MAXIMUM SUSTAINABLE SPEEDS AND COST OF SWIMMING IN JUVENILE KAWAKAWA TUNA (*EUTHYNNUS AFFINIS*) AND CHUB MACKEREL (*SCOMBER JAPONICUS*)

CHUGEY SEPULVEDA AND KATHRYN A. DICKSON*

Department of Biological Science, California State University Fullerton, Fullerton, CA 92834, USA

*Author for correspondence (e-mail: kdickson@fullerton.edu)

Summary

Tunas (Scombridae) have been assumed to be among the fastest and most efficient swimmers because they elevate the temperature of the slow-twitch, aerobic locomotor muscle above the ambient water temperature (endothermy) and because of their streamlined body shape and use of the thunniform locomotor mode. The purpose of this study was to test the hypothesis that juvenile tunas swim both faster and more efficiently than their ectothermic relatives. The maximum sustainable swimming speed (U_{max}, the maximum speed attained while using a steady, continuous gait powered by the aerobic myotomal muscle) and the net cost of transport (COT_{net}) were compared at 24 °C in similar-sized (116–255 mm fork length) juvenile scombrids, an endothermic tuna, the kawakawa (*Euthynnus affinis*) and the ectothermic chub mackerel (*Scomber japonicus*). U_{max} and COT_{net} were measured by forcing individual fish to swim in a temperature-controlled, variable-speed swimming tunnel respirometer. There were no significant interspecific differences in the relationship between U_{max} and body mass or fork length or in the relationship between COT_{net} and body mass or fork length. Muscle temperatures were elevated by 1.0–2.3 °C and 0.1–0.6 °C above water temperature in the kawakawa and chub mackerel, respectively. The juvenile kawakawa had significantly higher standard metabolic rates than the chub mackerel, because the total rate of oxygen consumption at a given swimming speed was higher in the kawakawa when the effects of fish size were accounted for. Thus, juvenile kawakawa are not capable of higher sustainable swimming speeds and are not more efficient swimmers than juvenile chub mackerel.

Key words: locomotion, endothermy, Scombridae, chub mackerel, *Scomber japonicus*, juvenile, kawakawa, tuna, *Euthynnus affinis*, cost of transport, standard metabolic rate, sustained swimming, swimming efficiency, energetics, respirometer.

Introduction

Tunas and mackerels, members of the teleost fish family Scombridae, are epipelagic predators capable of attaining high swimming speeds as well as undertaking long-distance migrations (for reviews, see Beamish, 1978; Magnuson, 1978; Joseph et al., 1988). All members of this family possess anatomical characteristics, such as a streamlined body shape and a high-aspect-ratio caudal propeller, that reduce drag or increase thrust production (Webb, 1975; Collette, 1978; Magnuson, 1978; Dewar and Graham, 1994). Scombrids also have caudal keels and finlets along their narrow caudal peduncles that are thought to aid in minimizing the turbulence encountered by the caudal fin as it moves laterally during swimming (Aleev, 1963; Collette, 1978; Magnuson, 1978). Although the tunas share these morphological traits with other scombrids, they alone can conserve metabolically derived heat to maintain the temperature of the slow-twitch, oxidative locomotor muscle significantly above that of the water and, thus, gain some independence from environmental temperature

(Carey et al., 1971; Graham, 1973). Thus, tunas are endothermic and are considered to be regional heterotherms. The tunas constitute a monophyletic clade within the family Scombridae, and all taxa of the sister groups, the bonitos, mackerels and Spanish mackerels, are ectothermic (Carey et al., 1971; Collette, 1978; Block et al., 1993; Graham and Dickson, 2000). Thus, the Scombridae provides an ideal system with which the selective advantages and the evolution of endothermy can be investigated.

Several hypotheses have been proposed to explain why tunas are endothermic. One hypothesis suggests that tunas maintain elevated temperatures to slow the rates of temperature change in their tissues when they swim into or spend brief times in cold water, thereby sustaining high activity levels when subjected to reduced water temperatures (Graham, 1975; Neill et al., 1976; Stevens and Neill, 1978; Brill et al., 1999). It has also been hypothesized that tunas evolved their endothermic capabilities to expand their ranges into cooler waters (Block

et al., 1993; Graham and Dickson, 2000). Alternatively, endothermy may have evolved to allow tunas to increase their rates of certain metabolic processes, including growth, digestion and processing of waste products such as lactic acid (Carey and Teal, 1966; Stevens and Carey, 1981; Stevens and McLeese, 1984; Brill, 1996). A final hypothesis is that warming the aerobic myotomal muscle tissue increases swimming performance by increasing muscle contraction velocity, power output and swimming efficiency (Carey et al., 1971; Graham, 1975; Brill and Dizon, 1979; Stevens and Carey, 1981; Johnston and Brill, 1984; Dewar and Graham, 1994; Altringham and Block, 1997). This could increase the maximum sustainable swimming speeds of tunas and enable them to be more efficient long-distance swimmers.

Although the swimming energetics of tunas larger than 320 mm in fork length (*FL*) have been described (Gooding et al., 1981; Graham et al., 1989; Dewar and Graham, 1994), the last hypothesis remains untested because there have been no comparisons between tunas and closely related ectothermic species that clearly identify the locomotor advantages associated with endothermy. Previous studies that have examined the energetics of tunas and then compared the results with those from an ectotherm of similar size have had to use data from salmonids for this comparison. Although a salmonid may offer a sized-matched comparison, the conclusions that may be drawn are limited because the two groups of fishes are so distantly related and because the studies were conducted at significantly different temperatures. The present study used juveniles (110–250 mm *FL*) of the kawakawa tuna *Euthynnus affinis* and the chub mackerel *Scomber japonicus* to test the hypothesis that aerobic swimming performance is greater in the tunas than in their ectothermic relatives. It is also the first study successfully to measure maximum sustainable swimming speeds of tunas under controlled conditions. Tunas of this size range represent those above and below the hypothesized minimum size for endothermy (207 mm *FL*) based on studies of the black skipjack tuna *Euthynnus lineatus* (Dickson, 1994). Thus, the present study also provides an intraspecific comparison of swimming performance in tunas that can and cannot elevate their muscle temperature.

Materials and methods

Fish collection and maintenance

Juvenile kawakawa *Euthynnus affinis* (Cantor, 1849), ranging in size from 110 to 250 mm fork length (*FL*), and one yellowfin tuna *Thunnus albacares* (Bonnaterre, 1788) were captured by traditional hook-and-line methods in July and August 1997 around fish-aggregating devices off the leeward side of the island of Oahu, Hawaii. The fish were immediately placed in a circular 110 l bait tank mounted to the transom of a sportfishing vessel. The water in the tank was maintained at the same ambient sea surface temperature at which the fish were caught (24±2 °C) and was supersaturated with oxygen. The fish were then transported to shore, transferred to a 380 l circular tank containing oxygenated sea water mounted in the

bed of a pickup truck, and transported to the National Marine Fisheries Service (NMFS) Kewalo Basin Research Facility, Honolulu, Hawaii. At the NMFS laboratory, the fish were maintained for 2–8 weeks in an 8 m diameter above-ground plastic-lined outdoor tank supplied with continuously flowing sea water at an ambient temperature of 24±2 °C and salinity of 33‰, and were subjected to a natural photoperiod. Initially, the tunas were fed live red-tailed guppies (Poeciliidae) until they began to eat chopped fish. They were then fed three times a day on an assortment of chopped fish [jack (*Decapterus macarellus* and *Selar crumenophthalmus*) and skipjack tuna (*Katsuwonus pelamis*)]. The amount of food consumed at each feeding was estimated to be approximately 10 % of body mass. Each tuna was feeding regularly in the tank for a minimum of 10 days before being chosen for an experimental trial.

Chub mackerel *Scomber japonicus* (Houttuyn, 1782) ranging in size from 133 to 250 mm *FL*, were collected in the coastal waters of southern California, USA, near Dana Point Harbor, between May and August 1998. The fish were transported from Dana Point Harbor in an 80 l round bait tank and were maintained in a 1.6 m diameter, 1500 l indoor fiberglass tank at California State University Fullerton, in water with a salinity of 34–35‰ and at a temperature of 24±2 °C. The mackerel were fed chopped fish [northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*)] and squid once a day, in an amount approximating 10 % of their body mass. The mackerel were subjected to a 12 h:12 h light:dark cycle and were feeding regularly in the tank prior to selection for any experimental trial. For all species, no feeding was performed for at least 12 h prior to selection for the respirometer.

