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STUDIES OF TROPICAL TUNA SWIMMING PERFORMANCE IN A LARGE WATER TUNNEL

I. ENERGETICS

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Summary

The metabolic rates ($\dot{V}_{O_2}$) of three tropical tunas [yellowfin tuna (*Thunnus albacares*), kawakawa (*Euthynnus affinis*) and skipjack (*Katsuwonus pelamis*)] were estimated using a large water-tunnel respirometer. Experiments lasting up to 31 h were used to determine the effects of velocity (U) on tuna $\dot{V}_{O_2}$ over a range of U ($17-150\,cm\,s^{-1}$) and temperatures (18–30 °C). Replicate tests were carried out on several fish. The swimming $\dot{V}_{O_2}$ of yellowfin is temperature-dependent (Q_{10}=1.67, determined over intervals of 3–5 °C). For yellowfin and skipjack, it was also possible to partition metabolic costs between maintenance and locomotion. The standard metabolic rate ($S\dot{V}_{O_2}$) was estimated by extrapolation of the $U/\dot{V}_{O_2}$ function to U=0. Comparisons of $S\dot{V}_{O_2}$ for different size groups of yellowfin show that the mass-specific scaling exponent for $\dot{V}_{O_2}$ is −0.40. The $S\dot{V}_{O_2}$ of tuna is comparable to values determined previously by stasis respirometry and is approximately three times higher than that of salmonids. Further comparisons with salmonids show that the slope of the $U/\dot{V}_{O_2}$ function is less for tunas, which demonstrate a greater swimming efficiency.

Introduction

Tunas are highly specialised predators that occur in the coastal and pelagic ecosystems of tropical and subtropical oceans (Collette and Nauen, 1983). The morphological, anatomical and biochemical specialisations of these fishes revolve around their continuous swimming, which they do to search out patchily distributed prey (Blackburn, 1968; Olson and Boggs, 1986), to maintain hydrostatic equilibrium (Magnuson, 1978) and to ventilate their gills (Brown and Muir, 1970; Roberts, 1978). Tunas are capable of high-performance swimming. Some species make annual migrations across ocean basins (Mather, 1962; Collette and Nauen, 1983), and studies suggest they can sustain greater cruising speeds (6–10 fork lengths s^{-1}; $L\,s^{-1}$) than most other teleosts (Yuen, 1970;

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summarised in Beamish, 1978). High burst speeds (20–27 $L\,s^{-1}$) have also been measured for some species (Fierstine and Walters, 1968; summarised in Magnuson, 1978).

Tunas possess a number of specialisations for increased swimming performance. Morphological adaptations include a fusiform body shape to reduce drag, median and paired fin grooves to increase streamlining, a high-aspect-ratio tail with a narrow and laterally keeled caudal peduncle, and finlets along the trailing edges of the body (Lindsey, 1978; Magnuson, 1978). Tunas are also unique among teleosts in their thunniform swimming mode, the anterior-central placement of their aerobic locomotor (red) muscle, and their ability to elevate body temperature (Carey and Teal, 1966; Stevens and Fry, 1971; Graham, 1975; Stevens and Neill, 1978). Added to these morphological adaptations for swimming is a series of functional characteristics implying that the metabolic capacity of tunas exceeds that of other fishes. These include an increased heart size and gill surface area and an elevated haematocrit (Muir and Hughes, 1969; Tota, 1978; Brill and Bushnell, 1991). Biochemical correlates of high energy turnover include a greater mitochondrial density, elevated levels of aerobic and anaerobic enzymes, and a high tissue buffering capacity (Bone, 1978; Dickson, 1988).

Although considerable evidence supports the contention that the aerobic metabolic capacity of tunas is heightened relative to that of other fishes, quantification of this difference has been complicated by the difficulties of handling these powerful fishes and of measuring metabolic rates during steady swimming.

This paper reports studies of tuna swimming energetics carried out using a large water-tunnel respirometer (Graham *et al.* 1990) that was set up at the US National Marine Fisheries Service, Kewalo Research Facility in Honolulu, Hawaii. The tunnel enabled maintenance of tunas for long periods while swimming stably at controlled speeds (U) and temperatures. Data were obtained for three tropical species, yellowfin tuna [*Thunnus albacares* (Bonnaterre)], kawakawa [*Euthynnus affinis* (Cantor)] and skipjack [*Katsuwonus pelamis* (Linnaeus)]. Our objectives were to determine the influence of body size, temperature and U on tuna metabolism, and to compare our values with those for other swimming vertebrates and with the power requirements predicted by hydrodynamic theory.

Materials and methods

All experiments were conducted using the large water tunnel described in detail by Graham *et al.* (1990). A number of modifications to the initial design were required for work in Hawaii. To eliminate cavitation and increase the unit's maximum velocity, the polyvinylchloride pipe diameter and propeller size were increased from 30.5 to 45.7 cm (from 12 to 18 inches). The top speed with the larger pipe diameter exceeds 3 m s^{-1}. The size (30–57 cm) of the tunas available in Hawaii necessitated a reduction in the cross-sectional area of the experimental working section (where the fish is maintained during tests) by use of a precisely fitted plastic floor and front and back side walls. Depending on the size of the tunas, the front wall could be set for three different working section widths (17.5, 22.5 and 28 cm). Reduction of swim-channel width necessitated correction for the

effects of solid blocking in cases where the maximal cross-sectional area of the body was greater than 10 % of the working section. Solid blocking correction methods are detailed in Webb (1975) and Graham and Laurs (1982).

Further modifications involved the addition of 3000 l heated and cooled water reservoirs which facilitated rapid temperature changes; this made it possible to examine thermal effects on tuna $\dot{V}_{O_2}$.

Selection of experimental subjects

Freshly caught tunas were purchased from local commercial fishing boats and maintained at ambient temperatures (T_a=24–26 ˚C) and photoperiod in outdoor holding tanks at the Kewalo Research Facility (Nakamura, 1972). Resident fish were fed once daily, but specimens to be used in a study were not fed for 24 h prior to testing. Fish were selected for experiments only if they swam normally in the holding tank, exhibited no excessive weight loss, had been in captivity for at least 24 h, and lacked significant abrasions. Tuna with a history of feeding were chosen preferentially.

