Marine Biology 72, 1–6 (1982)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Metabolic Rate of the Albacore Tuna *Thunnus alalunga*

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Abstract

The oxygen consumption rates ($\dot{V}O_2$) of 6 specimens (6 to 13 kg) of the albacore tuna *Thunnus alalunga* were measured at sea, using specimens collected 300 km west of San Diego, California (USA) during July and August, 1981. Fish were tested in a closed continuous-flow respirometer, where they swam at about 1.3 body lengths s^{-1} velocity in 15° to 19 °C water. The albacore tuna is a temperate pelagic species experiencing water temperatures from about 10° to 20 °C and attaining a maximum weight of 45 kg. The $\dot{V}O_2$ ranged from 1 249 to 3 336 ml h^{-1} (the mean $\dot{V}O_2$ for the 6 fish was 2 228 ml h^{-1}); such values approach those of mammals of a similar size and are 3 to 4 times those of most active fishes (e.g. sockeye salmon). Among fishes, the only higher $\dot{V}O_2$ values yet recorded were for the skipjack tuna *Katsuwonus pelamis*, a tropical species. The remarkably high metabolic rates of tunas are presumably correlated with their continuous swimming activity and the maintenance of endothermy. The exponent relating $\dot{V}O_2$ to body weight (1.18), although large, is not statistically different from the exponents for most other active vertebrates.

Introduction

Tunas, the most advanced and highly specialized group of fishes in the teleost family Scombridae, must swim continuously to maintain hydrostatic equilibrium (Magnuson, 1973, 1978) and to ventilate their gills (Roberts, 1978). Continuous swimming by tunas doubtlessly entails a large energetic investment (Gooding *et al.*, 1981; Stevens and Dizon, 1982). Moreover, the anatomical, physiological and biochemical specializations that are unique to tunas are all consistent with the hypothesis that these fish require high rates of oxygen consumption to sustain their body maintenance and locomotory costs (Gooding *et al.*, 1981; Stevens and Dizon, 1982; Graham *et al.*, unpublished observations). Verification of this hypothesis by direct measurement of the swimming metabolic rates of tunas is, however, technically difficult due to their generally large body size, fast swimming speeds, and poor survivorship in captivity.

Gooding *et al.* (1981) were the first to measure the swimming $\dot{V}O_2$ of tuna. They studied 0.4 to 6.0 kg specimens of skipjack tuna (*Katsuwonus pelamis*) swimming at speeds ranging from 50 to 75 cm s^{-1} in temperatures from 23° to 25 °C. The work by Gooding *et al.* revealed the following remarkable characteristics of skipjack tuna metabolism and swimming energetics: (1) skipjack tuna $\dot{V}O_2$ (0.522 mg O_2 g h^{-1}) was nearly the same as that of a mammal of similar size and thus much higher than that of most active fishes; (2) compared to a sockeye salmon (*Oncorhynchus nerka*, family Salmonidae) swimming at similar speeds but in 15 °C water, a skipjack tuna has a $\dot{V}O_2$ that is 2 to 5 times higher; (3) the rate of increase in $\dot{V}O_2$ with swimming velocity was proportionally less in skipjack tuna than in a sockeye salmon, implying that tunas, relative to salmonids, may be more efficient swimmers; (4) the $\dot{V}O_2$ of skipjack tuna was proportional to wet-body weight raised to a power of 1.19 (i.e. $\dot{V}O_2 \simeq W^{1.19}$), an exponent much higher than values (0.6 to 1.0) typical for active metabolism-body weight relationships in other vertebrates (Brett and Groves, 1979; Schmidt-Nielsen, 1979).

The notable results obtained for skipjack tunas by Gooding *et al.* (1981) invite additional experimentation with tuna swimming metabolism in order to verify these findings and understand how swimming energetics may vary among tuna species. Although their work was of extremely high quality, many of the $\dot{V}O_2$ determinations made by Gooding *et al.* were with groups rather than individual swimming skipjack tuna, and fish swimming speed could not be precisely controlled. Also, conclusions about the relative magnitude of the $\dot{V}O_2$ of skipjack tuna (and therefore all tuna species) relative to the $\dot{V}O_2$ of other active fishes (e.g. salmonids) may be biased somewhat by the

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water temperature differences (skipjack 23° to 25 °C, sockeye 15 °C) present in the existing comparative data.

