

## Effects of temperature on sustained swimming performance and swimming kinematics of the chub mackerel *Scomber japonicus*

Kathryn A. Dickson\*, Jeanine M. Donley†, Chugey Sepulveda† and Lisa Bhoopat‡  
*Department of Biological Science, California State University Fullerton, Fullerton, CA 92834, USA*

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

†Present address: Marine Biology Research Division, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA

‡Present address: Anaheim High School, 811 W. Lincoln Avenue, Anaheim, CA 92805, USA

Accepted 24 January 2002

### Summary

The effects of a 6 °C difference in water temperature on maximum sustained swimming speed, swimming energetics and swimming kinematics were measured in the chub mackerel *Scomber japonicus* (Teleostei: Scombridae), a primarily coastal, pelagic predator that inhabits subtropical and temperate transition waters of the Atlantic, Pacific and Indian Oceans. New data for chub mackerel acclimated to 18 °C are compared with published data from our laboratory at 24 °C. Twelve individuals acclimated to each of two temperatures (15.6–26.3 cm fork length, *FL*, and 34–179 g at 18 °C; 14.0–24.7 cm *FL* and 26–156 g at 24 °C) swam at a range of speeds in a temperature-controlled Brett-type respirometer, at the respective acclimation temperature. At a given fish size, the maximum speed that *S. japonicus* was able to maintain for a 30-min period, while swimming steadily using slow, oxidative locomotor muscle ( $U_{\max,c}$ ), was significantly greater at 24 than at 18 °C (52.5–97.5 cm s<sup>-1</sup> at 18 °C and 70–120 cm s<sup>-1</sup> at 24 °C). At a given speed and fish size, the rate of oxygen consumption ( $\dot{V}_{O_2}$ ) was significantly higher at 24 than at 18 °C because of a higher net cost of transport (1073–4617 J km<sup>-1</sup> kg<sup>-1</sup> at 18 °C and 2708–14895 J km<sup>-1</sup> kg<sup>-1</sup> at 24 °C). Standard metabolic rate, calculated by extrapolating the log  $\dot{V}_{O_2}$  versus swimming speed relationship to zero speed, did not vary significantly with temperature or fish mass (126.4 ± 67.2 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> at 18 °C and 143.2 ± 80.3 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> at 24 °C; means ± s.d., *N*=12). Swimming kinematics was quantified from high-speed (120 Hz) video recordings

analyzed with a computerized, two-dimensional motion-analysis system. At a given speed and fish size, there were no significant effects of temperature on tail-beat frequency, tail-beat amplitude or stride length, but propulsive wavelength increased significantly with temperature as a result of an increase in propulsive wave velocity. Thus, the main effects of temperature on chub mackerel swimming were increases in both  $U_{\max,c}$  and the net cost of swimming at 24 °C. Like other fishes, *S. japonicus* apparently must recruit more slow, oxidative muscle fibers to swim at a given sustainable speed at the lower temperature because of the reduced power output. Thus, the 24 °C mackerel reach a higher speed before they must recruit the fast, glycolytic fibers, thereby increasing  $U_{\max,c}$  at 24 °C. By quantifying *in vivo* the effects of temperature on the swimming performance of an ectothermic species that is closely related to the endothermic tunas, this study also provides evidence that maintaining the temperature of the slow, oxidative locomotor muscle at 6 °C or more above ambient water temperature in tunas should significantly increase sustainable swimming speeds, but also increase the energetic cost of swimming, unless cardiac output limits muscle performance.

Key words: Scombridae, chub mackerel, *Scomber japonicus*, locomotion, kinematics, cost of transport, metabolism, sustained swimming, energetics, respirometer, temperature.