Tuna selected for experiments were dip-netted from the holding tank and placed head first into a tube-shaped plastic bag filled with hyperoxic water. The fish was then rushed the distance of approximately 50 m to the water tunnel where the bag was opened and the fish released head first into the working section. Water flow at the time of introduction was set at a low U of approximately 25 cm s^{-1}. In preparation for a test, the water tunnel was run for at least 1 h while the water was filtered and trapped air removed through bleeder valves.

Maintenance of tuna in the working section

The fish was closely monitored while in the water tunnel. Over the first hour or more, one person placed their hand at the back of the working section between the fish's caudal fin and the back grating to prevent accidental fin abrasion. If fish did not swim, tickling its tail was sometimes effective. In general, however, touching the fish seemed to impede its adjustment to the working section and was minimised.

Conditions in the working section

Ambient conditions in the working section were critical for inducing stable swimming. Light fluctuations generally disturbed the fish and were reduced by draping dark cloths over the working section and by placing a light at its upstream end. Modulation of water flow was used to help the fish assume a stable swimming mode and to influence its position, preferably away from the back grating. The optimal initial conditions were normoxic or slightly hyperoxic water (20–25 kPa) at a T_a of 25 ˚C, which approximate ambient holding tank conditions.

Experimental protocols

After the minimum 1 h post-handling recovery period, if the fish was swimming stably, the water tunnel was sealed and U, water O_2 concentration and T_a were recorded every 10–15 min. Ports on the side of the working section were used to pump a stream of water past a YSI (Yellow Springs Instruments) temperature-compensated O_2 probe and

thermistor (5450/5758) that was connected to a model 54A meter. Electrode calibration was carried out daily in 100 % water-vapour-saturated air.

The O_2 consumption (mg O_2 h^{-1}) was determined by monitoring the rate of O_2 removal from the system in ‰ h^{-1} (‰=mg l^{-1}), and multiplying this value by the tunnel volume (3000 l; measured by dye dilution). When the water O_2 level fell to 80 % saturation, the tunnel was unsealed and O_2 bubbled in until levels reached approximately 25 kPa. The tunnel was then resealed and, after a 30 min equilibration period, O_2 measurements were resumed.

Effects of velocity

Measurements of swimming $\dot{V}_{O_2}$ usually commenced 3 h after the introduction of the tuna into the water tunnel. The steadily swimming fish was held at a constant U for a minimum of 45 min (measurements were generally made over a 1 h period) while the O_2 level was recorded. Following this, the speed was increased or decreased by at least 4 cm s^{-1}, and O_2 measurements were again made for at least 45 min. The new U was maintained only if steady swimming continued. If U was too high the fish often made small swimming bursts. If U was too low the fish sometimes moved to the front of the working section and shifted from side to side. If the selected U could not be maintained, speed was returned to the previous level or changed in the opposite direction (by at least 4 cm s^{-1}), or the experimental focus was shifted to the examination of thermal effects. Alternating between high and low U proved helpful for inducing faster swimming speeds (Fig. 1). During U tests, T_a was maintained within approximately 1 °C.

Thermal effects on active $\dot{V}_{O_2}$

The influence of T_a on $\dot{V}_{O_2}$ was examined by implementing changes in T_a of 3–5 °C and,

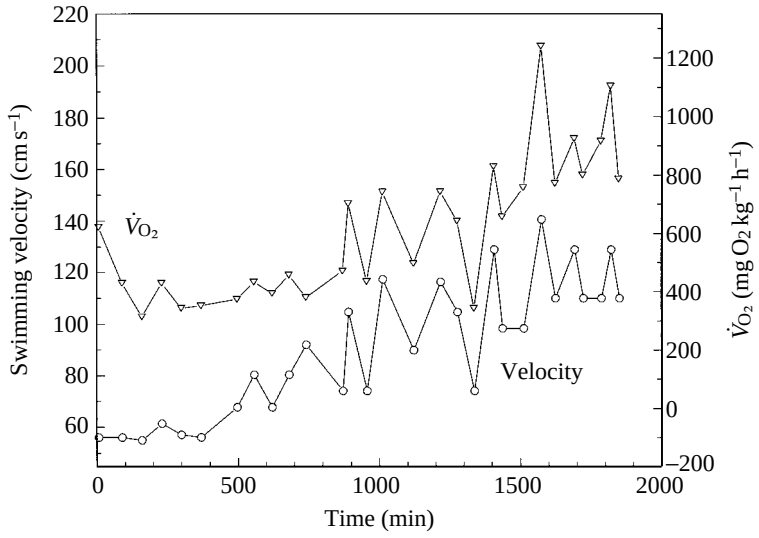

Fig. 1. Swimming velocity and $\dot{V}_{O_2}$ are plotted as a function of time for a 31 h investigation with a 50 cm yellowfin tuna. T_a was maintained at 25±0.5 °C.

after a 30 min equilibration period, measuring O_2 decline at a constant U for at least 45 min. After this period, U was increased or decreased following the regimen detailed above, or T_a was again changed by 3–5 °C.

Removal of fish from water tunnel

Each test was concluded when swimming became unstable (as described above). The tuna was then removed from the working section and immediately returned to the holding tank. Following removal of the fish, the tunnel was resealed and background (i.e. microbial) respiration was measured over 40 min. In cases of T_a change, this was only possible at the final T_a. In general, background respiration was negligible in relation to tuna $\dot{V}_{O_2}$.

Results

Respirometry studies on the three species involved a total of 47 specimens. Table 1 summarises data for the body size, number, feeding status, time in captivity and experimental durations of these tests. Yellowfin tuna were the most useful because they had the longest experimental durations and the greatest size range. It was also possible to perform replicate tests with seven yellowfin.

Table 2 summarises the studies where yellowfin swam in the water tunnel on more than one occasion. It shows the successive dates, the study type, the experimental duration and the maximum U. In general, only two replicates were possible, except that yellowfin no. 1 was used four times and no. 6, five times. In most cases, the return of the fish to the water tunnel was marked by an increase in both the maximal U and the experimental duration. A number of kawakawa were also used in replicate tests.