Respirometry

The respirometer

A Brett-type swimming tunnel respirometer was used to measure the rate of oxygen consumption rate ($\dot{V}_{O_2}$) of the fish as a function of swimming speed (Fig. 1). The respirometer, similar to but smaller than that used by Dewar and Graham (1994), is a swimming tunnel that constantly recirculates 35 l of water. A variable-speed motor propels the water, so that a fish maintaining its position in the center of the chamber is swimming at the same speed as the flowing water. A General Oceanics mechanical flow meter (model 2030 R) mounted in the center of the chamber was used to calibrate respirometer speeds prior to any respirometry trials and each time the chamber was moved or disassembled. Flow characteristics were also assessed visually by observing dye flow patterns at various speeds without fish swimming in the respirometer. Corrections for solid blocking effects were not necessary because the experimental subjects had cross-sectional areas that were less than 10 % of the cross-sectional area of the chamber (Brett, 1964; Webb, 1971).

The respirometer system can be used in both an open and a closed mode. When open, the water in the respirometer is circulated to and from a reservoir, where it can be oxygenated to the desired level. When closed, the $\dot{V}_{O_2}$ of the fish can be measured. Water oxygen concentration ($±0.3$ mg O_2 l^{-1}) was
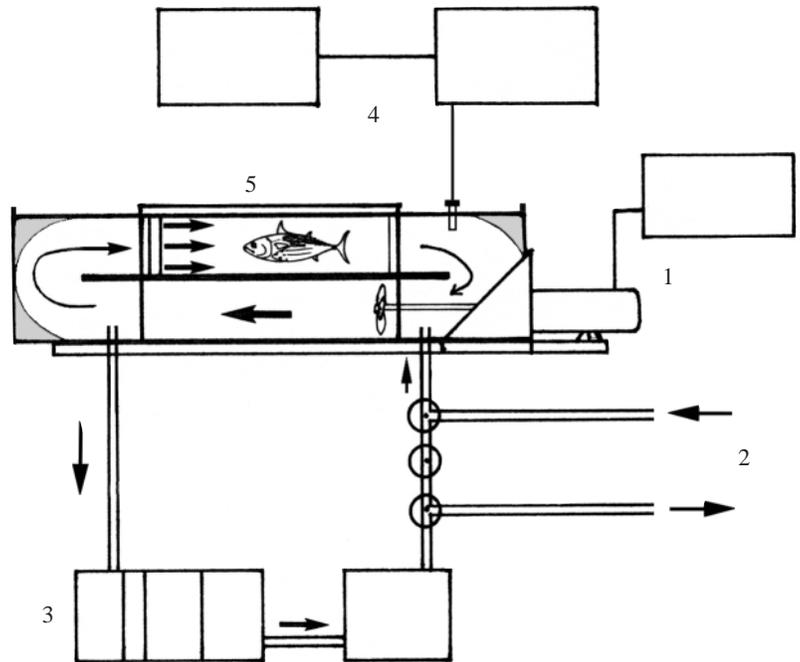
Fig. 1. A diagrammatic representation of the respirometer system: 1, variable-speed motor and controller; 2, reservoir of oxygenated water that can be isolated during metabolic rate measurements using a valve system; 3, filtration apparatus and in-line heater and chiller; 4, oxygen analysis system and chart recorder; 5, test chamber (13.5 cm×13.5 cm×50.8 cm) in which the fish swims, with honeycomb 'flow-straighteners' and a plastic grid positioned upstream and downstream, respectively. The respirometer holds a total volume of 35 l (drawing by Gary Hunt).

recorded continuously by a Yellow Springs Instruments (YSI) polarographic oxygen electrode (YSI model 5750) connected to an oxygen meter (YSI model 58), which then relayed the signal to a chart recorder. The $\dot{V}_{O_2}$ of the fish at each speed was calculated from the rate of change in water oxygen concentration. Prior to each experimental run, the YSI electrode membrane was replaced, and the probe was calibrated in air.

For all species, each experimental run began with the introduction of a fish into the respirometer. This was accomplished by hooking the fish with a baited barbless hook and transferring it to the chamber in a plastic pail liner filled with oxygenated sea water. The respirometer was then covered with a black cloth to minimize outside disturbance to the fish. Each fish underwent an initial 4 h recovery period at a speed of approximately 20 cm s^{-1} during which the oxygen level was maintained at approximately 200 % saturation for the first 3 h and was then allowed to decline to 100 % saturation over a further 1 h. The initial high O_2 concentration was used to ensure that the fish would recover from capture and transfer to the respirometer while at the initially low water speeds. Dewar and Graham (1994) noted a marked change in tuna behavior and a decrease in $\dot{V}_{O_2}$ after 2 h inside a respirometer; furthermore, it has been found that skipjack tuna can clear lactate produced during exhaustive exercise within 2 h (Perry et al., 1985; Arthur et al., 1992).

To ensure adequate time for these scombrids to adjust to the chamber, to process any lactate produced during the transfer procedure and for $\dot{V}_{O_2}$ to drop and stabilize, a 4 h recovery period was chosen. Each experimental run consisted of a 30 min period at each of the designated speeds up to the maximum sustainable speed. The rate at which the speed was increased depended on the size of the fish: 7.5 cm s^{-1} for fish

less than 120 mm *FL* and 10 cm s^{-1} for larger fish. $\dot{V}_{O_2}$ was measured during the second 10 min of each 30 min period at each speed. During the final 10 min period, the respirometer water oxygen content was brought back to the original 100 % saturation level by allowing water to flow to and from the reservoir. The level of oxygen saturation in the respirometer never dropped below 70 % for any of the trials. All experiments were conducted using filtered sea water maintained at an ambient temperature of 24±1 °C with an in-line heater and chiller. After each experimental run, the fish was removed, and the respirometer was re-sealed for the determination of the background respiration rate, which was subtracted from all $\dot{V}_{O_2}$ measurements to determine fish $\dot{V}_{O_2}$ at each speed.

Maximum sustainable swimming speed

The maximum swimming speed that the fish was able to maintain for a complete 30 min period while swimming using a gait characterized by steady, continuous tail beats (U_{max}), assumed to be powered by the slow-twitch, oxidative myotomal muscle (Videler, 1993; Rome, 1995; Webb, 1998), was determined by direct observation. The criterion for defining U_{max} was when the fish shifted from a steady tail beat to a 'burst-and-glide' swimming mode three times within 30 s. When the fish reached this point, it changed positions in the chamber, drifting back towards the back grating, brushing its tail against the grating and bursting forwards or swimming from side to side near the back of the chamber. Behavioral observations from the posterior of the fish, viewed through a hole cut into the black cloth covering the respirometer, were recorded throughout the experiment. Subsequent analysis of the $\dot{V}_{O_2}$ *versus* speed relationship for each individual was used to confirm a continuous increase in $\dot{V}_{O_2}$ with velocity up to U_{max}.

For some individuals, the $\dot{V}_{O_2}$ decreased slightly or stayed the same at the highest speeds, indicating that the fish was not actually swimming at the recorded water speed. This was confirmed by checking the observation records, which indicated that, at the highest motor speeds, these individuals swam from one side of the chamber to the other or that they avoided the center of the chamber and positioned themselves close to one side, but did not yet exhibit burst-and-glide behavior. When the fish is positioned against the sides of the chamber, interactions between the fish and the walls of the chamber produce frictional forces that can reduce the speed of the water flowing near the fish (Webb, 1993). For this reason, the fish was able to complete a period at a higher motor speed without consuming any more oxygen than it had consumed at the previous speed, because it was not actually swimming at the higher speed. In such cases, we did not attribute the leveling off of $\dot{V}_{O_2}$ to the fish having reached its anaerobic threshold because these active fishes are unlikely to be able to power continuous swimming for as long as 30 min with anaerobic metabolism. Moreover, we would have expected the fish to switch to a burst-and-glide gait if they recruited the fast, glycolytic muscle fibers (Rome, 1995; Webb, 1998), but the behavioral observations indicated that all individuals swam by beating their tails continuously at those speeds. For these individuals, U_{max} was determined to be the highest speed at which the fish swam before $\dot{V}_{O_2}$ leveled off or declined. For all other individuals, the highest speed at which the fish swam for a full 30 min period was considered to be the U_{max}.

Swimming efficiency

The net cost of transport (COT_{net}, in $J\,km^{-1}\,kg^{-1}$), or incremental cost of swimming, was used to quantify swimming efficiency; the lower the COT_{net} value, the more efficient the fish. COT_{net} was calculated by first subtracting the background respiration rate from each $\dot{V}_{O_2}$, then plotting $\dot{V}_{O_2}$ *versus* swimming speed for each fish; the slope of the best-fitting linear regression of the resulting graph is proportional to the mean net cost of transport for the fish. The slope units ($mg\,O_2\,min^{-1}\,cm^{-1}\,s$) were converted to $J\,km^{-1}\,kg^{-1}$ by multiplying by an oxycalorific equivalent ($3.24\,cal\,mg^{-1}\,O_2$; Beamish, 1978) and converting cal to J ($4.18\,J\,cal^{-1}$).