### Introduction

This paper reports the effects of a 6 °C difference in water temperature on sustained swimming in the chub mackerel *Scomber japonicus* Houttuyn (Teleostei: Scombridae). Like all scombrid fishes, *S. japonicus* is an epipelagic predator specialized for rapid and efficient swimming. Scombrids have a streamlined body shape, a high-aspect-ratio caudal fin, a hypural complex with caudal fin rays completely covering the hypural plate, a narrow caudal peduncle, caudal keels and

dorsal and ventral finlets – all of which are thought to reduce drag or increase thrust production during swimming (Aleev, 1969; Webb, 1975; Collette, 1978; Magnuson, 1978; Nauen and Lauder, 2000). *S. japonicus* is primarily a coastal species and is widely distributed, inhabiting subtropical and temperate transition waters of the Atlantic, Pacific and Indian Oceans (Schaefer, 1980; Collette and Nauen, 1983). Conventional tagging studies have documented migrations by *S. japonicus*

along the west coast of the United States and the east coast of Japan (for a review, see Schaefer, 1980). The lower and upper lethal temperatures for *S. japonicus* acclimated to 16–17°C and subjected to a 1°C day<sup>-1</sup> temperature change were 6.1±0.9°C and 28.8±1.1°C, respectively; the fish ceased feeding at 9.9±1.0°C and 26.7±0.5°C, respectively (Schaefer, 1986).

Quantifying the effects of temperature on swimming performance is important for active ectothermic species such as *S. japonicus* that experience wide ambient temperature ranges as well as for the few endothermic fish species that maintain the temperature ( $T_m$ ) of their slow-twitch, oxidative locomotor muscle significantly above water temperature. Among teleost fishes, only the tunas have been documented to maintain an elevated  $T_m$  using vascular counter-current heat exchangers (Carey et al., 1971) (for a review, see Block, 1991). Steady-state  $T_m$  values measured by acoustic telemetry in tunas are elevated above water temperature by as much as 6–13°C (Carey and Lawson, 1973; Holland et al., 1992; Stevens et al., 2000; Marcinek et al., 2001). Although it has been hypothesized that elevating  $T_m$  enhances swimming performance in tunas, no study has yet been able to test this hypothesis directly by comparing the swimming performance of tunas possessing significantly elevated muscle temperatures with that of closely related ectothermic fishes of similar size (see Sepulveda and Dickson, 2000). Because the ectothermic chub mackerel and the tunas are members of the family Scombridae, the effects of temperature on swimming in the chub mackerel may be used to model the potential enhancing effects of maintaining an elevated  $T_m$  on sustainable swimming performance in tunas. The present study examined continuous swimming, which is assumed to be powered by the slow-twitch, oxidative myotomal muscle (for reviews, see Rome, 1995; Jayne and Lauder, 1996; Webb, 1998) because that muscle is perfused *via* vascular counter-current heat exchangers and maintained at significantly elevated temperatures in the tunas (Carey et al., 1971).

Several previous studies that have quantified the effects of temperature on continuous swimming in teleost fishes have shown that metabolic rate and maximum sustainable swimming speed generally increase with temperature [e.g. in sockeye salmon *Oncorhynchus nerka* (Brett and Glass, 1973); carp *Cyprinus carpio* (Rome et al., 1984); scup *Stenotomus chrysops* (Rome et al., 1992); striped bass *Morone saxatilis* (Sisson and Sidell, 1987); rainbow trout *Oncorhynchus mykiss* (Kieffer et al., 1998); Atlantic menhaden *Brevoortia tyrannus* (Macy et al., 1999)]. In some cases, there is a decrease in these variables at high temperatures that approach the maximum environmental temperature experienced by the species [sockeye salmon (Brett and Glass, 1973); juvenile walleye *Stizostedion vitreum vitreum* (Beamish, 1990); rainbow trout (Taylor et al., 1996)]. Surprisingly, some studies have failed to show a significant effect of temperature on sustainable swimming performance [e.g. for the delta smelt *Hypomesus transpacificus* (Swanson et al., 1998)].

