

THE EFFECT OF BODY SIZE ON
THE STANDARD METABOLIC RATE OF
SKIPJACK TUNA, *KATSUWONUS PELAMIS*

The standard metabolic rate (SMR) of fish is the energy requirement of a postabsorptive animal completely at rest (Beamish and Mookherjee 1964; Fry 1971; Brett 1972). It approximates the energy demand of all metabolic processes except swimming and digestion. The SMR (and its relation to fish size) is an important input parameter for energetics, growth, and population models (Kitchell et al. 1974; Kitchell et al. 1977). The SMR may also be used to predict optimal fish cruising speed (Weihs 1973, 1977). I undertook this study to provide SMR measurements for skipjack tuna, *Katsuwonus pelamis*. These measurements may be incorporated into models such as those described in Sharp and Francis (1976), Kitchell et al. (1978), and Sharp and Vlymen (1978).

The SMR is generally determined by extrapolation of a metabolic rate versus swimming activity curve back to a zero activity level (Beamish 1964; Brett 1965; Muir et al. 1965). However, because it is difficult simultaneously to measure metabolic rate and activity level of large, highly active, pelagic species such as skipjack tuna, SMR was measured directly.

Methods and Materials

Skipjack tuna, purchased from local fishermen, were maintained at the Kewalo Research Facility of the National Marine Fisheries Service (described in Nakamura 1972). Fish were kept in outdoor tanks from 2 days to several weeks before use. Food was presented to all fish daily; however, a fish was not fed for at least 20 h prior to its use in an experiment. This allowed sufficient time for an animal to clear its stomach and intestine and for its blood glucose level to return to prefeeding levels (Magnuson 1969).

To reduce struggling and minimize injury during handling, each fish was injected with the neuromuscular blocking agent gallamine triethiodide (approximately 1 mg kg^{-1}). The animal was then placed in a Plexiglas¹ flow-through box respirometer, similar to that described in Stevens (1972). The spinal cord was cut immediately behind the skull to stop all overt muscular activity

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the wound packed with foam rubber to minimize bleeding. Electrocardiogram (ECG) leads were mounted subcutaneously on the ventral body surface and an 18-gage hypodermic needle, with a thermistor bead mounted in its tip, was pushed through the dorsal musculature to the vertebral column. The ECG signal was displayed on an oscilloscope and the red muscle temperature determined by balancing a wheatstone bridge circuit containing the needle mounted thermistor and a 5-decade resistance substitution box.

Oxygen concentration of the water upstream and downstream of the fish was monitored simultaneously with two Yellow Springs Instruments (model 51A) dissolved oxygen meters equipped with Clark-type, polarographic electrode, oxygen-temperature probes. Water flow through the respirometer was maintained at approximately 3 l kg^{-1} (body weight) min^{-1} , and was measured by recording the time required to fill a 1 l graduated cylinder. The source of the seawater was the same as that which supplied the holding tanks. No at-

tempt was made to control water temperature which ranged from 23.5° to 25.5° C .

Dissolved oxygen levels, water flow rate, heart rate, red muscle temperature, and water temperature were determined every 10 min and measurements were continued until the fish's metabolic rate remained relatively stable for at least 1 h.

Results and Discussion

The SMR of each fish was determined by finding the minimum predicted metabolic rate based on a second degree polynomial fitted to observed metabolic rate measurements. This method is an acceptable approximation for asymptotic curve fitting (Snedecor and Cochran 1967). To illustrate this technique, the observed and predicted metabolic rate, body temperature, and heart rate are presented in Figure 1.