Muscle temperatur+e measurements

Muscle temperature measurements were taken for both species with a digital thermocouple thermometer (Omega Engineering, model HH-72 T). After the respirometry trial and subsequent videotaping for a companion kinematic study (Donley and Dickson, 2000), which took approximately 30 min, the motor speed was reduced to approximately 1 body length s^{-1}, the chamber lid was removed, and the fish was quickly grasped around the opercular region. A thermocouple embedded in a 21-gauge hypodermic needle was immediately inserted into the deep red muscle of the kawakawa, penetrating to the vertebral column, or into the superficial red muscle of the chub mackerel, at a series of locations along the length of the body, and temperatures were

recorded. The temperature of the water was then taken with the same thermocouple, and the difference between the water and the maximum red muscle temperature recorded was defined as the maximum muscle temperature elevation (T_x).

All procedures were conducted with the approval of the CSUF Institutional Animal Care and Use Committee.

Statistical analyses

The U_{max} data for both species were first examined for normality in Minitab (version 10.5), and it was determined that the data did not need to be transformed prior to analysis. The U_{max} data were then analyzed with analysis of covariance (ANCOVA) in Minitab, with fish fork length (FL) and mass as covariates. Both linear and exponential regression equations were fitted by least squares to the $\dot{V}_{O_2}$ *versus* speed data for each individual. A repeated-measures multiple regression analysis in SAS (version 6.12) was used to determine whether the relationship between $\dot{V}_{O_2}$ and speed differed significantly between the two species when the effects of fork length and mass were accounted for. The initial statistical model tested for significant effects on $\dot{V}_{O_2}$ of species, speed, fork length and mass and for all possible two- and three-way interaction terms: species×speed, species×fork length, species×mass, speed×fork length, speed×mass, mass×fork length, species×speed×fork length, species×speed×mass. Variables and interaction terms that did not contribute significantly to the multivariate regression were dropped, one at a time, from the model, and a new regression was calculated until a final model that included only variables with significant effects on $\dot{V}_{O_2}$ was obtained. In all statistical analyses, a significance level of P=0.05 was used.

Results
Maximum sustainable swimming speeds

The maximum sustainable swimming speeds at a gait characterized by continuous tail beats (U_{max}) for juvenile kawakawa *Euthynnus affinis*, ranging in size from 116 to 255 mm FL and from 24 to 265 g, were 45–110 cm s^{-1} and 3.4–5.1 FL s^{-1} (Table 1). No marked increase in U_{max} occurred at the hypothesized minimum size for endothermy of 207 mm FL (Fig. 2). Chub mackerel (*Scomber japonicus*), ranging in size from 140 to 240 mm FL and from 26 to 156 g, had maximum continuous swimming speeds of 70–120 cm s^{-1} or 3.8–5.8 FL s^{-1} (Table 1). In both species, U_{max} increased significantly with FL (Fig. 2) and with mass (Table 1), but there was no significant interspecific difference in the relationship between U_{max} and fish FL or mass (ANCOVA). The single yellowfin tuna (*Thunnus albacares*) (202 mm FL and 111 g) had a U_{max} of 80 cm s^{-1} or 4.0 FL s^{-1}, similar to that of similar-sized kawakawa and chub mackerel (Fig. 2).

Energetics

The relationships between $\dot{V}_{O_2}$ (mg O$_2$ min^{-1}) at 24 °C and swimming speed (cm s^{-1}) for the individual scombrids in the present study are shown in Fig. 3. These data were modeled with both linear and exponential regressions (Table 2). The

Table 1. *Fork length, body mass, maximum sustained swimming speeds (U$_{max}$), net cost of transport and red muscle temperature elevation (T$_x$), for kawakawa, chub mackerel and one yellowfin tuna at 24 °C*

Species	Fork length (mm)	Mass (g)	U_{max} (cm s^{-1})	U_{max} (*FL* s^{-1})	COT_{net} (J kg^{-1} km^{-1})	T_x (°C)
Kawakawa, *Euthynnus affinis*						
	116	24	45	4.06	11521.9	
	151	43	67.5	4.47	9246.2	1.3
	170	67				1.0
	182	73	60	3.37	4641.9	1.3
	182	85	67.5	3.86	4295.5	2.3
	185	59	67.5	3.65	4941.0	1.3
	212	160	100	4.71	6610.6	1.5
	220	145	105	5.08	4885.0	1.7
	232	225	80	3.51	3782.3	
	240	195	110	4.58	1933.5	2.0
	255	265	90	3.75	2912.9	2.0
Yellowfin tuna, *Thunnus albacares*						
	202	111	80	3.96	3124.7	
Chub mackerel, *Scomber japonicus*						
	140	26	82.5	5.8	14895.2	0.6
	166	38	90	5.4	2708.1	
	170	45	70	4.1	8286.3	0.1
	175	53	80	4.5	6836.1	
	190	64	100	5.2	7794.4	0.4
	210	97			4716.6	0.4
	213	103	80	3.8	6857.3	
	215	108	90	4.1	3399.7	
	233	129	120	5.1	3137.8	0.5
	234	147	100	4.3	3843.2	
	240	156	110	4.5	3060.1	
	245	155			1976.9	
	247	144			5517.2	

Blanks mean that no data were collected.

COT_{net}, net cost of transport.

theoretical mechanical cost of swimming should increase exponentially with speed, with plots of $\dot{V}_{O_2}$ *versus* swimming speed taking the form of a 'J' (Webb, 1998). However, empirical data for swimming fishes do not necessarily fit this model and, in most studies, metabolic costs increase with speed at a lower rate than is predicted (for a review, see Webb, 1998). In the present study, a linear increase in $\dot{V}_{O_2}$ with speed was often found, with a linear regression modeling the data for approximately 60 % of the individuals as well as or better than the exponential regression (see r^2 values in Table 2). With a linear fit, COT_{net} is directly proportional to the slope of the linear regression (see Materials and methods). With an exponential fit, COT_{net} varies with speed, and it is possible to determine a minimum COT_{net} and the speed at which COT_{net} is minimal. To do so, one first subtracts the standard metabolic rate (SMR), which can be estimated by extrapolating the $\dot{V}_{O_2}$ *versus* speed curve to zero speed (e.g. Dewar and Graham, 1994), from the $\dot{V}_{O_2}$ at each speed. However, extrapolation of the data results in large confidence intervals around the estimates, and the extrapolated SMR values differ greatly

depending on whether a linear or exponential curve fit is used (see Table 2). Therefore, for consistency, we chose to use the slope of the computer-generated linear regression of $\dot{V}_{O_2}$ *versus* speed as an estimate of the average COT_{net} of each individual (Tables 1, 2).

In both species, as fish size increased, mass-specific net cost of transport (COT_{net}) decreased (Fig. 4) and non-mass-specific net cost of transport increased (Fig. 5). No marked change in COT_{net} was recorded at the hypothesized minimum size for endothermy of 207 mm *FL* (Fig. 4), and the relationships between COT_{net} at 24 °C and fish size did not differ significantly between kawakawa and chub mackerel (Figs 4, 5). The one yellowfin tuna studied had COT_{net} values comparable with those of similar-sized kawakawa and chub mackerel.

We also calculated the total cost of transport (COT_{total}) at each speed for each fish by dividing the $\dot{V}_{O_2}$ (mg O$_2$ min^{-1}) at each speed by speed (cm s^{-1}) and then converting to J km^{-1} kg^{-1} using the conversion factors given in the Materials and methods section. The speed at which COT_{total} is a
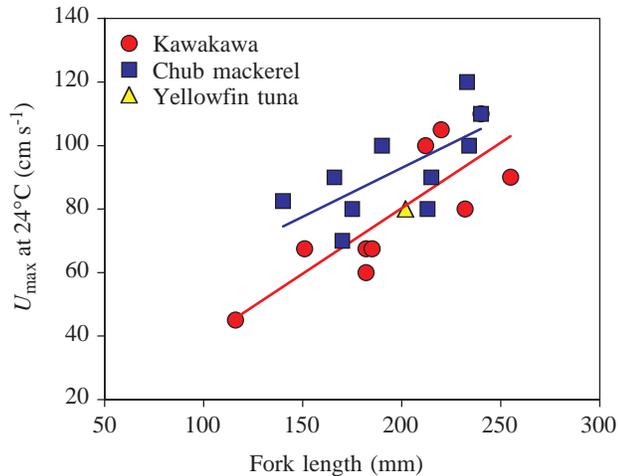
Fig. 2. Maximum continuous swimming speeds (U_{max}), measured at a water temperature of 24 °C, for juvenile kawakawa tuna (*Euthynnus affinis*), chub mackerel (*Scomber japonicus*) and one yellowfin tuna (*Thunnus albacares*) as a function of fish fork length (*FL*). The lines are the best-fitting linear regressions: $y=0.413x–2.29$, $r^2=0.68$, $P<0.01$, for the kawakawa (red) and $y=0.308x+31.38$, $r^2=0.48$, $P<0.05$, for the chub mackerel (blue). In both kawakawa and chub mackerel, U_{max} increased with fork length over the size range studied (116–255 mm *FL* and 140–240 mm *FL*, respectively). There was no significant difference in the U_{max} *versus* fork length relationship between the kawakawa and chub mackerel (ANCOVA; $P>0.05$).

minimum varied considerably among individuals, ranging from 40 to 110 cm s^{-1} (67±22 cm s^{-1}; mean ± S.D.) for the kawakawa and from 30 to 110 cm s^{-1} (55±25 cm s^{-1} mean ± S.D.) for the chub mackerel. There was no significant difference between these mean values (*t*-test).