Effects of recovery and velocity on $\dot{V}_{O_2}$

Fig. 1 illustrates the basic features of our $U/\dot{V}_{O_2}$ observations. These data are for a 50 cm yellowfin tuna that swam in the tunnel for 31 h (U=25–150 cm s^{-1};

Table 1. *Summary of the mean fork length (*L*), body mass, number and feeding individuals and the mean time in captivity before an experiment and in the water tunnel*

	Length (cm)	Mass (kg)	*N*	Number feeding	Time in captivity (days)	Time in tunnel (h)
Thunnus albacares						
I	31.8±0.27	0.47±0.03	6	2	11	7.6±2.4
II	41.6±2.7	1.1±0.21	11	9	18	11.2±4.9
III	51.3±3.0	2.17±0.50	12	9	26	14.6±9.1
Katsuwonus pelamis	48±3.3	1.7±0.26	8	1	5	6.3±2.2
Euthynnus affinis	38±1.4	0.79±0.26	10	8	19	8.1±3.8

Values are mean ± S.D.

Table 2. *Summary of replicate studies for seven yellowfin tuna*

Fish number	Type of study	Date	Time (min)	Velocity (cm s^{-1})
1	O_2	27/8/90	310	48
	O_2	7/9/90	506	59
	O_2	16/9/90	1265	77
	O_2	14/10/90	784	75
2	O_2	3/12/90	500	52
	O_2	17/12/90	840	54
3	O_2	13/12/90	440	49
	O_2	22/1/91	970	63
4	TR	7/2/91	930	40
	f_H	12/2/91	400	55
5	TR	18/2/91	960	78
	TR	28/2/91	630	95
6	TR	19/8/91	120	26
	TR	29/8/91	405	35
	TR	7/9/91	525	34
	O_2	17/9/91	1515	83
	TR/O_2	26/9/91	1640	130
7	O_2	23/9/91	945	150
	TR/O_2	29/9/91	1860	130

Included is the study type (O_2, energetics; TR, thermoregulation; f_H, heart rate), the dates of subsequent studies, the experimental duration and the maximum velocity.

T_a=24.5–25.5 °C). After the first 3 h, the $\dot{V}_{O_2}$ of this fish became more closely correlated with U. This pattern was observed in most tuna, and the mean $\dot{V}_{O_2}$ for individuals swimming at or near the same U (±4 cm s^{-1}) dropped (over a similar time interval) by 32 % for skipjack, 25 % for yellowfin and 21 % for kawakawa. We interpreted the reduction in $\dot{V}_{O_2}$ as demonstrating a recovery phase from the stresses of capture and handling, and thus waited 2–3 h before attempting to acquire data describing the relationship of $\dot{V}_{O_2}$ to variables such as body size, temperature and U.

Fig. 2 shows $\dot{V}_{O_2}$ data for all yellowfin tuna plotted as a function of U. Data are presented for three size groups of fish (32, 42 and 51 cm fork length) and are separated into pre-recovery (before 3 h) and post-recovery (after 3 h) values. The least-squares regression lines [determined only for the post-recovery data (Table 3)] for the 42 cm and 51 cm groups lie well below mean pre-recovery $\dot{V}_{O_2}$ levels. For both groups $\dot{V}_{O_2}$ increases significantly with U (P<0.05). Because the post-recovery data for the 51 cm group were not distributed evenly throughout the U range, assumptions for regression analysis were not met. Thus, the mean U and $\dot{V}_{O_2}$ for all fish, over each interval of approximately 4 cm s^{-1}, were calculated and regression analysis performed on these adjusted data (Fig. 2). Although the slope for the adjusted-data regression line (Table 3) is higher than that for the non-adjusted data, this increase is not significant. In the case of the 32 cm

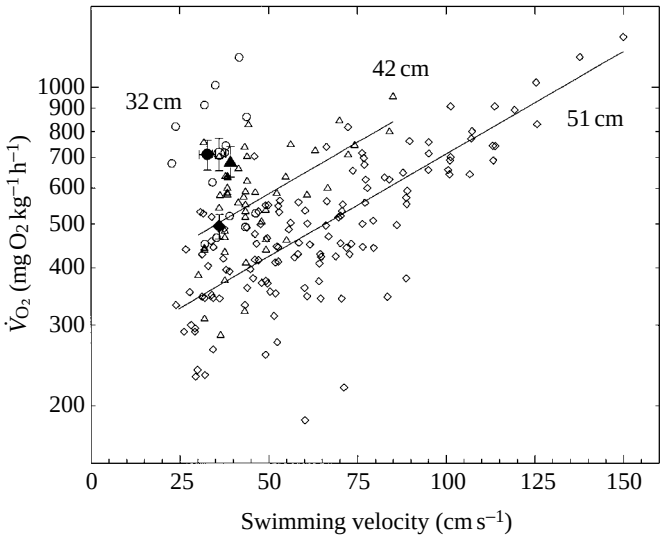

Fig. 2. Post-recovery $\dot{V}_{O_2}$ data (24 ±2°C) for the yellowfin tuna are plotted as a function of swimming velocity (U: cm s^{-1}); 51 cm group (diamonds); 42 cm group (triangles); and 32 cm group (circles). Regression lines are shown for the 51 cm group (calculated from the adjusted data which are not shown) and the 42 cm group. The mean $\dot{V}_{O_2}$ and U (±S.E.M.) for the 32 cm fish is also indicated (hollow circle). The filled symbols are the mean pre-recovery $\dot{V}_{O_2}$ and U (±S.E.M.).

group, the test velocity range was too small to allow regression analysis, and a single value for mean U and $\dot{V}_{O_2}$ is plotted.

Fig. 3 shows the pre- and post-recovery $\dot{V}_{O_2}$ data for the skipjack and kawakawa. As for the yellowfin, the mean pre-recovery values fall above the respective regression line. $\dot{V}_{O_2}$ increases significantly with U for the skipjack (P<0.05) but not for the kawakawa, which had a narrower speed range. Thus, only mean U and $\dot{V}_{O_2}$ are reported for kawakawa, along with the regression variables for the skipjack (Table 3).

Standard metabolic rate

The standard metabolic rate estimates ($S\dot{V}_{O_2}$) shown in Table 3 were determined by extrapolating the linear regression equations to U=0. Values for yellowfin range from 253 mg O_2 kg^{-1} h^{-1} (51 cm group) to 476 mg O_2 kg^{-1} h^{-1} (32 cm group; estimated using the slope for the 42 cm group). The 48 cm skipjack $S\dot{V}_{O_2}$ is 315 mg O_2 kg^{-1} h^{-1}.