The present paper reports investigations of the swimming $\dot{V}O_2$ of the North Pacific albacore tuna *Thunnus alalunga*, conducted on board the "David Starr Jordan", research vessel of the National Oceanic and Atmospheric Administration-National Marine Fisheries Service. Our objectives were to measure $\dot{V}O_2$ as soon as possible after capture. We have studied the albacore because it, unlike the skipjack tuna, is a temperate-zone species and thus would provide $\dot{V}O_2$ data directly comparable, in terms of habitat temperature, to that for sockeye salmon. Another objective of our work was to investigate the scaling of $\dot{V}O_2$ with body weight in *T. alalunga*. We also report some observations on the effects of temperature and hypoxia on the albacore. In addition to increasing our knowledge of the specializations of tunas for locomotion, investigations of tuna swimming physiology are important to an understanding of the migration and movements of these fishes and to ensure proper management of the fishery.

Materials and Methods

Specimens of *Thunnus alalunga* were caught by trolling feathered jigs in surface waters approximately 300 km west of San Diego, California (USA) in July and August, 1981. Sea surface temperatures in the area ranged from 17.5° to 19.0 °C. Hooked fish were brought on board within 60 s of striking a jig, and a hose with running seawater was immediately placed in the mouths to irrigate the gills during hook removal. Only fish without serious hook injury were selected for respirometer tests.

Swimming $\dot{V}O_2$ measurements were made on 6 albacore, ranging in weight from 6 to 13 kg. Each fish was initially submerged in a 200 liter tank containing chilled (15° to 17 °C), oxygenated seawater, and its gills were ventilated with flow from a submersible pump. After initial observations revealed the fish to be in good condition, it was transferred to the working section of a tunnel respirometer (Fig. 1), where continuously flowing water required it to swim in order to maintain a stationary position. A single-speed centrifugal pump (capacity 4 000 liters min^{-1}) circulated water from the reservoir (2 800 liters) through the working section of the respirometer and back to the reservoir. The parallel bypass channel and gate valve in the system (Fig. 1) permitted some modulation of flow through the working section. This was necessary initially to "train" fish to swim in the chamber (10 to 30 min) and to stimulate swimming throughout each experiment. A removable clear Lucite lid, fitted with a rubber gasket and held in place by wingnuts, was used to introduce or remove a fish from the respirometer. A black plastic cover over the front half of the lid darkened the chamber during experiments. This had a calming effect on the fish and, together with vertical black and white stripes painted inside the front part of the working section, may have provided orientation cues for maintaining station.

Refrigeration units in the reservoir maintained temperature between 14° and 18 °C. All pipes used in respirometer construction were PVC (15.2 cm i.d.). The 110 cm long aluminium working section (Fig. 1) was square in cross-section (26×26 cm), and tapered at each end (for 42 cm) to permit direct attachment to PVC flanges. A 23 cm long stack of 2 cm (i.d.) diam PVC collimator tubes in the anterior part of the working section helped to reduce turbulence. A small 45° grating was also installed anterior to the collimator (Fig. 1) to deflect water to the inner side of the working section and straighten flow from the upstream union with the bypass channel (Fig. 1). Dye injections were used to verify rectilinear flow through the working section.

A calibrated flow meter was used to determine water velocity in the working section. The average velocity was 0.73 m s^{-1}. Actual experimental velocities were higher, however, because of the solid blocking effects of fish body cross-sectional area (Webb, 1975). To take this into account, size-dependent velocity relationships had to be calculated as follows for each fish tested, using the methods described by Bell and Terhune (1970). Chamber velocity, U, is proportional to the product of the rated tunnel velocity, U_t, and the velocity factor speed increment, K, imposed by fish cross-sectional area,

$$U = U_t(1 + K). \quad (1)$$

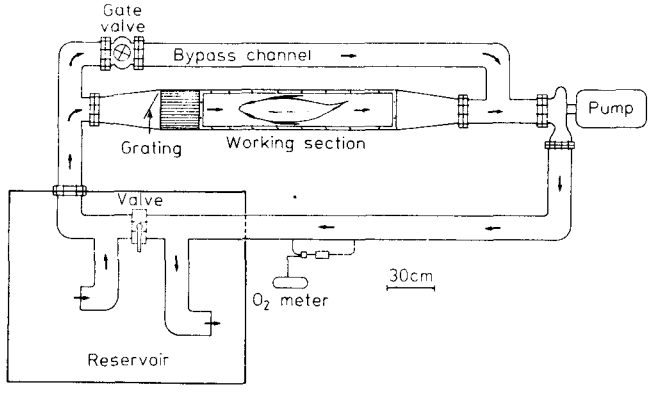

Fig. 1. Top view of albacore swimming respirometer. Arrows show direction of flow. Main return pipe is located at top of reservoir