Repeated-measures analysis of covariance was used to describe the interrelationships between $\dot{V}_{O_2}$ at 24 °C (mg O$_2$ min^{-1}), speed (cm s^{-1}) and body size (both fish mass and *FL*) for the juvenile kawakawa and chub mackerel. In both species, $\dot{V}_{O_2}$ at 24 °C increased significantly with both swimming speed and fish mass ($P\leqslant0.0001$); the rates of increase did not differ interspecifically. There was no significant effect of *FL* on $\dot{V}_{O_2}$ when the effects of fish mass and speed were accounted for. Total $\dot{V}_{O_2}$ was significantly higher at a given speed and size in the kawakawa than in the chub mackerel, by an average of 1.19 mg O$_2$ min^{-1} ($P<0.0001$). To illustrate these relationships, the minimum and maximum values for both fish mass and speed were used to solve the final multiple regression for each species for $\dot{V}_{O_2}$, and these values were plotted as the four corners of planes in three-dimensional space, together with the data points for each individual fish (Fig. 6). The difference in position along the *y*-axis between the planes for the kawakawa and the chub mackerel represents the magnitude of the interspecific difference in total metabolic rate. Because the COT_{net} values do not differ significantly between the two species, the interspecific difference in total $\dot{V}_{O_2}$ can be attributed to the standard metabolic rate being
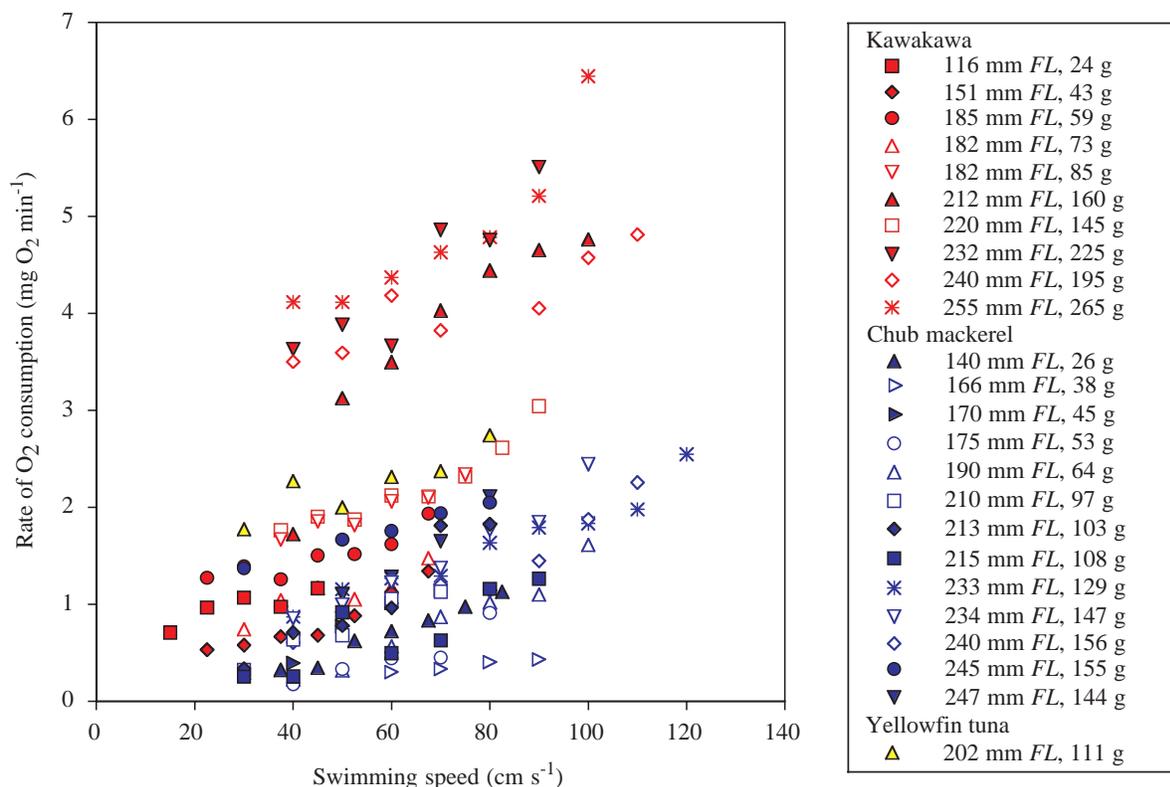

Fig. 3. Rates of oxygen consumption at a water temperature of 24 °C *versus* swimming speed for all individuals studied. The fork length (*FL*) and mass of each individual are indicated. The best-fitting regressions for each individual are presented in Table 2.
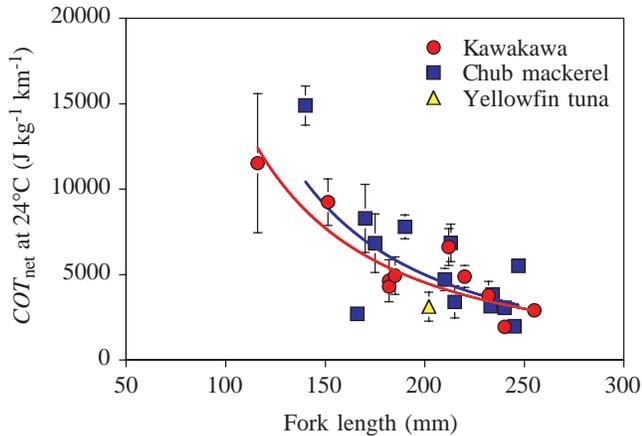
Fig. 4. The mass-specific net cost of transport (COT_{net}), measured at a water temperature of 24 °C, for juvenile kawakawa (*Euthynnus affinis*), chub mackerel (*Scomber japonicus*) and one yellowfin tuna (*Thunnus albacares*) as a function of fish fork length (*FL*). The lines are the best-fitting exponential equations: $y=8.16\times10^7 x^{-1.85}$, $r^2=0.72$, $P<0.01$, for the kawakawa (red) and $y=2.89\times10^8 x^{-2.07}$, $r^2=0.37$, $P<0.05$, for the chub mackerel (blue). When the one outlying point, for the 166 mm *FL* chub mackerel, is excluded, the equation is $y=5.51\times10^9 x^{-2.61}$, $r^2=0.70$, $P<0.001$. There was no significant interspecific difference in the relationship of COT_{net} *versus* fork length (ANCOVA; $P>0.05$). Because the larger kawakawa had a greater mass than chub mackerel of similar fork length, net cost of transport was also plotted as a function of fish mass in Fig. 5.
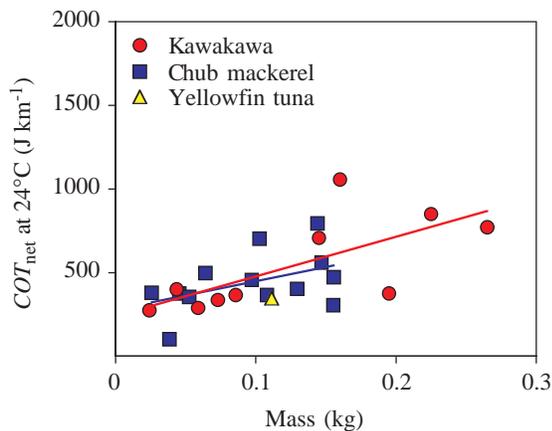

Fig. 5. The net cost of transport ($J\,km^{-1}$), measured at a water temperature of 24 °C, for juvenile kawakawa tuna (*Euthynnus affinis*), chub mackerel (*Scomber japonicus*) and one yellowfin tuna (*Thunnus albacares*) plotted as a function of fish mass. The lines are the best-fitting linear equations: $y=2359x+243$ ($r^2=0.495$, $P<0.05$) for the kawakawa (red) and $y=1688x+281$ ($r^2=0.209$, $P>0.05$) for the chub mackerel (blue). A similar increase in net cost of transport with fish mass was found for the two species (ANCOVA; $P>0.05$).