Scaling effects

The effect of body size on yellowfin tuna metabolism was estimated by calculating the dependence of $S\dot{V}_{O_2}$ on body mass for log-transformed data. The resultant mass-specific $\dot{V}_{O_2}$ exponent is −0.40 ±0.23 (S.E.M.).

Thermal effects

Temperature effects on the swimming $\dot{V}_{O_2}$ of 19 yellowfin tuna are summarised in

Table 3. *Parameters (±S.E.M.) for the regression equation log$\dot{V}_{O_2}$ (mg O_2 kg^{-1} h^{-1}) = b + m×U (cm s^{-1}) for the larger yellowfin and skipjack, including the sample size, regression coefficient and estimated $S\dot{V}_{O_2}$*

	N	*m*	*b*	r^2	$S\dot{V}_{O_2}$ (mg O_2 kg^{-1} h^{-1})
Thunnus albacares					
42 cm	50	0.0046±0.001	2.6±0.08	0.29	344
51 cm	131	0.0042±0.0003	2.41±0.10	0.56	257
51 cm	23	0.0045±0.0001	2.40±0.04	0.95	253
Adjusted					
Katsuwonus pelamis					
48 cm	18	0.0066±0.0024	2.5±0.14	0.33	315

		U (cm $s^{-1)}$	$\dot{V}_{O_2}$ (mg O_2 kg^{-1} h^{-1})	$S\dot{V}_{O_2}$ (mg O_2 kg^{-1} h^{-1})
Thunnus albacares				
32 cm	14	36±1.9	712±59	476
Euthynnus affinis				
38 cm	26	57±1.3	796±29	

The mean $\dot{V}_{O_2}$ and *U* (±S.E.M.) for the kawakawa and small yellowfin are also reported.

Data for the 51 cm tuna were 'adjusted' as described in the text to account for the uneven distribution of the *U* range.

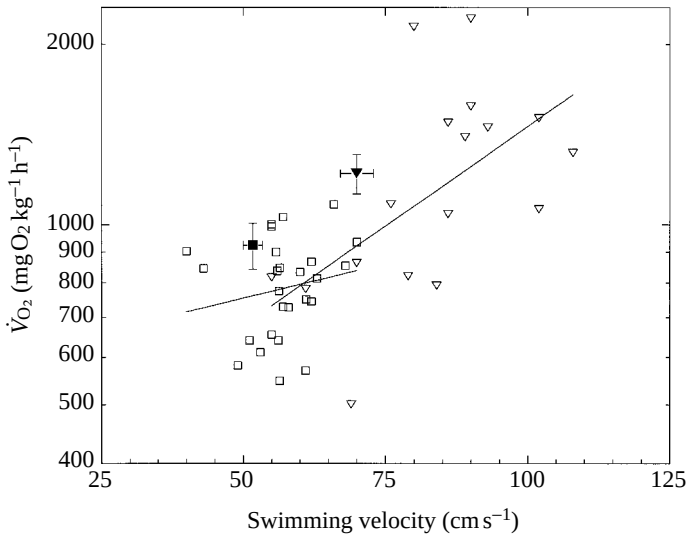

Fig. 3. Post-recovery $\dot{V}_{O_2}$ data and regression lines for the kawakawa (*Euthynnus affinis*) (squares) and skipjack (*Katsuwonus pelamis*) (inverted triangles). Also shown (filled symbols) are the mean pre-recovery $\dot{V}_{O_2}$ and *U* (±S.E.M.).

Table 4. *Summary of the sample size, mean* U, *and the Q_{10} values determined over 18–24 °C and 24–30 °C*

Yellowfin	*N*	*U* (cm s^{-1})	Q_{10} 18–24 °C	Q_{10} 24–30 °C
1	1	32	2.21	
2	3	52	1.59	
3	2	65	1.68	
4	1	36		1.28
5	1	43		2.99
6	2	38		1.08
7	3	43		1.26
8	1	35		1.30
9	3	44		1.34
10	3	41		1.18
11	3	43		1.80
12	2	45		1.77
13	2	36		1.99
14	2	36		1.80
15	3	29		2.17
16	1	29		1.66
17	2	39	1.38	
18	2	60	1.41	
19	2	100		1.79
Mean		44.5±16.4	1.65±0.34	1.67±0.50
S.E.M.				

The mean *U* and the Q_{10} (±S.E.M.) for each thermal interval are also given.

Table 4 which shows the Q_{10} values, mean *U* (±4 cm s^{-1}) and sample size. The mean values for each thermal interval are nearly identical (18–24 °C, 1.65; 24–30 °C, 1.67).

Discussion

The first measurements of tuna $\dot{V}_{O_2}$ as a function of swimming speed were made by Gooding *et al.* (1981) on small groups of skipjack at sea and after time in captivity. Although their experiments did not control velocity, opportunistic measurements covered a range of speeds from 0.9 to 2.2 *L* s^{-1} in captivity, with a mean at-sea value of 3.5 *L* s^{-1}. In other experiments at sea with albacore tuna (*Thunnus alalunga*), the use of a water tunnel permitted velocity to be controlled (Graham and Laurs, 1982; Graham *et al.* 1989), but these studies were done on recently captured and probably stressed fish. Metabolic estimates have also been made from reductions in caloric density during starvation for skipjack and yellowfin tuna swimming in large circular tanks (Boggs, 1984; Boggs and Kitchell, 1991). While all of these studies indicate that tuna metabolism is higher than that of other teleosts, the separate effects of body size, *U* and temperature on swimming energetics are not well defined (Boggs, 1984; Brill, 1987; Graham *et al.* 1989; Boggs and Kitchell, 1991). Quantification of velocity effects, specifically, has been complicated by

the relatively low and narrow range of velocity over which it has been possible to measure tuna $\dot{V}_{O_2}$.

Our study has combined experimental access to healthy, feeding tunas acclimated to captivity with use of the large water tunnel to carry out extended observations of tuna swimming energetics and to determine the effects of body mass, T_a and velocity on $\dot{V}_{O_2}$.