Heart rate was monitored only as a check on the health of the animal. Experiments were terminated if the heart rate became erratic or slowed

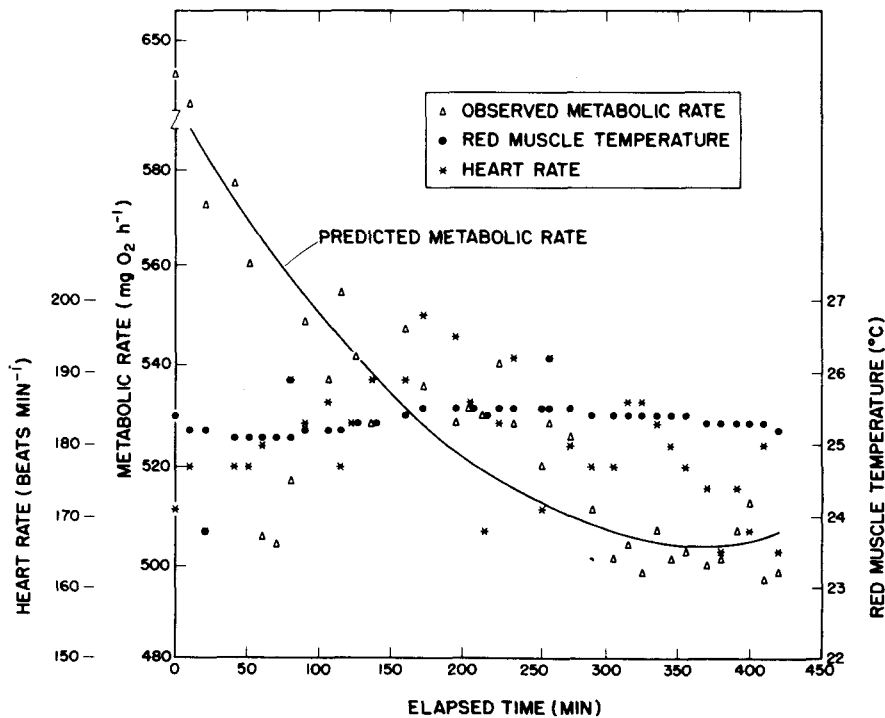


FIGURE 1.—Changes in metabolic rate, heart rate, and red muscle temperature of a 1.456 kg skipjack tuna during an experiment to determine standard metabolic rate (SMR). The predicted metabolic rate is based on a least-squares fitted second degree polynomial. The minimum predicted metabolic rate (i.e., SMR) is $505 \text{ mg O}_2 \text{ h}^{-1}$.

significantly. Red muscle temperature was monitored to test if changes in metabolic rate reflected changes in it. All fish showed red muscle temperatures as stable as those shown in Figure 1. Fish were in the respirometry box approximately 15 to 30 min before data recording began and red muscle temperatures generally approached thermal steady state during this period.

The SMR of 33 fish (0.317-4.737 kg) was successfully determined. A regression line of SMR versus body weight was fitted by Gauss-Newton iteration technique (Biomedical Computer Programs, program number BMDP 3R), rather than by a linear regression technique based on log-log transformation of the data (Figure 2). The advantages of the former method and disadvantages of the latter have been discussed by Zar (1968) and Glass (1969).

The best-fitting allometric equation was found to be:

$$\text{SMR} = 412.0 (\pm 27.1) W^{0.563 (\pm 0.07)} \quad (1)^2$$

where SMR = standard metabolic rate in milligrams O₂ per hour and
W = body weight in kilograms;

values in parentheses are the standard deviations of the parameters. The coefficient of determination (r^2) is 0.72.

The exponent in the allometric equation describing the effect of body size on the SMR of other teleosts ranges from approximately 0.65 to >1 (Winberg 1956; Fry 1957; Beamish and Mookherjee 1964; Beamish 1964; Glass 1969; Brett 1972). The lower value for the exponent in Equation (1) indicates that the weight specific SMR (i.e., milligrams O₂ per gram per hour) of skipjack tuna decreases more steeply as body size increases than does the weight specific SMR of other species.