significantly greater in the kawakawa than in the chub mackerel. Thus, on average, SMR in the juvenile kawakawa exceeds that of the chub mackerel by 1.19 mg O_2 min^{-1}. Because of the limitations to estimating SMR by extrapolation
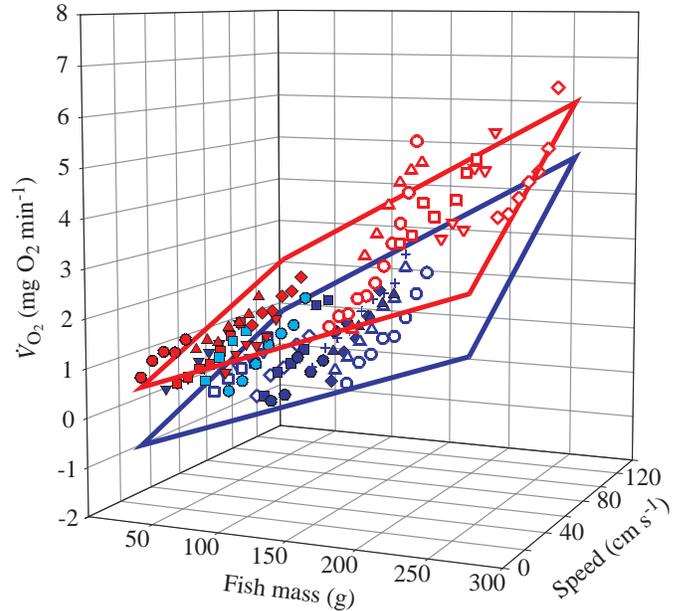

Fig. 6. Rates of oxygen consumption ($\dot{V}_{O_2}$) at a water temperature of 24 °C as a function of both swimming speed and fish mass for all individuals studied. The kawakawa are represented by red symbols and the chub mackerel by blue symbols. The best-fitting regressions of $\dot{V}_{O_2}$ (mg O_2 min^{-1}) *versus* speed (*U*; cm s^{-1}) for each individual are presented in Table 2. The planes outlined in red and blue represent the final models for the kawakawa and chub mackerel, respectively, of the repeated-measures multivariate regression analysis (see text). The equations describing the planes (with ± 1 S.E.M. for each coefficient) are: for kawakawa at 24 °C, $\dot{V}_{O_2}=0.0395\pm0.0202+0.0089\pm0.0017M+0.0153\pm0.0033U+0.000058\pm0.000025UM$; for chub mackerel at 24 °C, $\dot{V}_{O_2}=-1.1493\pm0.2283+0.0089\pm0.0017M+0.0153\pm0.0033U+0.000058\pm0.000025UM$, where *M* is mass (g). The plane for the kawakawa is parallel to but above that for the mackerel, indicating that the effects of speed and of mass are similar in both species, but the total $\dot{V}_{O_2}$ values are significantly greater in the kawakawa. The difference in position between the two planes relative to the *y*-axis represents the mean interspecific difference in standard metabolic rate.

to zero speed (see above), we did not calculate an SMR value for each individual. We consider the mean interspecific difference in the $\dot{V}_{O_2}$ *versus* speed relationships (Fig. 6) to be the best estimate possible from these data of the difference in SMR between the juvenile kawakawa and chub mackerel.

Red muscle temperature measurements

The maximum red muscle temperature elevations (T_x values, Table 1) for the kawakawa ranged from 1.0 to 2.3 °C (1.5±0.3 °C, mean ± S.D., *N*=9). For the chub mackerel, red muscle temperatures were elevated by only 0.1–0.6 °C (0.4±0.2 °C, *N*=5).

Discussion

This project is the first to measure directly the maximum sustainable swimming speed of tunas of any size under

Table 2. *Equations and* r^2 *values for linear and exponential regressions for the plots of rates of oxygen consumption* ($mg\,O_2\,min^{-1}$) *versus swimming speed* ($cm\,s^{-1}$) *for juvenile kawakawa (*Euthynnus affinis*), chub mackerel (*Scomber japonicus*) and yellowfin tuna (*Thunnus albacares*)*

Fish FL (mm)	Fish mass (g)	Linear	r^2	P	Exponential	r^2	P
Kawakawa, *Euthynnus affinis*							
116	24	$y=0.012x+0.609$	**0.728**	<0.10	$y=0.645\times10^{0.006x}$	0.708	<0.10
151	43	$y=0.018x+0.028$	0.903	<0.01	$y=0.307\times10^{0.009x}$	**0.951**	<0.001
182	73	$y=0.015x+0.379$	**0.782**	<0.05	$y=0.549\times10^{0.006x}$	0.768	<0.05
182	85	$y=0.014x+1.150$	**0.891**	<0.01	$y=1.273\times10^{0.003x}$	**0.888**	<0.01
185	59	$y=0.013x+0.921$	0.802	<0.01	$y=1.021\times10^{0.004x}$	**0.817**	<0.01
212	160	$y=0.047x+0.465$	**0.883**	<0.01	$y=1.286\times10^{0.006x}$	0.780	<0.01
220	145	$y=0.012x+1.312$	0.852	<0.001	$y=1.402\times10^{0.003x}$	**0.855**	<0.001
232	225	$y=0.038x+1.934$	**0.839**	=0.01	$y=2.493\times10^{0.004x}$	**0.838**	=0.01
240	195	$y=0.017x+2.836$	0.815	<0.01	$y=2.995\times10^{0.002x}$	**0.819**	<0.01
255	265	$y=0.034x+2.413$	0.816	<0.01	$y=2.952\times10^{0.003x}$	**0.864**	<0.01
Chub mackerel, *Scomber japonicus*							
140	26	$y=0.017x-0.298$	**0.967**	<0.001	$y=0.119\times10^{0.012x}$	0.950	<0.001
166	38	$y=0.005x+0.023$	**0.969**	<0.05	$y=0.141\times10^{0.005x}$	0.967	<0.05
170	45	$y=0.025x-0.536$	**0.952**	<0.05	$y=0.115\times10^{0.015x}$	0.882	<0.05
175	53	$y=0.016x-0.491$	0.839	<0.05	$y=0.047\times10^{0.016x}$	**0.915**	=0.01
190	64	$y=0.022x-0.733$	**0.962**	<0.001	$y=0.071\times10^{0.014x}$	0.949	<0.001
210	97	$y=0.020x-0.250$	**0.947**	<0.01	$y=0.156\times10^{0.013x}$	0.903	<0.015
213	103	$y=0.031x-0.648$	0.907	<0.01	$y=0.151\times10^{0.014x}$	**0.925**	<0.01
215	108	$y=0.016x-0.266$	0.726	<0.05	$y=0.120\times10^{0.012x}$	**0.743**	<0.05
233	129	$y=0.018x+0.156$	0.941	<0.001	$y=0.602\times10^{0.005x}$	**0.955**	<0.001
234	147	$y=0.025x-0.250$	0.952	<0.001	$y=0.433\times10^{0.007x}$	**0.986**	<0.001
240	156	$y=0.021x-0.277$	0.916	<0.001	$y=0.349\times10^{0.007x}$	**0.946**	<0.001
245	155	$y=0.014x+0.966$	**0.994**	<0.001	$y=1.089\times10^{0.004x}$	**0.990**	<0.001
247	144	$y=0.035x-0.759$	**0.982**	=0.001	$y=0.227\times10^{0.012x}$	0.947	<0.01
Yellowfin tuna, *Thunnus albacares*							
202	111	$y=0.016x+1.385$	**0.774**	<0.05	$y=1.510\times10^{0.003x}$	0.766	<0.05

FL, fork length.

The *y*-intercept of each linear regression and the coefficient *a* of the exponential regression ($y=a\times10^{bx}$) can be used as estimates of the rate of oxygen consumption at zero speed (standard metabolic rate) for each individual.

For each individual, a bold r^2 value indicates the better fit.

controlled conditions. Furthermore, it is also the first to compare the maximum sustainable speed and the cost of locomotion in tunas with those in a closely related, similar-sized ectothermic teleost at the same temperature. The results do not support the hypothesis that juvenile tunas are faster or more efficient swimmers than their ectothermic relatives. The kawakawa of the size range studied did not have higher maximum sustainable swimming speeds nor did they possess lower net cost of transport values than did the chub mackerel. In fact, the metabolic rate at a given speed and fish size and the standard metabolic rate were greater in the juvenile kawakawa than in the chub mackerel. The finding of similar U_{max} values in juvenile tunas and chub mackerel does support previous hypotheses (Bushnell and Brill, 1991; Block et al., 1992; Brill, 1996; Korsmeyer et al., 1996b) that the maximum sustainable swimming speeds of tunas should approximate those of other active teleosts and provides evidence against earlier proposals that tunas are capable of extraordinary

sustained speeds (Walters, 1962; Yuen, 1966; Magnuson, 1978).