Temperature effects

Predictions about temperature effects on swimming $\dot{V}_{O_2}$ in tuna are complicated by the ability of these fish both to elevate and to control body temperature (Carey and Teal, 1966; Dizon and Brill, 1979; Dewar *et al.* 1994). Irrespective of water temperature, metabolic heat retention can influence swimming $\dot{V}_{O_2}$ by affecting tissue metabolism and locomotor muscle efficiency.

This study shows that the swimming metabolism of the yellowfin tuna is temperature-dependent (Table 4). Although the mean Q_{10} for yellowfin $\dot{V}_{O_2}$ (1.67) is below values reported for most ectotherms, including teleosts (Q_{10}=2–3; Brett, 1965; Brett and Glass, 1973; Bennett and Ruben, 1979), the difference is not significant. While our results are consistent with the observed thermal dependence of enzyme activity in a number of tuna species (Dickson, 1988), previous findings for skipjack based on isolated muscle preparations (Gordon, 1968) and respirometry in free-swimming fish (R. Chang, unpublished results) suggest that $\dot{V}_{O_2}$ is temperature-independent. Whether this discrepancy reflects interspecific differences [as suggested by Stevens and Neill (1978) on the basis of differences in the thermal dependence of volitional swimming speeds for skipjack and yellowfin tuna], or is a consequence of the differing methodologies used, requires further study.

Standard metabolic rate

$S\dot{V}_{O_2}$ for yellowfin and skipjack was estimated by extrapolating the $U/\dot{V}_{O_2}$ regression to zero velocity. Although extrapolation to zero velocity is potentially problematic for tunas, which never stop swimming, this exercise is useful for comparative purposes and for isolating locomotor costs. This method may, however, bias $S\dot{V}_{O_2}$ estimates because of the complications of extrapolating beyond the measured U range. Also, $S\dot{V}_{O_2}$ could be overestimated if the $U/\dot{V}_{O_2}$ function was elevated or the slope reduced as a result of unsteady or inefficient swimming at slow speeds (Brett, 1964, 1985; Webb, 1975; Webb *et al.* 1984, Dewar and Graham, 1994).

Validation for zero extrapolation is found in work by Brill (1987), who reported no differences between the ‘stasis $\dot{V}_{O_2}$’ (i.e. the $\dot{V}_{O_2}$ of specimens paralysed with the neuromuscular blocking agent Flaxedil and ventilated in a flow stream) and the $S\dot{V}_{O_2}$ determined by extrapolating to zero velocity for two species [the rainbow trout (*Oncorhynchus mykiss*) and aholehole (*Kuhlia sandvicensis*)]. Brill also measured the stasis $\dot{V}_{O_2}$ of the three tuna species used in this study. Our $S\dot{V}_{O_2}$ values (Table 3) do not differ from Brill’s stasis values. In addition, our $S\dot{V}_{O_2}$ values for the 48 cm skipjack and 51 cm yellowfin equal the estimates for skipjack (267 $mg\,kg^{-1}\,h^{-1}$) obtained by extrapolating to zero velocity (Gooding *et al.* 1981).

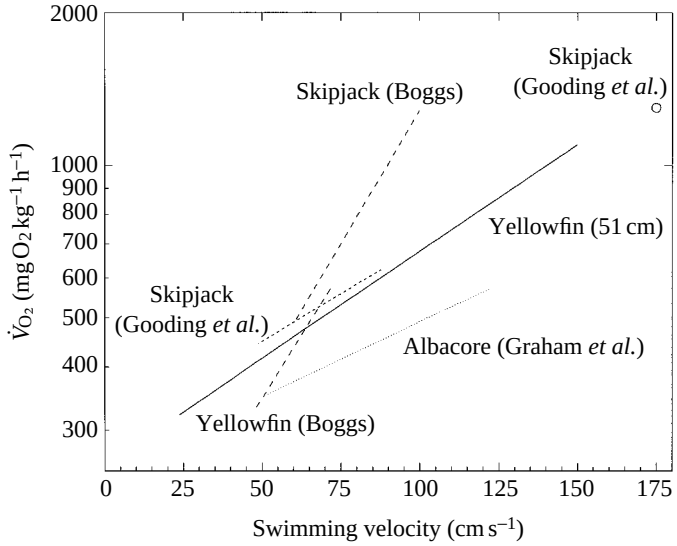

Fig. 4. Summary of all tuna $U/\dot{V}_{O_2}$ relationships; Boggs (1984) data for yellowfin and skipjack (long dashed lines); Gooding *et al.* (1981) for skipjack (dashed line and open circle); Graham *et al.* (1989) for Pacific albacore (dotted line). Also shown is the adjusted regression line (solid line) for the 51 cm yellowfin tuna from this study.

Body size effects

The mass-specific exponent for $S\dot{V}_{O_2}$ ($M^{-0.40}$, where M is body mass), estimated for yellowfin is similar to the exponent of -0.43 reported by Brill (1987). Our yellowfin exponent is also similar to Brill's (1987) values for skipjack ($M^{-0.44}$) and kawakawa ($M^{-0.50}$), which suggests that metabolic scaling in tunas is not unique but is similar to the values for most other vertebrates (i.e. $M^{-0.10}$ to $M^{-0.40}$, Brett, 1964, 1965). Gooding *et al.* (1981) and Graham and Laurs (1982) reported positive mass-specific exponents of $M^{0.2}$ for skipjack and albacore, respectively.

Tuna $\dot{V}_{O_2}$ and velocity

Fig. 4 and Table 5 compare our results for the 51 cm yellowfin group with previous tuna swimming energetics data. This group was selected because it had the largest sample size, the greatest U range and exhibited the best ability to adjust to the water tunnel (see Table 1). All metabolic values lie within the same range [the slightly lower values for the albacore may be explained by the lower experimental temperature (15 °C) and greater body mass]. However, discrepancies are apparent among the slopes (Tables 3 and 5). The slopes of the lines determined by respirometry increase at half the rate of those estimated from calorific reduction; this may result, in part, from differences in fish size (Table 5).