Fewer studies of the effects of temperature on the kinematics

of sustained swimming in teleosts exist, but most show small or insignificant effects. At a given sustainable speed, neither tail-beat frequency nor tail-beat amplitude varied with temperature in carp (Rome and Sosnicki, 1990). Similarly, no temperature effect on tail-beat frequency was found in scup (Rome et al., 1992) or in goldfish *Carassius auratus* (Smit et al., 1974). However, the tail-beat frequency *versus* swimming speed relationships varied with temperature in rainbow trout (Stevens, 1979; Taylor et al., 1996), largemouth bass *Micropterus salmoides* (Stevens, 1979) and striped bass (Sisson and Sidell, 1987), and Swank and Rome (2000) found a small but significant increase at 20°C compared with 10°C in tail-beat frequency measured at a swimming speed of 50 cm s<sup>-1</sup> but not at 40 cm s<sup>-1</sup> for scup. The latter findings suggest that swimming efficiency may change with temperature.

We know of no published study that has simultaneously examined the effects of temperature on sustainable swimming, swimming energetics and swimming kinematics for a species as well adapted for rapid and continuous swimming as the chub mackerel. Thus, the objective of the present study was to compare the previously reported data for chub mackerel at 24°C (Donley and Dickson, 2000; Sepulveda and Dickson, 2000) with data for the same species at 18°C to determine the effect of a temperature change of that magnitude on sustainable swimming performance and swimming kinematics of scombrid fishes.

## Materials and methods

### *Fish collection and maintenance*

The present study compares new data for chub mackerel *Scomber japonicus* Houttuyn at 18°C with data at 24°C that were previously reported in a comparison of swimming performance in chub mackerel and kawakawa tuna *Euthynnus affinis* (Donley and Dickson, 2000; Sepulveda and Dickson, 2000). Chub mackerel were captured by hook and line off the coast of southern California, USA, and were transported to California State University Fullerton (CSUF) in an 80 litre cylindrical bait tank in aerated sea water. The sea surface temperatures at capture for the two groups of mackerel were approximately 18 and 22°C. Fish were maintained for at least 2 weeks with a 12 h:12 h light:dark photoperiod cycle, in a 1500 l indoor fiberglass tank 1.6 m in a diameter, in filtered, recirculating sea water with a salinity of 32–34‰ and temperature of 18.5±0.5°C or 24.0±1.0°C. Fish were fed chopped fish and/or squid once a day, in an amount approximating 5–10% of their body mass; generally, the 18°C-acclimated mackerel were fed less than those held at 24°C. No feeding occurred for at least 12 h prior to removal of a fish for an experiment.

### *Respirometry*

All experiments were conducted in a Brett-type, temperature-controlled, variable-speed respirometer containing a total volume of 35 litre (13.5 cm×27.0 cm×101.6 cm), as described

previously (Donley and Dickson, 2000; Sepulveda and Dickson, 2000). Individual fish swam against water currents of known velocities, determined by calibration with a General Oceanics mechanical flow meter (model 2030 R). Corrections for solid blocking effects were not necessary because all fish had maximal cross-sectional areas that were less than 10% of the cross-sectional area of the 13.5 cm×13.5 cm×50.8 cm fish test chamber (Brett, 1964; Webb, 1971). Each fish was removed from the holding tank by capture with a baited, barbless hook and placed, with minimal handling, into the respirometer. Before starting an experiment, each fish was allowed to adjust to the respirometer chamber for 4 h in the case of the 24 °C mackerels or for 12–19 h (overnight) for the 18 °C mackerels. Water temperature within the respirometer system was maintained at 18.4±0.2 °C or 24.0±0.2 °C, respectively, with an in-line heater and chiller system.