K is estimated by

$$K = \tau\lambda \frac{A_0^{3/2}}{A_t}, \quad (2)$$

where τ is 0.8, λ is 0.5 x (fish fork length ÷ body thickness), and A_0 and A_t are the cross-sectional areas of the fish and tunnel, respectively (Bell and Terhune, 1970).

The condition of albacore in the respirometer was continually monitored and tail-beat frequency was determined at regular intervals. Metabolic rate measurements were begun only after a fish had swum continuously for 1 to 2 h. Oxygen consumption rate ($\dot{V}O_2$) was estimated by monitoring the decline in respirometer O_2 level during 15 to 25 min intervals when the respirometer was closed and no water exchange occurred between it and the reservoir. The respirometer was closed by opening a gate valve between the intake and outflow pipes and capping the two reservoir ports (Fig. 1). The rate of O_2 decline (slope) when corrected for closed respirometer volume (342.5 liters), fish wet weight (volume), and background respiration, indicated fish $\dot{V}O_2$. Respirometer oxygen level was measured with a temperature-compensated Yellow Springs O_2 electrode (Model 54) in a housing which was circulated with water pumped from and back into the respirometer (Fig. 1). Before each test, the electrode was calibrated in air and water. Replicate $\dot{V}O_2$ measurements were made on all but one fish, and 20 to 30 min elapsed between each run. Because water temperature rose when the system was closed, runs had to be kept short and all albacore $\dot{V}O_2$ measurements were made under conditions where temperature increased by 2 or 3 C° during the run. The temperature-compensated probe permitted correction for the effects of heating on O_2 solubility, and tests with freshly killed fish were conducted to estimate background respiration.

All tests were carried out at water O_2 concentrations above 60% air saturation. In addition, observations were made on the behavioral responses to decreasing O_2 concentration to the point of suffocation for one fish. Also 3 inadvertent "tests" with fish at respirometer water temperatures of 11° to 12 °C provided additional information about the probable tolerance limits of albacore to low temperature.

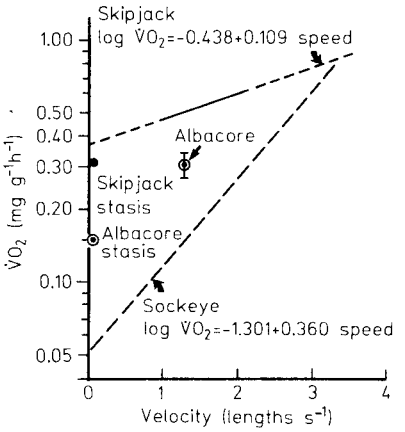

Fig. 2. Relationship between swimming speed and $\dot{V}O_2$ determined for 0.4 to 6.0 kg skipjack tuna (*Katsuwonus pelamis*) by Gooding *et al.* (1981) and the weighted mean $\dot{V}O_2$ (mg g^{-1} h^{-1} ±95% confidence intervals) determined for 6 to 13 kg albacore (*Thunnus alalunga*) swimming at 1.3 lengths s^{-1} in present study. Stasis $\dot{V}O_2$ estimates for albacore (Brill, personal communication) and skipjack tuna (Brill, 1979) are included for comparison, as is the $\dot{V}O_2$-velocity relationship of sockeye salmon (*Oncorhynchus nerka*) at 15 °C (Brett and Glass, 1973; Gooding *et al.*, 1981). Albacore data were obtained at 15° to 19 °C, skipjack at 23° to 25 °C