The similarity between the present work and previous respirometry studies supports our quantitative description of the dependence of tuna $\dot{V}_{O_2}$ on U. This assertion is strengthened by the factors underlying these metabolic measurements. We were able to

Table 5. *Summary of the mean body mass*, L, U *range and the regression variables [log$\dot{V}_{O_2}$ (mg O_2 kg^{-1} h^{-1})* = b + m × U *(cm* s^{-1}*)] for various tunas and the sockeye salmon (*Oncorhynchus nerka*)*

Mass (kg)	Length (cm)	*N*	*U* range (cm s^{-1})	*m*	*b*	r^2
Thunnus albacares[1]						
1.35±0.36	40±3.4	21	48–72	0.0099±0.0035	2.03±0.08	0.37
Thunnus alalunga[2]						
8.5–12	87	28	52–122	0.003	2.40	–
Katsuwonus pelamis[1]						
1.60±0.40	43±3.1	21	60–86	0.0104±0.003	2.06±0.15	0.31
Katsuwonus pelamis[3]						
1.98	47±6.9	40	49–88	0.0038±0.0013	2.46±0.07	0.43
Oncorhynchus nerka[4]						
1.43	53	–	0–140	0.0086	1.62	–

[1]Boggs (1984); [2]Graham *et al.* (1989); [3]Gooding *et al.* (1981); [4]Brett (1965).
Values in parentheses represent S.D. for mass and fork length (*L*) and S.E.M. for *m* and *b*.

control *U*, to make measurements over a broader continuous *U* range than was previously possible, and to conduct long-term experiments that allowed a sufficient time for fish to adjust to the water tunnel and to recover from capture and handling.

An underlying assumption of our yellowfin $U/\dot{V}_{O_2}$ function is that swimming, specifically at the highest speeds, is powered solely by aerobic metabolism. That this requirement was met is suggested by three facts. First, a $\dot{V}_{O_2}$ asymptote, apparent as the aerobic limit is reached, was not observed. Second, Brill and Dizon (1979) showed that skipjack white muscle is active only above $3\,L\,s^{-1}$; so, assuming that yellowfin and skipjack have similar patterns of muscle recruitment, only the aerobic locomotor muscle was active over the range of swimming speeds measured. Finally, we detected no differences in $\dot{V}_{O_2}$ at a slow speed before and after a period of swimming at a higher *U*. If anaerobic metabolism contributed to high-speed swimming, then $\dot{V}_{O_2}$ during the second control period should have been elevated.

Comparisons with hydrodynamic theory

Rigid body hydrodynamic theory has been used to estimate power requirements for swimming fish (Weihs, 1973; Dizon and Brill, 1979; Gooding *et al.* 1981). This model assumes that total drag is equal to the surface friction drag on a flat plate oriented parallel to flow such that:

$$\text{Power} = 0.5dAU^3C_D\,, \tag{1}$$

where *d* is water density, *A* is surface area, and C_D is the drag coefficient. If the boundary layer conditions are laminar, then:

$$C_D = 1.33Re^{-0.5}\,, \tag{2}$$

and if turbulent:

$$C_D = 0.072Re^{-0.2}, \quad (3)$$

where *Re* (Reynolds number)=$U\times L\times$(kinematic viscosity)$^{-1}$ (Webb, 1975, 1978).

Although this model does not accurately describe swimming costs for other teleosts (Webb, 1975, 1978; Beamish, 1978), it could be applicable to tunas because their thunniform swimming mode more closely conforms to the model's assumption of no lateral motion. However, our empirically determined U exponent of 1.4 for 51 cm yellowfin is considerably less than the 2.5–2.8 predicted by equations 1–3. Also, if we compare the actual power requirements, the model predicts that a 51 cm fish swimming at 100 cm s^{-1} would expend (assuming a turbulent boundary) 0.267 W. This underestimates empirical power determinates by twofold [($\dot{V}_{O_2}$ at 100 cm s^{-1})$-S\dot{V}_{O_2}$ (mg O_2 kg^{-1} h^{-1})$\times$ (1 W kg^{-1})/(256 mg O_2 kg^{-1} h^{-1})$\times$2.1 kg=0.667 W]. These results indicate that, even for tunas, estimation of surface friction drag alone is not sufficient for accurate quantification of locomotor costs.

Maximum metabolic rate

Estimation of the maximum aerobic metabolic rate for a tuna has both comparative and theoretical relevance. For most ectotherms and homeotherms, the maximum aerobic capacity approaches 10 times the $S\dot{V}_{O_2}$ (Bennett and Ruben, 1979). Applying this to the 51 cm (2.2 kg) yellowfin group provides an estimate of 2570 mg O_2 kg^{-1} h^{-1}. This agrees with the maximum rates predicted by Bushnell and Brill (1991) which are 2500 mg O_2 kg^{-1} h^{-1} for yellowfin and 2700 mg O_2 kg^{-1} h^{-1} for skipjack. The highest measured rates are for skipjack: 2200 mg O_2 kg^{-1} h^{-1} (this study) and 2500 mg O_2 kg^{-1} h^{-1} (Gooding *et al.* 1981).

Another means of estimating the maximum $\dot{V}_{O_2}$ is by extrapolating the $U/\dot{V}_{O_2}$ function to the maximum aerobic speeds reported for tunas. We have not done this because of the potential complications of extrapolating far above the measured range. As U increases, changes in the pectoral fin angle, as well as muscle temperature, recruitment and efficiency, will probably affect the $U/\dot{V}_{O_2}$ function.

Comparing tunas and other teleosts

Much of our current understanding of tuna energetics derives from comparisons with salmonids, the best-studied group of cruise-adapted teleosts (Brett, 1964, 1965; Webb, 1971; Brett and Glass, 1973). Fundamental differences in the methods of data analysis for most of the salmonid and tuna data (i.e. in salmonid studies only the minimum $\dot{V}_{O_2}$ at each U was included for analysis, whereas in tuna studies all data were used), have raised reservations about direct comparability (Boggs and Kitchell, 1991). However, experiments by Bushnell *et al.* (1984) validated this general comparative approach (Fig. 5). Metabolic measurements reported by Bushnell *et al.* (1984) for *O. mykiss* (determined using all data) are not significantly different from the minimum values for *O. nerka* (Brett, 1965).