#### Maximum sustainable swimming speed

In total, 12 chub mackerel at each temperature [15.6–26.3 cm fork length (*FL*) (20.9±4.0 cm, mean ± S.D.) and 34–179 g at 18 °C; 14.0–24.7 cm *FL* (20.3±3.4 cm) and 26–156 g at 24 °C] were used in swimming performance experiments. A modification of the Brett (1964) procedure for measuring critical swimming speed ( $U_{crit}$ ) was used to determine the maximum sustainable speed. Each fish was forced to swim for sequential 30-min periods at specific speeds, starting at 15–40 cm s<sup>-1</sup>. Speed was increased in increments of 7.5 or 10 cm s<sup>-1</sup>. We attempted to use a speed increment of approximately 10% of the expected maximum sustainable speed; the increments were actually 10.7±1.7% and 10.8±1.9% (mean ± S.D.) of that value for fish at 18 °C and 24 °C, respectively. The maximum speed that each fish was able to maintain for an entire 30-min period while swimming using a gait characterized by steady, continuous tail beats ( $U_{max,c}$ ), assumed to be powered by the slow-twitch, oxidative myotomal muscle, was determined.

Several investigators have shown that the aerobic myotomal muscle powers sustainable swimming in fish and that recruitment of the fast-twitch, glycolytic muscle fibers at higher speeds is evident in a change in gait from a continuous tail beat to intermittent bursts of high-frequency tail beats followed by gliding (for reviews, see Videler, 1993; Rome, 1995; Webb, 1998). Thus, when the fish shifted from a steady tail beat to a 'burst-and-glide' gait three times within 30 s, we assumed that it could not maintain speed using the aerobic muscle alone and had to recruit the fast-twitch muscle fibers. The preceding speed that the fish had maintained for 30 min was designated as  $U_{max,c}$  (maximum continuous or cruising speed) for that fish. Thus,  $U_{max,c}$  values in the present study are lower than  $U_{crit}$  values determined using the Brett (1964) formula, which takes into account the period the fish swam at the speed at which it switched to burst-and-glide swimming.

#### Swimming energetics

Fish oxygen consumption rate ( $\dot{V}_{O_2}$ ) was measured at each speed during the  $U_{max,c}$  trials using a Yellow Springs

Instruments polarographic oxygen electrode and meter connected to a chart recorder, as described by Sepulveda and Dickson (2000).  $\dot{V}_{O_2}$  was measured during the middle 10–27 min of each 30-min period at each speed; the time required depended upon the fish's  $\dot{V}_{O_2}$  and thus varied with fish size, speed and temperature. The minimum level of oxygen saturation in the respirometer for all trials for each fish was 79–95% at 18 °C and 88–98% at 24 °C, and all tracings of water oxygen concentration *versus* time were linear. During the remainder of the 30-min period at each speed, the respirometer water oxygen content was brought back to the original 100% saturation level by allowing water to flow to and from a reservoir of oxygenated or aerated sea water connected to the respirometer by a valve system. The valves to the reservoir were closed whenever  $\dot{V}_{O_2}$  was measured. After each experiment, 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.

The net cost of transport ( $COT_{net}$ , in J km<sup>-1</sup> kg<sup>-1</sup>), or incremental cost of swimming, was calculated by 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 average net cost of transport for the fish (see Sepulveda and Dickson, 2000). The slope units (mg O<sub>2</sub> min<sup>-1</sup> cm<sup>-1</sup> s) were multiplied by (1 min×60 s<sup>-1</sup>) to remove time and then converted to J km<sup>-1</sup> kg<sup>-1</sup> by multiplying by 13.54 J mg<sup>-1</sup> O<sub>2</sub> and dividing by fish mass.

Each fish's standard metabolic rate (SMR) was estimated by extrapolating the log  $\dot{V}_{O_2}$  *versus* swimming speed relationship to zero speed. Although these estimates are associated with considerable error, it has been shown for tunas that SMRs calculated in this way are similar to oxygen consumption rates of paralyzed, restrained individuals (Brill, 1987; Dewar and Graham, 1994).