Results and Discussion

Table 1 summarizes *Thunnus alalunga* body-size information, corrected respirometer swimming speeds (Eqs. 1 and 2), mean tail beat frequencies, and the $\dot{V}O_2$ estimates obtained for the 6 albacore in this study. The mean combined $\dot{V}O_2$ for all fish is 2 228 ml h^{-1} fish^{-1}. Expressed in terms of unit body weight, mean $\dot{V}O_2$ is 0.212 ml g^{-1} h^{-1} (=0.303 mg g^{-1} h^{-1}, Fig. 2). Calculated swimming speeds vary directly with size and range from 93 to 115 cm s^{-1}, and there is no correlation between $\dot{V}O_2$ and swimming speed (Table 1). Each albacore maintained a steady tail-beat frequency during the test period, and the range of rates observed (2.13 to 2.36 Hz) for all fish is similar to values reported for other scombrids swimming at 1.3 lengths

Table 1. *Thunnus alalunga.* Body size, swimming speed and respiration data at 15° to 19 °C. $\dot{V}O_2$ data are weighted means

Fish No.	Weight (g)	Fork length (cm)	Swimming velocity (cm s^{-1})	Swimming velocity (lengths s^{-1})	Tail-beat frequency Hz±(95%)	Mean $\dot{V}O_2$ (ml g^{-1} h^{-1})	SD	N	Mean total O_2 consumption (ml h^{-1})	Minimum speed[a] (lengths s^{-1})
1	6 245	67.6	92.6	1.37	2.31 (0.20)	0.200	0.049	3	1 249	0.72
2	9 740	79.5	104.9	1.32	2.14 (0.07)	0.159	0.044	4	1 553	0.57
3	11 810	83.7	109.6	1.31	2.24 (0.04)	0.175	0.003	4	2 070	0.51
4	13 600	87.5	114.6	1.31	2.23 (0.05)	0.245	0.020	4	3 336	0.47
5	9 170	77.0	101.6	1.32	2.13 (0.10)	0.179	–	1	1 643	0.62
6	9 890	82.0	108.2	1.32	2.36 (0.07)	0.286	0.020	4	2 831	0.54
$\bar{X}$	10 076	79.6	105.3	1.33	2.24	0.212[b]			2 227.5	

[a] Estimated from Dotson (1976): $V_{min} = \frac{l_f}{D_e/2(A)}$, where A is body lifting area, l_f is lift required for hydrostatic equilibrium, D_e is sea-water density (see Magnuson, 1973)

[b] 0.212 ml O_2 g^{-1} h^{-1} = 0.303 mg O_2 g^{-1} h^{-1}

s^{-1} (Fig. 16 in Magnuson, 1978). Stride length coefficients (i.e., the number of body lengths moved per tail beat) of the albacore in Table 1 range from 0.56 to 0.62, which is within the range of values found for other scombrids (Magnuson, 1978; Brill and Dizon, 1979). The variation in tail-beat frequency observed among different fish was not correlated with either body size or corrected swimming velocity.

The swimming velocities of albacore tuna in these tests ($\bar{x}$ 1.3 lengths s^{-1}) were similar to the mean speeds of the skipjack tuna *Katsuwonus pelamis* tested by Gooding *et al.* (1981; range 0.9 to 2.0 lengths s^{-1}). Table 1 also indicates the minimum swimming speed estimates for each fish based on the relationship determined for albacore tuna by Dotson (1976). Minimum speed is defined as the slowest speed a negatively buoyant fish (such as all tuna) could swim and still maintain hydrostatic equilibrium (Dotson, 1976). Minimum speed varies among species, and depends primarily upon morphological features such as the presence or absence of a gas bladder, pectoral fin size (area) and body shape (Magnuson, 1978). It is apparent that the velocity of each fish in the respirometer was faster than its minimum speed requirement by a mean factor of 2.4.

Fig. 2 compares the mean weight-specific $\dot{V}O_2$ (0.303 mg O_2 g^{-1} h^{-1}) of the 6 albacore tuna swimming at a mean speed of 1.3 lengths s^{-1} with the $\dot{V}O_2$-velocity linear regression for skipjack tuna (Gooding *et al.*, 1981). Also shown in Fig. 2 is the "stasis" $\dot{V}O_2$ for a 1.96 kg skipjack tuna (the mean weight of fish tested by Gooding *et al.*) calculated from the $\dot{V}O_2$-weight regression determined by Brill (1979) for sedated spinalectomized fish. (Stasis $\dot{V}O_2$ is determined from measurements on sedated immobilized fish in order to provide an estimate of maintenance metabolic activities that are otherwise masked by swimming metabolism.) Brill (personal communication) also allowed us to include his unpublished stasis $\dot{V}O_2$ measurements for two albacore (3.3 and 3.5 kg) in Fig. 2. Finally, and for additional comparison, the $\dot{V}O_2$-velocity regression for a 1.8 kg sockeye salmon (*Oncorhynchus nerka*) at 15 °C is included (as shown in Gooding *et al.*, 1981; data from Brett and Glass, 1973).