Maximum sustainable swimming speeds

There are few published measurements that are directly comparable with the U_{max} data of the present study. Because swimming speed varies with both temperature (for a review, see Rome, 1995) and fish size, valid interspecific comparisons require that acclimation and measurement temperatures and fish size be closely matched. Furthermore, to elucidate the selective advantage of specific characteristics such as endothermy and thunniform locomotion, comparisons must be made with closely related taxa in a phylogenetic context. Thus, the present study directly compared the aerobic swimming performance of tunas with that of similar-sized individuals of a closely related ectothermic species under similar conditions. The U_{max} values for *S. japonicus* measured in the present study (Table 1) are similar to maximum sustainable speeds measured

previously in *S. japonicus* and the Atlantic mackerel *Scomber scombrus*. Roberts and Graham (1979) swam *S. japonicus* (343–392 mm *FL*) at maximum sustainable speeds of 3.2–4.5 *FL* s^{-1} (125–171 cm s^{-1}) in a 12 cm diameter swimming tunnel at 16.1–21.8 °C, but the duration that each fish swam at those speeds was not given. At 11.7 °C, *S. scombrus* (29–33 cm *FL*) maintained a maximum speed of 3.5 *FL* s^{-1} for 200 min and 4.3 *FL* s^{-1} for 30 min (He and Wardle, 1988). For kawakawa (38±1.4 cm *FL*, mean ± S.D.), individuals swam in a respirometer at a mean (± S.D.) velocity of 57±1.3 cm s^{-1} (range approximately 40–70 cm s^{-1}) at 24±2 °C (Dewar and Graham, 1994). This is the only other study that we know of that attempted to measure maximum sustainable swimming speeds in tunas in a swimming tunnel.

A number of methods have been used to quantify the sustained or prolonged swimming performance of fishes (for reviews, see Beamish, 1978; Videler, 1993). Maximum sustainable swimming speeds are often measured using the Brett (1964) protocol to measure critical speed (U_{crit}) in which speed is incrementally increased until the fish fatigues, but such studies have not been conducted with scombrids. The U_{crit} calculation takes into account the fraction of time the fish swam at the final speed at which it fatigued. Although our procedures approximated this, the U_{max} values from the present study will be lower than those that use the Brett (1964) procedure to determine U_{crit}, because we did not push any fish to its fatigue point and we did not take into account the fraction of time that the fish swam at the speed at which it shifted to a burst-and-coast gait. Nevertheless, our U_{max} measurements are within the ranges of U_{crit} determined for other active species, primarily salmonids, of similar sizes (for reviews, see Beamish, 1978; Videler, 1993).

The U_{max} values for the scombrids in the present study are greater than voluntary speeds that have been recorded for the same or similar species. Larger kawakawa (approximately 42 cm *FL*) swam at speeds of 56–68 cm s^{-1} in 7.3 m diameter tanks at 22.8–25.9 °C, but swam at 126 cm s^{-1} when stimulated by food flavor added to the tank (Magnuson, 1970). Typical speeds for kawakawa (mean length 36 cm *FL*) swimming in a 7.2 m diameter tank at 23–26 °C were 2.0–2.4 *FL* s^{-1} (Magnuson, 1973). Dizon et al. (1977) measured voluntary swimming speed *versus* water temperature, as water temperature was changed at a rate of 5 °C h^{-1}, in a doughnut-shaped tank with inner and outer diameters of 4.5 m and 6 m, respectively. At 23–25 °C, kawakawa (40–50 cm *FL*) swam at 1.25–1.70 *FL* s^{-1}. *Euthynnus lineatus* (46.0–54.8 cm *FL*) swam at mean speeds of 68–79 cm s^{-1} (1.35–1.71 *FL* s^{-1}) in a 2.5 m long × 2.3 m wide × 2.2 m deep bait well (Schaefer, 1984). For mackerel, Schaefer (1986) measured voluntary swimming speeds of fish subjected to a 1 °C day^{-1} temperature change in a 1.52 m diameter tank. When at 24 °C, chub mackerel (22–26 cm *FL*) swam at approximately 1.2 *FL* s^{-1} (approximately 26–31 cm s^{-1}) at 13:00 h, prior to feeding, and at approximately 1.9–2.1 *FL* s^{-1} (approximately 42–55 cm s^{-1}) at 17:00 h. Preferred speeds of schooling Atlantic mackerel (*Scomber scombrus*) swimming in a 10 m diameter gantry tank were 0.9–1.2 *FL* s^{-1} and

0.9–3.5 *FL* s^{-1} for two groups, 28.5–39.5 cm *FL* and 28.5–40 cm *FL*, respectively (He and Wardle, 1988). The highest speeds for the second group of *S. scombrus* were associated with feeding. Because all these measurements were made on fish in confined conditions, they may not represent typical voluntary speeds for scombrids in the wild.

The present study set out to test the hypothesis that tunas swim faster and more efficiently than their ectothermic relatives. The focus on juveniles was based on the hypothesized minimum size for endothermy of 207 mm *FL* in *Euthynnus lineatus* (Dickson, 1994) and on the need to conduct size-matched interspecific comparisons. However, the red muscle temperatures measured in the present study for *E. affinis* are lower than those recorded by Dickson (1994) for *E. lineatus* of similar sizes. This discrepancy is probably due to the difference in methods used to obtain the temperature data, but could also be due to different amounts of red muscle in the two species [11 % in *E. lineatus* 289–570 mm *FL*, *N*=14 (Graham et al., 1983) *versus* 8 % in *E. affinis* 360 mm *FL*, *N*=1 (Magnuson, 1973), for larger individuals]. The temperature measurements were collected with the same thermocouple thermometer for both species, but the *E. lineatus* data were collected after the fish had been chased at a moderate speed for approximately 1 min. The latter temperature measurements are similar to acute temperature measurements in the literature, which represent values from freshly caught fish (e.g. Carey et al., 1971).

The muscle temperature data for the kawakawa and mackerel in the present study were collected at the end of the experiment in a manner that results in T_x measurements that are probably more indicative of *in vivo* conditions. The mean red muscle T_x of only 1.5 °C in the juvenile kawakawa in the present study may not have been sufficient measurably to enhance aerobic swimming performance. On the basis of the temperature effects between 25 °C and 30 °C on contraction time for red muscle fibers isolated from yellowfin tuna (Altringham and Block, 1997), a red muscle temperature elevation of 1.5 °C in juvenile kawakawa would result in an increase in U_{max} of approximately 7 %. Given the variability in the data, it may not have been possible to detect an increase in speed of that magnitude in the present study. However, the kawakawa tended to have lower, not higher, U_{max} values than did the chub mackerel (Fig. 2). The ability of tunas to elevate muscle temperatures above water temperature increases with fish size. For example, Lindsey (1968) reported a T_x as high as 5.4 °C for a 485 mm *FL* kawakawa. Thus, we cannot rule out the possibility that, at larger sizes, when the kawakawa can elevate red muscle temperature to a greater degree, there will be a significant difference in maximum sustainable swimming speeds. Future studies of larger tunas and similar-sized, closely related ectotherms, such as the bonitos, swimming at the same water temperature, are needed to determine unequivocally whether endothermy enables tunas to increase swimming speed.

Energetics

The present study compared swimming energetics of

juvenile kawakawa and chub mackerel on the basis of $\dot{V}_{O_2}$ *versus* speed *versus* fish size relationships described as multiple linear regressions. Because these variables covary, such an analysis is necessary to account simultaneously for the effects of speed and size. However, because few previous studies have used a similar type of analysis for fish of a similar size range and temperature, it is difficult to make comparisons with published data. Dewar and Graham (1994) measured $\dot{V}_{O_2}$ as a function of speed and mass in larger kawakawa (366–400 mm FL, 770–1000 g) at a water temperature of 24.4±0.2 °C (mean ± s.e.m.). They provided us with their raw data so that we could compare the energetics data for the juvenile kawakawa with those for larger individuals in which muscle temperature should be elevated significantly above water temperature. The multiple regression of $\dot{V}_{O_2}$ *versus* speed and mass for the kawakawa in the present study was solved for $\dot{V}_{O_2}$ using the data of Dewar and Graham (1994), and these extrapolated values were compared with their measured $\dot{V}_{O_2}$ values. Although we acknowledge the limits of this extrapolation, there was good agreement between the calculated and empirical data, with a mean difference of -0.14 ± 0.44 mg O_2 min^{-1} (mean ± s.e.m., 25 measurements). There are no published $\dot{V}_{O_2}$ *versus* speed data that we know of for any *Scomber* species.

To estimate mean COT_{net} for each individual, we modeled the data with linear regressions, rather than a 'J'-shaped exponential relationship (Webb, 1998). Many of the values fitted the linear model well, probably because we specifically chose to study a single gait, when fish swam with a steady, continuous tail beat, which resulted in speed ranges in the most linear portion of the J-shaped curve. We also started most experiments at a moderate speed, rather than at lower speeds, for the following reasons. Because tunas are obligate ram ventilators and are negatively buoyant, it was necessary to commence all respirometry trials at a speed high enough to ensure adequate ventilation and hydrodynamic equilibrium (Magnuson and Weininger, 1978). In initial trials, low speeds were used, and they resulted in high $\dot{V}_{O_2}$ values. These low speeds often elicited erratic fluttering of the pectoral fins and unsteady swimming in the tunas (visual observations) which, in combination with the inefficiency of muscle contraction at low strain rates (Webb, 1998), probably caused the elevated $\dot{V}_{O_2}$ values. In those cases, $\dot{V}_{O_2}$ measurements at the lowest swimming speeds were not included in the linear regressions used to estimate COT_{net}. All future trials commenced at a higher speed, because we were interested only in continuous, sustainable swimming (i.e. a single gait). Furthermore, mackerel actively ventilate their gills by buccal pumping at low speeds (Boutilier et al., 1983), whereas kawakawa do not. Thus, the added cost of the contractions associated with this behavior could increase the $\dot{V}_{O_2}$ of the mackerels and thus bias the interspecific comparison at low speeds.