#### Swimming kinematics

Individual chub mackerel were videotaped at 120 Hz using a Peak Performance Technologies high-speed video camera (model TM640) positioned in front of a mirror mounted at 45° above the respirometer to obtain a dorsal view of the fish. The swimming kinematics of 13 chub mackerel (15.6–26.3 cm *FL*) at 18 °C and eight chub mackerel (14.0–23.4 cm *FL*) at 24 °C were analyzed. Video recordings were made onto Maxell Professional SVHS tapes over a 2- to 10-min period at each speed at which the fish swam during its  $\dot{V}_{O_2}$  measurements. Videotapes were analyzed using a Peak Performance Technologies two-dimensional motion-analysis system, as described by Donley and Dickson (2000).

Video segments in which the fish was swimming steadily for 8–10 tail beats and was positioned in the center of the chamber, away from the walls and bottom of the chamber, were selected for analysis. Six points along the dorsal midline of each fish that could be identified consistently were digitized in sequential video fields for 8–10 tail beats at each speed: the tip of the snout, the points along the dorsal midline

between both the anterior and the posterior insertion points of the eyes, the midpoint between the anterior insertions of the pectoral fins, the caudal peduncle and the tip of the upper lobe of the caudal fin. The kinematic variables tail-beat frequency, tail-beat amplitude, stride length (the distance traveled per tail beat) and propulsive wavelength were calculated for each individual at each speed by analyzing the progression of these digitized points over time, as described by Donley and Dickson (2000). Propulsive wave velocity ( $C$ ), the speed of the wave of undulation that travels down the body during swimming, was calculated from the time (s) between the peaks in lateral displacement at two points, the tip of the snout and the tip of the tail. For each individual at each speed, 7–10 measurements were averaged to calculate progression time. The distance between the two points (which is equal to fish total length) was divided by the average progression time to obtain the propulsive wave velocity ( $C$ ) in  $\text{cm s}^{-1}$  at each speed for each individual. Propulsive wavelength ( $\lambda$ ) was calculated by dividing  $C$  by the fish's tail-beat frequency at that speed.

*Statistical analyses*

Differences between the two mackerel groups in the relationships between  $U_{\text{max,c}}$ ,  $\text{COT}_{\text{net}}$  or  $\text{SMR}$  and fish size (both fork length and mass) were assessed using a general linear model (GLM) analysis of covariance (ANCOVA) in Minitab (version 10.5). Because speed and size covary and both may affect  $\dot{V}_{\text{O}_2}$  and each of the kinematic variables, it was necessary to use a multivariate analysis to determine whether temperature had a significant effect on these variables (see Donley and Dickson, 2000). We determined whether there was

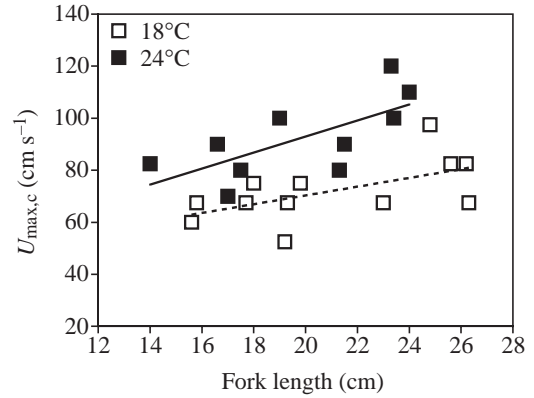


Fig. 1. Maximum continuous swimming speed ( $U_{\text{max,c}}$ ) versus fork length ( $FL$ ) in chub mackerel (*Scomber japonicus*) acclimated to 18 °C (open squares) or 24 °C (filled squares) measured at the respective acclimation temperature. The lines are the best-fitting linear regressions (with coefficients  $\pm$  S.E.M.):  $U_{\text{max,c}} = (0.168 \pm 0.075)FL + (36.6 \pm 16.0)$ ,  $r^2 = 0.33$ ,  $N = 12$ ,  $P = 0.049$ , at 18 °C (dashed line);  $U_{\text{max,c}} = (0.308 \pm 0.114)FL + (31.4 \pm 22.9)$ ,  $r^2 = 0.48$ ,  $N = 10$ ,  $P = 0.027$ , at 24 °C (solid line). At a given  $FL$ ,  $U_{\text{max,c}}$  was significantly greater at 24 °C (ANCOVA;  $P = 0.001$ ), but  $U_{\text{max,c}}$  increased with  $FL$  at the same rate at the two temperatures.

