ($\text{cm} \cdot \text{sec}^{-1}$), and C_D = coefficient of total drag. Similarly, thrust force is $T = 0.5 \cdot S \cdot \rho \cdot V^2 \cdot C_T$ where S = surface area of caudal fin (cm^2), V^2 = lateral velocity of fin ($\text{cm} \cdot \text{sec}^{-1}$), and C_T = coefficient of total thrust.

Power is the time rate of doing work, and work is the application of force through a given distance. But since the propulsion system is not 100% efficient, more power input is required for the power output necessary to propel a given fish at a given speed. Total aerobic efficiency is generally taken (30) as 0.2, which means of course that about 80% of the input power is lost as heat and does no usable work (Figure 1). Thus $P_i = (D \cdot V \cdot 10^{-7})/n$, and $P_o = (T \cdot V \cdot 10^{-7})/n$, where P_i = input power (watts) and n = total aerobic efficiency = 0.2. To this input power must be added the power necessary to fuel the nonswimming processes described in the previous section.

Table 1 The metabolic cost of locomotion of tunas compared to other endotherms of similar mass

Animal	Mass	Speed ($\text{km} \cdot \text{day}^{-1}$)	Fat used ($\text{g fat} \cdot \text{day}^{-1}$)	Fuel economy ($\text{km} \cdot \text{g fat}^{-1}$)
Small endotherms				
Skipjack	320 g	82	2.52	32
Pigeon	384 g	1374	117	11.7
Rat	384 g	54	13.8	3.9
Large endotherms				
Bluefin	385 Kg	259	1237	0.21
Salmon ^a	385 Kg	397	1283	0.31
Mammal	385 Kg	259	2510	0.10

^a Extrapolated from salmon data (2) at the maximum activity level

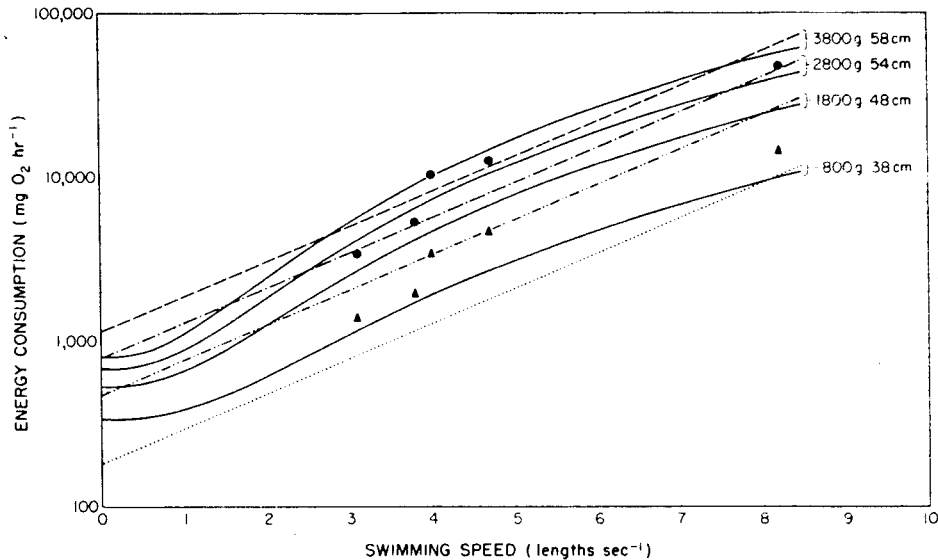


Figure 3 Comparison between measured oxygen uptake extrapolated to 8.5 l. sec^{-1} (broken lines) and the theoretically calculated power consumption based on hydrodynamic considerations (solid lines). Triangles (\blacktriangle) are the theoretical power consumption based on an analysis of drag forces, and points (\bullet) are based on an analysis of thrust forces for a 40 cm, 1003 g skipjack tuna (17). Figure adapted from (10).

Precise estimates of body surface area exist for many species of tuna, along with regression relationships based on length (18). Remaining are estimates of the coefficients of drag and thrust; these are the most questionable and subject to error. For the construction of the solid lines in Figure 3, a simple relationship was used (6,10). The simple drag model produces conservative values.

The measured oxygen-uptake relationship in Figure 2 extrapolated to 8.5 l./sec^{-1} compares well to the theoretical projections of energy consumption based on the simple drag model (Figure 3). Magnuson's (17) estimates of the theoretical power consumption of a 40 cm, 1003 g skipjack tuna, based on either model of thrust forces or based on an accurate estimate of total drag, are also presented in the figure. These compare well and are conservative, predicting even larger expenditures of energy.

THERMOCONSERVATION, LOCOMOTION, AND ENERGETICS IN TUNAS

The feature that most sets tunas apart from other fishes is the fact that they are warm-bodied. Is this fact related to locomotion and/or the energetics of locomotion? Arguments concerning the adaptive advantage of being warm relative to the water have been discussed in detail (27). Recently Stevens & Carey (25) developed a new argument.

Tuna are especially well adapted to sustain high speeds (they have many morphological features that reduce drag) rather than to achieve high burst speeds (which require low mass, and for which frictional resistance is less important). Yuen (31) reported a school of skipjack tuna that travelled 28 km in 107 min—i.e. fish 40–50 cm long can swim at speeds of about $10 \text{ l}\cdot\text{sec}^{-1}$ for at least an hour.

Stevens & Carey (25) argue that being warm-bodied confers an adaptive advantage because it increases the amount of oxygen that can be delivered to active cells. Passive diffusion of oxygen has a Q_{10} of about 1. The Q_{10} of transport of oxygen by myoglobin is higher, probably between 1.5 and 2 (E. D. Stevens, unpublished). Skipjack tuna muscle temperature changes with activity level, at least when we compare extreme activity levels. Tuna muscle has much red muscle that contains a high concentration of myoglobin. Thus the warmth may increase the rate at which myoglobin delivers oxygen to the mitochondria of active cells.

Although the above reasonably explains the advantage of warm muscle, it does not explain that of a warm stomach. Telemetric observations of free-swimming bluefin tuna (F. G. Carey, E. D. Stevens, and J. W. Kanwisher, unpublished data) show that these tunas increase stomach temperature after a cold meal and keep it warm for hours during digestion (stomach temperature 25–30°C, water temperature 12°C). In this case it seems that being warm-bodied confers an adaptive advantage because it permits an increase in the rate at which food can be physiologically processed.

All tunas, from the small tropical tunas to the giant bluefin, also have elevated brain temperatures. Brain temperature of skipjack increases from about 0.1°C to 4°C above ambient during rapid swimming (26).

Thus although being warm is what makes tuna unique among fishes, no single function can be attributed to the warmth. Tunas inhabit parts of the ocean where food is dilute and patchily distributed. They maximize energy gain by “gambling” large energy expenditures (high sustained activity) on the “expectation” of proportionately large energy returns (25, 27). Being warm is one aspect of this “gamble.”

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