There was no significant difference in the incremental cost of swimming (COT_{net}) between the juvenile kawakawa and chub mackerel (Figs 4, 5). However, total metabolic costs and standard metabolic rates were higher in the kawakawa (Figs 3,

6). The high metabolic rates of tunas have been documented in the literature (Gooding et al., 1981; Brill, 1987; Brill and Bushnell, 1991; Dewar and Graham, 1994; for a review, see Brill, 1996), but it was not until the present study that tunas were compared with a closely related ectothermic teleost of the same size range at the same ambient temperature. Prior investigations have been limited in that they have had to compare their results with the only available data from similar-sized ectothermic fishes, which has been from salmonids. Salmonids are active ectothermic teleosts, but they differ morphologically from tunas and they are only distantly related to scombrids. When Dewar and Graham (1994) compared energetic data from yellowfin tuna (416±27 and 513±30 mm FL) at 24±2 °C with those of similar-sized salmonids at 15 °C (Brett, 1965; Bushnell et al., 1984), tunas had higher standard metabolic rates, but their net cost of swimming (COT_{net}) was actually lower than that of the salmonids. This provided support for the hypothesis that tunas were more efficient swimmers than ectotherms, possibly because of the streamlined bodies of the tunas, the thunniform mode of locomotion and/or warm aerobic locomotor muscle. However, the results from the present study, a more appropriate comparison because we have used a member of one of the tunas' sister groups and studied both species under the same conditions, provides evidence that tunas are not faster or more efficient swimmers, at least as juveniles. Since the kawakawa swam with less lateral displacement than the chub mackerel, it appears that the thunniform mode of locomotion is not more energetically efficient than the carangiform mode used by mackerels (Donley and Dickson, 2000).

The finding of higher standard metabolic rates in the juvenile kawakawa compared with the chub mackerel is probably related to the high aerobic capacity of tunas (Gooding et al., 1981; Dewar and Graham, 1994; Dickson, 1996; Korsmeyer et al., 1996a; Mathieu-Costello et al., 1996; Brill, 1996). Tunas possess anatomical, biochemical and physiological characteristics that have led researchers to conclude that they are high-performance fishes (for reviews, see Dickson, 1995; Brill, 1996). The need to maintain the high-performance 'machinery' is probably, at least in part, responsible for the high standard metabolic rates of tunas compared with mackerels. Tunas have high gill surface areas with a thinner gill epithelium than most teleosts, including mackerels (Gray, 1954; Muir and Hughes, 1969; Hughes, 1984). This thin barrier enables oxygen transfer from the water to the blood to occur twice as fast in tunas as it does in other teleosts (for a review, see Bushnell and Jones, 1994), but may also result in high rates of ion flux across the gills, which should result in high osmoregulatory costs (Brill, 1996; Korsmeyer et al., 1996a). A recent study showed that the combined costs of running the Na^+/K^+-ATPase pumps in both the intestines and gills, which are primarily responsible for ion regulation in teleosts, account for 16 % of the total SMR in yellowfin tuna (J. Y. Swimmer and R. W. Brill, personal communication).

The heart of tunas is larger than that of other similar-sized ectothermic teleosts, including mackerels, and is capable of

generating greater blood pressures (Brill and Bushnell, 1991; for reviews, see Bushnell and Jones, 1994; Farrell, 1996). A high cardiac output, coupled with the elevated hemoglobin and myoglobin levels found in tunas, provides for an enhanced oxygen delivery system (for reviews, see Bushnell and Jones, 1994; Dickson, 1996). The activity of the enzyme citrate synthase, which catalyzes the first step in the citric acid cycle and is an index of tissue mitochondrial density, was significantly higher in the red muscle of the juvenile kawakawa than in the chub mackerel used in this study (Herrick, 1999). Thus, maintenance costs for the cardiovascular system and aerobic locomotor muscle may be greater in the kawakawa than in the chub mackerel. In addition, the kawakawa in the present study were probably growing at a faster rate than were the mackerel because of the approximately threefold difference in feeding rates, which could have contributed to their elevated $\dot{V}_{O_2}$. It is also possible that the kawakawa experienced more stress during the experiments than the mackerel did, even though we attempted to minimize stress by handling the fish as little as possible and to control the amount of stress by handling both species in an identical manner. If this were true, it could have contributed to the higher metabolic rates of the kawakawa relative to the chub mackerel.

Although a recent study (Freund, 1999) found that routine rates of oxygen consumption at 20 °C of the eastern Pacific bonito (*Sarda chiliensis*) were similar to those of similar-sized skipjack tuna, swimming speeds were not controlled and were not measured for the bonito. Future studies of $\dot{V}_{O_2}$ *versus* speed *versus* fish size relationships of similar-sized bonitos at the same temperature are needed to determine whether members of tunas' sister taxon have an elevated standard metabolic rate like the tunas or whether they are more like the mackerels. Only then will it be possible to ascertain whether high SMRs are associated with the tunas only, and if this trait is more likely to have evolved before or after the divergence of the tunas and bonitos. Such future studies will allow us to determine whether the high standard metabolic rates of tunas were a prerequisite for the evolution of endothermy.

The increased metabolic cost in tunas, without any measurable benefit in terms of swimming performance, at least in juveniles, leads one to ask, 'why be a tuna?' The answer to this question is not known, but tunas are one of the most abundant apex predators throughout the world's oceans, despite the low quantity and patchy distribution of nutrients (Sund et al., 1981). Their sheer abundance and coexistence with other similarly derived piscivorous fishes suggest that this added metabolic cost could, at least in part, be overcome by other factors that contribute to their evolutionary success.

References

Aleev, Y. G. (1969). *Function and Gross Morphology in Fish*. Jerusalem: Keter Press.

Altringham, J. D. and Block, B. A. (1997). Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200**, 2617–2627.

Arthur, P. G., West, T. G., Brill, R. W., Schulte, P. M. and Hochachka, P. W. (1992). Recovery metabolism of skipjack tuna (*Katsuwonus pelamis*) white muscle: Rapid and parallel changes of lactate and phosphocreatine after exercise. *Can. J. Zool.* **70**, 1230–1239.

Beamish, F. W. H. (1978). Swimming capacity. In *Fish Physiology*, vol. VII (ed. W. S. Hoar and D. J. Randall), pp. 101–187. New York: Academic Press.

Block, B. A., Booth, D. and Carey, F. G. (1992). Direct measurement of swimming speeds and depth of blue marlin. *J. Exp. Biol.* **166**, 267–284.

Block, B. A., Finnerty, J. R., Stewart, A. F. R. and Kidd, J. (1993). Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. *Science* **260**, 210–214.

Boutilier, R. G., Aughton, P. and Shelton, G. (1983). O_2 and CO_2 transport in relation to ventilation in the Atlantic mackerel, *Scomber scombrus*. *Can. J. Zool.* **62**, 546–554.

Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd Can.* **21**, 1183–1226.

Brett, J. R. (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd Can.* **22**, 1491–1501.

Brill, R. W. (1987). On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. *Fish. Bull.* **85**, 25–35.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes and dolphin fish. *Comp. Biochem. Physiol.* **113A**, 3–15.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V. and Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: Implications for the physiological ecology of pelagic fishes. *Mar. Biol.* **133**, 395–408.

Brill, R. W. and Bushnell, P. G. (1991). Metabolic and cardiac scope of high energy demand teleosts, the tunas. *Can. J. Zool.* **69**, 2002–2009.

Brill, R. W. and Dizon, A. E. (1979). Red and white muscle fiber activity in swimming skipjack tuna, *Katsuwonus pelamis*. *J. Fish Biol.* **15**, 679–685.

Bushnell, P. G. and Brill, R. W. (1991). Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas exposed to acute hypoxia and a model of their cardiorespiratory function. *Physiol. Zool.* **64**, 787–811.

Bushnell, P. G. and Jones, D. R. (1994). Cardiovascular and respiratory physiology of tuna: Adaptations for support of exceptionally high metabolic rates. *Env. Biol. Fish.* **40**, 303–318.

Bushnell, P. G., Steffensen, J. G. and Johansen, K. (1984). Oxygen consumption and swimming performance in hypoxia-acclimated rainbow trout *Salmo gairdneri*. *J. Exp. Biol.* **113**, 225–235.

Carey, F. G. and Teal, J. M. (1966). Heat conservation in tuna fish muscle. *Proc. Natl. Acad. Sci. USA* **56**, 1464–1469.

Carey, F. G., Teal, J. M., Kanwisher, J. W., Lawson, K. D. and Beckett, J. S. (1971). Warm-bodied fish. *Am. Zool.* **11**, 135–143.