Fig. 2 shows the lower rate of increase in $\dot{V}O_2$ with velocity found for skipjack tuna (Gooding *et al.* 1981) relative to sockeye salmon. At low speed, skipjack tuna at 23 ° to 25 °C clearly have higher maintenance costs than do sockeye salmon at 15 °C; however, the energetic cost of swimming faster is proportionately less in skipjack tuna, possibly because of their streamlined body and improved mechanical efficiency (Gooding *et al.*, 1981; Stevens and Dizon, 1982). Although there are no $\dot{V}O_2$ data for skipjack tuna swimming slower than 0.9 lengths s^{-1}, extrapolation of the Gooding *et al.* $\dot{V}O_2$-velocity line to zero velocity gives a "resting" $\dot{V}O_2$ estimate of 0.365 mg g^{-1} h^{-1}, which is 1.2 times greater than Brill's stasis $\dot{V}O_2$ estimate for a 1.96 kg fish (0.307 mg g^{-1} h^{-1}). Assuming that the $\dot{V}O_2$ velocity relationship of albacore parallels that of skipjack tuna, one can extrapolate to zero velocity to obtain a "resting" $\dot{V}O_2$ of about 0.224 for albacore (Fig. 2), which is 1.5 times above the stasis rate determined for this species by Brill (personal communication), and only slightly more than the ratio between resting and stasis $\dot{V}O_2$ in skipjack tuna. The overall similarity between these ratios in both *Thunnus alalunga* and *Katsuwonus pelamis* suggests that these species incur comparable increases in metabolic cost during swimming.

Fig. 2 additionally shows that at 1.3 lengths s^{-1} swimming speed, albacore weight-specific $\dot{V}O_2$ is twice the rate of sockeye salmon and 60% of that of skipjack tuna. Thus, even though albacore typically occur in cooler waters than do tropical skipjack tuna (Laurs and Lynn, 1977), their metabolic rate at 15 ° to 19 °C is nearly as high as that of a skipjack tuna at 23 ° to 25 °C. Also, the maintenance by the albacore of a metabolic rate twice that of a sockeye salmon at 15 °C suggests that an elevated metabolic rate is typical of all tuna species.

The following factors may explain the differences between albacore and skipjack tuna $\dot{V}O_2$. Both these species are endothermic (Graham and Dickson, 1981). Skipjack tuna tested at 23 ° to 25 °C would be expected to have a core body temperature of about 26 °C (Dizon and Brill, 1979), which is slightly warmer than deep core and red muscle temperatures expected to prevail in an albacore (21 ° to 25 °C) in 17 ° to 18 °C water (Graham and Dickson, 1981). Because it is warmer, the skipjack tuna may use more O_2 (Stevens and Dizon, 1982) and thus have a higher $\dot{V}O_2$ at a given speed and water temperature. Albacore have lower amounts of aerobically active red muscle than skipjack, 4.1% of body mass vs 7.3%, respectively (Graham *et al.*, unpublished observations). Based on published values for red muscle $\dot{V}O_2$ (Stevens and Neill, 1978), we calculate that this difference in red muscle accounts for 20% of the $\dot{V}O_2$ difference. However, relative activity differences between albacore and skipjack tuna in the two swimming experiments do not correlate with $\dot{V}O_2$ differences. Although swimming velocities were similar in tests with albacore and skipjack tuna (see above), albacore swam 2.4 times faster than their minimum speed for hydrostatic equilibrium (Table 1) while skipjack tuna tested by Gooding *et al.* (1981) swam at only 85% of their minimum speed. Gooding *et al.* attributed differences in the observed and expected speeds of skipjack tuna in their experiments to condition factors (e.g. reductions in body fat and thus density and average gut fullness) that occur in captivity as a result of feeding schedule, nutrition, and exercise.