The strong influence of body size on the SMR may be a unique characteristic of thermoconserving species such as skipjack tuna. However, the value of the weight exponent could also be influenced by the technique used to measure SMR. For comparative purposes, it would be useful to determine the SMR's (and corresponding allometric equation) of species (e.g., salmonids) where

²If the allometric equation to describe the effect of body size on whole body SMR is: $\text{SMR} = aW^b$ then the corresponding equation to describe weight-specific SMR versus body weight is: $\text{SMR}/W = aW^{b/W}$ or $\text{SMR}' = aW^{b-1}$ where SMR' = weight-specific SMR, W = body weight, and a and b are fitted parameters.

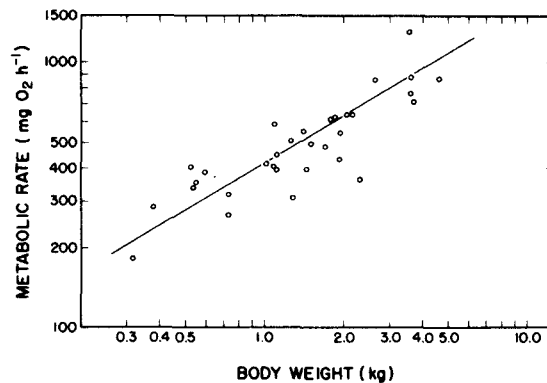


FIGURE 2.—A double logarithmic plot of the standard metabolic rate (SMR) versus body weight (W). The line represents the allometric equation $\text{SMR} = 412.0 W^{0.563}$. The coefficient of determination is 0.72.

these parameters are already known, but employing the methodology outlined in this study.

The SMR has been postulated to be a function of: the diffusing capacity of the respiratory system, whole blood sugar concentration, and the rate at which the circulatory system can deliver substrates and oxygen to the cells (Schmidt-Nielsen 1970; Ulsch 1973; Coulson et al. 1977; Wilkie 1977; Hughes 1977; Umminger 1977). Specifically which of these factors most influence the SMR of skipjack tuna is unknown at this time. Selection pressures apparently favor significant reductions in the weight-specific SMR of skipjack tuna as body size increases (hence the lower exponent in Equation (1)). How the factors that determine SMR could be affected by such selection pressures is also unknown.

The SMR's for skipjack tuna are approximately 5 to 10 times greater than those reported for other teleosts of equal body size (Pritchard et al. 1958; Beamish 1964; Brett 1965, 1972). However, the great difference in the effect of weight on SMR, and the unique methodology employed in this study, makes direct comparisons tenuous.

Application of the Results

Careful application of my results in energetics models is advised for several reasons. First, skipjack tuna attain maximum body size of approximately 22 kg (Kitchell et al. 1978); although the weight range of fish I used in this study covers more than an order of magnitude, there is still a large untested size range. Because skipjack tuna

>4 to 5 kg are extremely difficult to capture and transport, it is unlikely that specimens larger than this will be tested in the foreseeable future.

Second, the SMR includes the energetic cost of osmoregulation and cardiac work. The energy requirement of both processes comprises a significant fraction of the SMR (Heath 1964) and more importantly, the energy demand of these processes is dependent on swimming speed (Rao 1968; Farmer and Beamish 1969; Nordlie and Leffler 1975). Therefore prediction of energy demand as a function of swimming speed may not be adequately determined by simple addition of the SMR and the energy cost of swimming based on a theoretical estimate of hydrodynamic drag; an estimate of the increased internal work, due to activity, should also be included.

Third, the scatter in the SMR's presented in Figure 2 is due, in part, to the difficulty of working with animals such as skipjack tuna, which are both highly active and physiologically delicate. There are, however, also at least two distinct subpopulations of skipjack tuna that occur around the Hawaiian Islands (Sharp³). It is reasonable to suspect the SMR of individuals from the various subpopulations might be significantly different when measured under identical conditions. Again, reasonable caution in application of the data presented here is urged.

Acknowledgments

I thank the following people for helpful criticisms of the manuscript and useful discussions: Andrew Dizon, Gary Sharp, Don Stevens, Causey Whittow, and Carol Hopper. Randolph Chang, Douglas Davies, and Victor Honda provided technical assistance.

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