Collette, B. B. (1978). Adaptations and systematics of the mackerels and tunas. In *The Physiological Ecology of Tunas* (ed. G. D. Sharp and A. E. Dizon), pp. 7–39. New York: Academic Press.

Dewar, H. and Graham, J. B. (1994). Studies of tropical tuna swimming performance in a large water tunnel. I. Energetics. *J. Exp. Biol.* **192**, 13–31.

Dickson, K. A. (1994). Tunas as small as 207 mm fork length can elevate muscle temperatures significantly above ambient water temperature. *J. Exp. Biol.* **190**, 79–93.

Dickson, K. A. (1995). Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Env. Biol. Fish.* **42**, 65–97.

Dickson, K. A. (1996). Locomotor muscle of high-performance fishes: What do comparisons of tunas with ectothermic sister taxa reveal? *Comp. Biochem. Physiol.* **113**A, 39–49.

Dizon, A. E., Neill, W. H. and Magnuson, J. J. (1977). Rapid temperature compensation of volitional swimming speeds and lethal temperatures in tropical tunas (Scombridae). *Env. Biol. Fish.* **2**, 83–92.

Donley, J. M. and Dickson, K. A. (2000). Swimming kinematics of juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J. Exp. Biol.* **203**, 3103–3116.

Farrell, A. P. (1996). Features heightening cardiovascular performance in fishes, with special reference to tunas. *Comp. Biochem. Physiol* **113**A, 61–67.

Freund, E. V. (1999). Comparisons of metabolic and cardiac performance in scombrid fishes: Insights into the evolution of endothermy. PhD dissertation, Stanford University, Stanford, CA, USA. 182pp.

Gooding, R. J., Neill, W. H. and Dizon, A. E. (1981). Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. *Fish. Bull.* **79**, 31–47.

Graham, J. B. (1973). Heat exchange in the black skipjack and the blood–gas relationship of warm bodied fishes. *Proc. Natl. Acad. Sci. USA* **70**, 1964–1967.

Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares* and skipjack tuna, *Katsuwonus pelamis* and the adaptive significance of elevated body temperatures in scombrid fishes. *Fish. Bull.* **73**, 219–229.

Graham, J. B. and Dickson, K. A. (2000). The evolution of thunniform locomotion and heat conservation in scombrid fishes: New insights based on the morphology of *Allothunnus fallai*. *Zool. J. Linn. Soc.* **129**, 419–466.

Graham, J. B., Koehrn, F. J. and Dickson, K. A. (1983). Distribution and relative proportions of red muscle in scombrid fishes: Consequences of body size and the relationships to locomotion and endothermy. *Can. J. Zool.* **61**, 2087–2096.

Graham, J. B., Lowell, R. W., Lai, N. C. and Laurs, R. M. (1989). O₂ tension, swimming velocity and thermal effects on the metabolic rate of the Pacific albacore, *Thunnus alalunga*. *Exp. Biol.* **48**, 89–94.

Gray, I. E. (1954). Comparative study of the gill area of marine fishes. *Biol. Bull.* **107**, 219–225.

He, P. and Wardle, C. S. (1988). Endurance at intermediate swimming speeds of Atlantic mackerel, *Scomber scombrus* L., herring, *Clupea harengus* L. and saithe, *Pollachius virens* L. *J. Fish Biol.* **33**, 255–266.

Herrick, B. (1999). Do biochemical indices of aerobic capacity correlate with swimming speeds of kawakawa tuna (*Euthynnus affinis*)? Master's thesis, California State University, Fullerton, USA. 41pp.

Hughes, G. N. (1984). General anatomy of the gills. In *Fish Physiology*, vol. 10A (ed. W. S. Hoar and D. J. Randall), pp. 1–72. New York: Academic Press.

Johnston, I. A. and Brill, R. W. (1984). Thermal dependence of contractile properties of singled skinned muscle fibers from Antarctic and various warm water marine fishes including skipjack tuna (*Katsuwonus pelamis*) and kawakawa (*Euthynnus affinis*). *J. Comp. Physiol.* **155**B, 63–70.

Joseph, J., Klawe, W. and Murphy, P. (1988). *Tuna and Billfish – Fish Without a Country*. La Jolla, CA: Inter-American Tropical Tuna Commission. 69pp.

Korsmeyer, K. E., Dewar, H., Lai, N. C. and Graham, J. B. (1996a). The aerobic capacity of tunas: Adaptations for multiple metabolic demands. *Comp. Biochem. Physiol.* **113**A, 17–24.

Korsmeyer, K. E., Dewar, H., Lai, N. C. and Graham, J. B. (1996b). Tuna aerobic swimming performance: Physiological and environmental limits based on oxygen supply and demand. *Comp. Biochem. Physiol.* **113**B, 45–56.

Lindsey, C. C. (1968). Temperatures of red and white muscle in recently caught marlin and other large tropical fish. *J. Fish. Res. Bd Can.* **25**, 1987–1992.

Magnuson, J. J. (1970). Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. *Copeia* **1970**, 56–85.

Magnuson, J. J. (1973). Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. *US Fish Wildl. Serv. Fish Bull.* **71**, 337–356.

Magnuson, J. J. (1978). Locomotion by scombroid fishes: Hydromechanics, morphology and behavior. In *Fish Physiology*, vol. VII (ed. W. S. Hoar and D. J. Randall), pp. 239–313. New York: Academic Press.

Magnuson, J. J. and Weininger, D. (1978). Estimation of minimum sustained speed and associated body drag of scombrids. In *The Physiological Ecology of Tunas* (ed. G. D. Sharp and A. E. Dizon), pp. 293–311. New York: Academic Press.

Mathieu-Costello, O., Brill, R. W. and Hochachka, P. W. (1996). Structural basis for oxygen delivery: Muscle capillaries and manifolds in tuna red muscle. *Comp. Biochem. Physiol.* **113**A, 25–31.

Muir, B. S. and Hughes, G. M. (1969). Gill dimensions for three species of tunny. *J. Exp. Biol.* **51**, 271–285.

Neill, W. H., Chang, R. K. C. and Dizon, A. E. (1976). Magnitude

and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). *Env. Biol. Fish.* **1**, 61–80.

Perry, S. F., Daxboeck, C., Emmett, B., Hochachka, P. W. and Brill, R. W. (1985). Effects of exhausting exercise on acid–base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. *Physiol. Zool.* **58**, 421–429.

Roberts, J. L. and Graham, J. B. (1979). Effect of swimming speed on the excess temperature and activities of heart and red and white muscles in the mackerel, *Scomber japonicus*. *Fish. Bull.* **76**, 861–867.

Rome, L. C. (1995). Influence of temperature on muscle properties in relation to swimming performance. In *Biochemistry and Molecular Biology of Fishes*, vol. 5 (ed. P. W. Hochachka and T. P. Mommsen), pp. 73–99. Amsterdam: Elsevier Science.

Schaefer, K. M. (1984). Swimming performance, body temperatures and gastric evacuation times of the black skipjack, *Euthynnus lineatus*. *Copeia* **1984**, 1000–1005.

Schaefer, K. M. (1986). Lethal temperatures and the effect of temperature change on volitional swimming speeds of chub mackerel, *Scomber japonicus*. *Copeia* **1986**, 39–44.

Stevens, E. D. and Carey, F. G. (1981). One why of the warmth of warm-bodied fish. *Am. J. Physiol.* **240**, R151–R155.

Stevens, E. D. and McLeese, J. M. (1984). Why bluefin tuna have warm tummies: Temperature effect on trypsin and chymotrypsin. *Am. J. Physiol.* **246**, R487–R494.

Stevens, E. D. and Neill, W. H. (1978). Body temperature relations of tunas, especially skipjack. In *Fish Physiology*, vol. VII (ed. W. S. Hoar and D. J. Randall), pp. 316–356. New York: Academic Press.

Sund, P. N., Blackburn, M. and Williams, F. (1981). Tunas and their environment in the Pacific Ocean: A review. *Oceanogr. Mar. Biol. Annu. Rev*. **19**, 443–512.

Videler, J. J. (1993). *Fish Swimming*. London: Chapman & Hall.

Walters, V. (1962). Body form and swimming performance in the scombroid fishes. *Am. Zool*. **2**, 143–149.

Webb, P. W. (1971). The swimming energetics of trout. I. Thrust and power output at cruising speeds. *J. Exp. Biol*. **55**, 489–520.

Webb, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can*. **190**, 1–159.

Webb, P. W. (1993). The effect of solid and porous channel walls on steady swimming of steelhead trout *Oncorhynchus mykiss*. *J. Exp. Biol*. **178**, 97–108.

Webb, P. W. (1998). Swimming. In *The Physiology of Fishes*, second edition (ed. D. Evans), pp. 1–24. Boca Raton, Florida: CRC Press.

Yuen, H. S. H. (1966). Swimming speeds of yellowfin and skipjack tuna. *Trans. Am. Fish. Soc*. **95**, 203–209.