Body size also has an effect on the $\dot{V}O_2$ differences seen between the albacore and skipjack tunas. Fig. 3 compares total $\dot{V}O_2$ (ml O_2 h^{-1}) vs body weight for both species. The equation for albacore is

$$\log \dot{V}O_2 = 1.395 + 1.18 \log W, \quad (3)$$

where W is weight in g. The correlation between $\dot{V}O_2$ and weight is significant ($r = 0.81$, $N = 20$, $p = < 0.05$; 95% confidence intervals for the slope value are ± 0.53). The line for skipjack tuna was taken from an equation relating $\dot{V}O_2$,

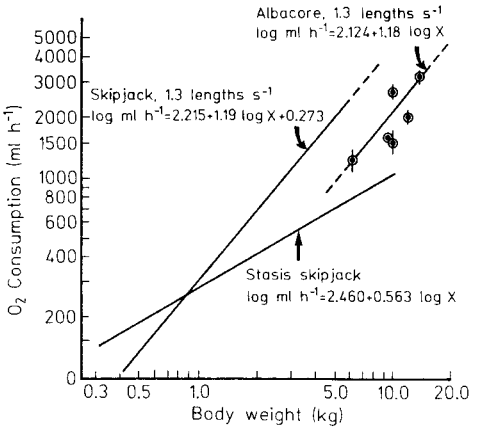

Fig. 3. *Thunnus alalunga* and *Katsuwonus pelamis*. Relationships between total O_2 consumption (ml h^{-1}) and body weight in albacore and skipjack tuna swimming at 1.3 lengths s^{-1} and the change in skipjack stasis $\dot{V}O_2$ with body weight (Brill, 1979). Vertical lines through points for albacore are standard errors of the mean $\dot{V}O_2$ estimate for each fish

weight, and speed (Gooding *et al.*, 1981),

$$\log \dot{V}O_2 = 1.20 + 0.19 \log W + 0.21 S, \quad (4)$$

where $\dot{V}O_2$ is in mg g^{-1} h^{-1}, W is weight (g) and S is speed (lengths s^{-1}). Corrections were applied to convert mg O_2 g^{-1} h^{-1} to ml O_2 h^{-1}, and to enable direct comparison with albacore, the equation was evaluated at $S = 1.3$ lengths s^{-1}. This resulted in a slope of 1.19 and a speed constant of 0.273 (Fig. 3). Also shown in Fig. 3 is the stasis $\dot{V}O_2$-body weight relationship for skipjack (Brill, 1979):

$$\log \dot{V}O_2 = 0.93 + 0.56 \log W, \quad (5)$$

where $\dot{V}O_2$ is in mg h^{-1} (converted to ml h^{-1} for comparison) and W is in g.

Fig. 3 reveals the striking similarity between the slopes of the $\dot{V}O_2$-body weight regression equations for albacore (1.18) and skipjack tuna (1.19). The $\dot{V}O_2$-size slope values determined for most vertebrates generally increase with activity, and approach and sometimes exceed 1.0 (Brett and Groves, 1979; Schmidt-Nielsen, 1979). Thus, the values for both tuna species are unusually high. It is noteworthy that independent studies with two different tuna species (Gooding *et al.*, 1981, with skipjack and the present work with albacore) both arrived at atypically high and very similar values for the $\dot{V}O_2$-weight exponent. However, in the case of the albacore, the 95% confidence intervals for the slope extend this value from 0.65 to 1.71. Thus, no significant difference is seen in the weight exponent for total active metabolism in the albacore and typical values for other active vertebrates (Brett and Groves, 1979; Schmidt-Nielsen, 1979). Gooding *et al.* (1981) did not indicate slope confidence intervals for their 1.19 weight exponent. This value was obtained from a multiple regression analysis (Eq. 4) in which the effects of both weight and speed on $\dot{V}O_2$ were evaluated. Size and speed are clearly interdependent in tunas (Magnuson, 1973, 1978), and Gooding *et al.* (1981) calculated a weight exponent probably biased by this analytical technique. This is shown by the lack of agreement in the data of Brill (1979) and Gooding *et al.* (1981) (present Fig. 3) where, at body weights smaller than 0.9 kg, the stasis $\dot{V}O_2$ of skipjack, as predicted by Eq. (5) actually exceeds predicted $\dot{V}O_2$ at 1.3 s^{-1} (from Eq. 4). When Gooding *et al.* (1981, their Fig. 3) applied a speed correction factor to their data, they found skipjack total metabolism (i.e., mg O_2 h^{-1}) to vary with a mass exponent of about 1 (zero if $\dot{V}O_2$ is computed as mg O_2 g^{-1} h^{-1}). We have estimated the confidence intervals to be about ± 0.3 for data presented in Fig. 3 of Gooding *et al.* (1981). While this exponent (1 ± 0.3) remains beyond the stasis $\dot{V}O_2$-mass exponent of Brill (0.56 ± 0.07), it is not excessively large or unexpected for an active fish. Thus, present evidence does not unequivocally support the conclusion that an unusually large metabolism-weight exponent is present in tunas. Gooding *et al.* (1981), however, did additionally cite several independent lines of evidence (e.g. the scaling of heat production and red muscle metabolism in skipjacks) to support their conclusion that the 1.19 weight exponent is valid. Further experimentation is thus required to discern fully the consequences of size and activity on the metabolism of tunas.