Comparison of the $U/\dot{V}_{O_2}$ regression for the 51 cm yellowfin group with that for a comparably sized sockeye salmon (Brett, 1965) reveals that the yellowfin has a higher

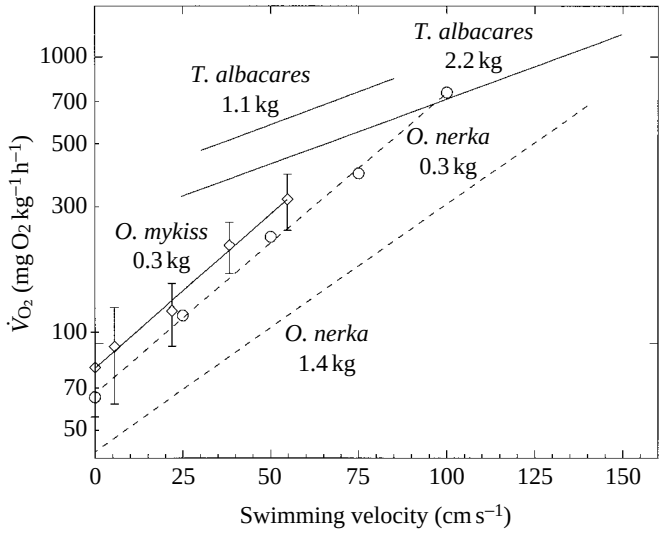

Fig. 5. Comparison of salmonid and scombrid $\dot{V}_{O_2}$ data plotted as a function of swimming velocity. Data for 0.3 kg (circles, dashed line) and 1.4 kg (dashed line) sockeye salmon (*O. nerka*, Brett, 1965) at 15 °C. Also shown are the mean $\dot{V}_{O_2}$ ± S.D. (diamonds, solid line) for 0.3 kg rainbow trout (*O. mykiss*, Bushnell *et al.* 1984) at 15 °C. The solid lines show the linear regressions for the 42 cm (1.1 kg) and the adjusted 51 cm (2.2 kg) yellowfin data at 24 °C.

intercept but lower slope (Fig. 5). Gooding *et al.* (1981) reported similar results for skipjack. At U=0, $S\dot{V}_{O_2}$ for the 51 cm (2.2 kg) yellowfin is 257 mg O_2 kg^{-1} h^{-1} (24 °C), which is considerably higher than that for the 53 cm (1.4 kg) sockeye (44 mg O_2 kg^{-1} h^{-1}, 15 °C, Brett, 1965). The observed metabolic differences are too great to be accounted for on the basis of the 9 °C water temperature difference ($S\dot{V}_{O_2}$ at 24 °C is 85 mg O_2 kg^{-1} h^{-1}; Brett and Glass, 1973).

The high intrinsic metabolic costs of tunas, as in mammals (Bennett and Ruben, 1979), is probably a consequence of adaptations for high energy turnover and metabolic scope expansion (Brill, 1987). Tunas, for example, have 6.6 times the gill surface area, and one-twelfth the gill epithelial thickness, of a comparably sized salmon (Muir and Hughes, 1969). Although this favours O_2 uptake, it probably also increases ion movements and thus elevates osmoregulatory costs. The heart's increased metabolic contribution is suggested by its large size (Tota, 1978; Brill and Bushnell, 1991), and the tuna's relatively high heart rates and ventral aortic pressures (Lai *et al.* 1987; Brill and Bushnell, 1991). It is improbable that endothermy elevates $S\dot{V}_{O_2}$, because at U=0, minimal heat will be produced in the aerobic locomotor muscle.

While $\dot{V}_{O_2}$ for the yellowfin tuna is elevated in comparison with that of the sockeye, its lower rate of $\dot{V}_{O_2}$ increase with U demonstrates a higher swimming efficiency (Fig. 5), and this is consistent with the numerous morphological adaptations for drag reduction and thrust enhancement. Another explanation may relate to endothermy and the associated increase in the contraction velocity at which muscle power output and efficiency are greatest (Johnston and Brill, 1984; Rome, 1990; Rome and Sosnicki,

1990). Because the locomotor muscle temperature increases with U (Stevens and Neill, 1978; Dewar *et al.* 1994), the contraction velocity, or tail-beat frequency (*TBF*), at which efficiency is maximal will also increase. Consequently, the simultaneous rise in U and locomotor muscle temperature may reduce the drop in muscular efficiency as *TBF* increases and thus reduce the slope of the $U/\dot{V}_{O_2}$ function.

Finally, comparisons of the maximum aerobic capacity and maximum aerobic scope (maximum aerobic capacity minus $S\dot{V}_{O_2}$) reveal that both are higher in the yellowfin than in the sockeye. With $\dot{V}_{O_2}$ measured over the entire aerobic range of the sockeye, Fig. 5 shows both its maximum aerobic capacity ($750\,mg\,O_2\,kg^{-1}\,h^{-1}$) and scope ($700\,mg\,O_2\,kg^{-1}\,h^{-1}$). Assuming $2500\,mg\,O_2\,kg^{-1}\,h^{-1}$ to be the maximum $\dot{V}_{O_2}$ of the yellowfin, this fish has the capacity to utilize O_2 four times faster than the sockeye, and its scope is three times larger.

Cost of transport and optimal swimming velocity

This section employs two indices of swimming performance, cost of transport (COT) and optimal swimming velocity (U_{opt}), to compare the swimming energetics of tunas with other vertebrates.

COT, the cost required to travel a unit distance, can be calculated from $\dot{V}_{O_2}$ (Schmidt-Nielsen, 1972; Beamish, 1978; Videler and Nolet, 1990) and has been used to compare the efficiencies of a diversity of locomotor modes. When plotted in relation to U, COT has a U-shaped function. It initially declines, due to a decrease in the relative contribution of $S\dot{V}_{O_2}$, goes through a minimum value defined as U_{opt}, and then increases as $\dot{V}_{O_2}$ rises with U. U_{opt} is directly related to $S\dot{V}_{O_2}$ and inversely related to the slope of the $U/\dot{V}_{O_2}$ function.

Optimal swimming velocity

On the basis of rigid body theory, Weihs (1973) calculated that the U_{opt} of fishes should be about $1\,L\,s^{-1}$, the velocity where $\dot{V}_{O_2}$ is approximately two times $S\dot{V}_{O_2}$. However, because the rigid body theory overestimates the change in $\dot{V}_{O_2}$ with U and because the slope of this function and U_{opt} are inversely related, actual values for tuna are probably higher. This is verified by Fig. 6, which shows that the U_{opt} ($100\,cm\,s^{-1}$) for 51 cm yellowfin [which is nearly identical to the $2.1\,L\,s^{-1}$ reported by Gooding *et al.* (1981)] is considerably higher than predicted ($67\,cm\,s^{-1}$; indicated by the vertical line). The tuna U_{opt} is also higher than that for a 50 cm salmonid (approximately $50\,cm\,s^{-1}$). It is emphasized that U_{opt} probably reflects $S\dot{V}_{O_2}$ and the $U/\dot{V}_{O_2}$ metabolic increment rather than the results of natural selective pressure on swimming performance. Nonetheless, the U_{opt} of $2.0\,L\,s^{-1}$ determined for the 51 cm yellowfin group is close to the mean U ($2.1\,L\,s^{-1}$) of four yellowfin tuna tracked at sea (Holland *et al.* 1990). This suggests that tuna do swim near U_{opt} and that U_{opt} values determined in the water tunnel may be useful for predicting the mean U of free-swimming tunas.

Cost of transport

The COT at U_{opt} provides a relative index of overall swimming efficiency and Videler and Nolet (1990) summarised COT and U_{opt} relationships for a number of ectothermic and homeothermic swimmers. Their compilation, which includes animals of varying size

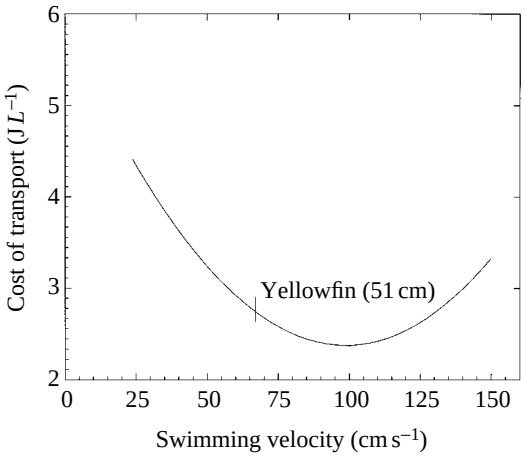

Fig. 6. Cost of transport ($J\,L^{-1}$) plotted as a function of swimming velocity (U) for the 51 cm yellowfin tuna. Weihs' (1973) predicted optimal U is indicated by the vertical line.

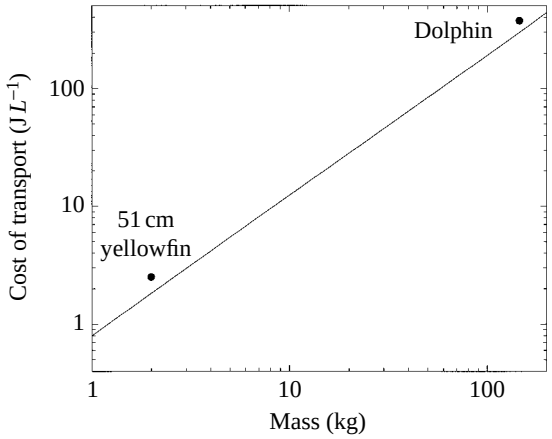

Fig. 7. The cost of transport at U_{opt} as a function of mass for ectothermic teleosts (COT=3.3×mass$^{1.05}$, adapted from Videler and Nolet, 1990). Points show the COT at U_{opt} for the 51 cm (2.2 kg) yellowfin tuna and for a 145 kg dolphin (adapted from Williams *et al.* 1992).

using a variety of swimming modes, provides a valuable data set for tuna comparisons. Fig. 7 shows that the COT at U_{opt} for our 51 cm (2.2 kg) yellowfin tuna and for a 145 kg bottlenose dolphin (*Tursiops truncatus*, Williams *et al.* 1992) both lie above the Videler and Nolet (1990) fish line. The actual comparative values (at specified mass) are: tuna (2.2 kg) 2.5 $J\,L^{-1}$, fish 1.83 $J\,L^{-1}$; dolphin (145 kg) 374 $J\,L^{-1}$, fish 298 $J\,L^{-1}$.

Comparisons of COT reveal *overall* transport efficiency. To examine *locomotor* efficiency requires partitioning of COT into its two component costs: $S\dot{V}_{O_2}$ and locomotion (net COT). For the yellowfin tuna, 37 % of COT is attributable to $S\dot{V}_{O_2}$ and

net COT is therefore 1.58 J L^{-1}. The estimated $S\dot{V}_{O_2}$ component in the Videler–Nolet fish line is 13 % which makes net COT 1.59 J L^{-1}. Thus, net COT values are similar in both groups. However, the U_{opt} of the yellowfin is approximately two times higher than that for fish, indicating a greater efficiency. Correction for $S\dot{V}_{O_2}$ also eliminates the COT difference between *Tursiops* (COT, 35 %=243 J L^{-1}) and the Videler–Nolet fish (COT, 13 %=259 J L^{-1}). The extent to which the dolphin value falls below that for fish is probably underestimated because 13 % $S\dot{V}_{O_2}$ may be too high [i.e. the estimate obtained by extrapolating Brett's (1965) salmonid mass versus $S\dot{V}_{O_2}$ line to 145 kg is 2.4 % $S\dot{V}_{O_2}$]. Although more data are needed, these comparisons show that, when corrected for $S\dot{V}_{O_2}$, the locomotor cost at U_{opt} for both tuna and bottlenose dolphin is lower than that for fish in general and suggests a strong evolutionary convergence for efficient continuous locomotion (Webb, 1975).

This study has shown that, relative to the sockeye salmon, the yellowfin tuna (and tunas in general) has a higher estimated $S\dot{V}_{O_2}$, but a greater locomotor efficiency. The high standard metabolic cost for tunas supports the biochemical and anatomical framework enabling heightened rate processes and expansion of their aerobic scope. An elevated maximum $\dot{V}_{O_2}$ in concert with adaptations for rapid, efficient swimming reduces potential energetic limitations on activity from processes such as growth, digestion, and reproduction. This maximises the probability of energy acquisition in habitats where prey are patchily distributed. In many respects the metabolic intensity of tunas parallels that of mammals; a substantial initial energetic investment is needed to support and enhance functions contributing to overall fitness.

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