Additional results obtained for albacore tuna in the respirometer suggest that adverse effects result from prolonged exposure to low temperature and also permit some preliminary conclusions about the effects of low ambient O_2 levels. Graham and Dickson (1981) showed that under the experimental conditions of their study, the albacore tuna is unable to regulate red muscle temperature for long periods below 12 °C. In the present study, 3 fish placed in the respirometer with initial water temperatures of from 11° to 12 °C lost equilibrium within 1 to 2 h. Since fish in these tests were in the same size range as those used by Graham and Dickson, size was not a factor and no other experimental procedures were implicated in the failure of these test fish. All 3 fish initially swam vigorously; however, within the confines of the respirometer they may not have been able to increase activity sufficiently to prevent hypothermia. Albacore swimming in nature spend from 10 to 90% of their time in 9° to 12 °C water (Laurs *et al.*, 1980). Unstressed free-swimming fish may be better able to control heat balance as well as alternate periods in cool and warm water (Graham and Dickson, 1981).

Fish No. 6 (Table 1) was kept in the sealed respirometer until it suffocated. Owing to changes in water temperature while the system was closed, we were unable to discriminate between the effects of elevated temperature and hypoxia on the lethal limit of this fish which occurred at about 37% of air saturation (57 mm Hg O_2 partial pressure) and at 22 °C. The first effects of hypoxia were noted at about 58% saturation (90 mm Hg) in 18° to 19 °C water when the fish increased its mouth gape and made occasionally larger tail thrusts. Between 55 and 45% saturation (85 to 70 mm Hg), intermittent opercular pumping was noted and caudal frequency sporadically increased. Since these

responses occurred at temperatures within the range typically encountered by albacore (Laurs and Lynn, 1977) behavioral aviodance responses to hypoxia might normally be initiated by this O_2 level in the natural environment. Gooding *et al.* (1981) found that skipjacks exhibited behavioral responses to hypoxia beginning at about 90 mm Hg (23 ° to 24 °C), and that about 4 h exposure to this level of hypoxia proved fatal. By contrast, Dizon (1977) determined that the yellowfin tuna (*Thunnus albacares*) is much more tolerant of low O_2 than is the skipjack tuna (*Katsuwonis pelamis*) which may be related to the frequent occurrence of yellowfin tuna in or near O_2 minimum zones.

Acknowledgements. We thank the captain and crew of the "David Starr Jordan" for their assistance and support during this study. We also thank H. Chin, W. Flerx, G. Hunt, and J. Moberly for technical assistance during experiments. Dr. M. Gordon loaned us the pump and reservoir and made numerous suggestions for experimental design. Drs. P. Webb and D. Weihs and R. Lynn advised us on the working section design. We thank K. Dickson, and Drs. A. Dizon, R. Brill, J. Hunter and P. Webb for commenting critically on drafts of this paper. Partial support (JBG) was by grants from the National Institutes of Health (BRSG S07-RR07011) and National Science Foundation (DEB 79-12235).

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Date of final manuscript acceptance: September 7, 1982.
Communicated by N. D. Holland, La Jolla