a significant difference between the two mackerel groups, indicating a significant effect of temperature, in the relationship between each variable and swimming speed and fish size. After determining that the data were normally distributed and thus did not need to be transformed, a repeated-measures multiple regression analysis (ANCOVA) was performed with SAS (version 6.12) using the regression

Table 1. Fork length, mass, maximum continuous swimming speed, net cost of transport and linear and exponential regression equations for the plots of rate of oxygen consumption versus swimming speed for individual chub mackerel (*Scomber japonicus*) at 18 °C

FL (cm)	Mass (g)	$U_{\text{max,c}}$		$\text{COT}_{\text{net}}$ ( $\text{J kg}^{-1} \text{ km}^{-1}$ )	Linear fit	$r^2$	$P$	Exponential fit	$r^2$	$P$
		( $\text{cm s}^{-1}$ )	( $FL \text{ s}^{-1}$ )							
15.6	34	60.0	3.8	4617	$y = 0.007x - 0.130$	0.956	<0.001	$y = 0.022 \times 10^{0.019x}$	<b>0.980</b>	<0.001
15.8	38	67.5	4.3	3550	$y = 0.006x + 0.068$	<b>0.962</b>	<0.001	$y = 0.128 \times 10^{0.009x}$	0.925	<0.001
17.7	50	67.5	3.8	4461	$y = 0.010x - 0.068$	0.937	<0.001	$y = 0.094 \times 10^{0.012x}$	<b>0.986</b>	<0.001
18.0	50	75.0	4.2	3218	$y = 0.007x - 0.011$	<b>0.949</b>	<0.001	$y = 0.093 \times 10^{0.011x}$	<b>0.953</b>	<0.001
19.2	54	52.5	2.7	3368	$y = 0.008x + 0.032$	0.931	<0.01	$y = 0.114 \times 10^{0.012x}$	<b>0.974</b>	<0.001
19.3	71	67.5	3.5	3392	$y = 0.011x - 0.028$	<b>0.808</b>	<0.01	$y = 0.150 \times 10^{0.010x}$	0.671	<0.025
19.8	77	75.0	3.8	4190	$y = 0.014x - 0.037$	<b>0.796</b>	<0.01	$y = 0.171 \times 10^{0.011x}$	0.781	<0.01
23.0	107	67.5	2.9	3494	$y = 0.017x - 0.207$	<b>0.875</b>	<0.01	$y = 0.094 \times 10^{0.016x}$	0.736	<0.05
24.8	145	97.5	3.9	2904	$y = 0.019x - 0.269$	0.930	<0.001	$y = 0.206 \times 10^{0.009x}$	<b>0.957</b>	<0.001
25.6	162	82.5	3.2	1621	$y = 0.012x + 0.054$	0.798	<0.01	$y = 0.279 \times 10^{0.007x}$	<b>0.842</b>	<0.01
26.2	170	82.5	3.1	1073	$y = 0.008x + 0.343$	0.716	<0.025	$y = 0.447 \times 10^{0.004x}$	<b>0.733</b>	<0.025
26.3	179	67.5	2.6	1186	$y = 0.009x + 0.794$	<b>0.825</b>	<0.025	$y = 0.865 \times 10^{0.003x}$	0.818	<0.025

Corresponding data for chub mackerel at 24 °C are in Sepulveda and Dickson (2000).

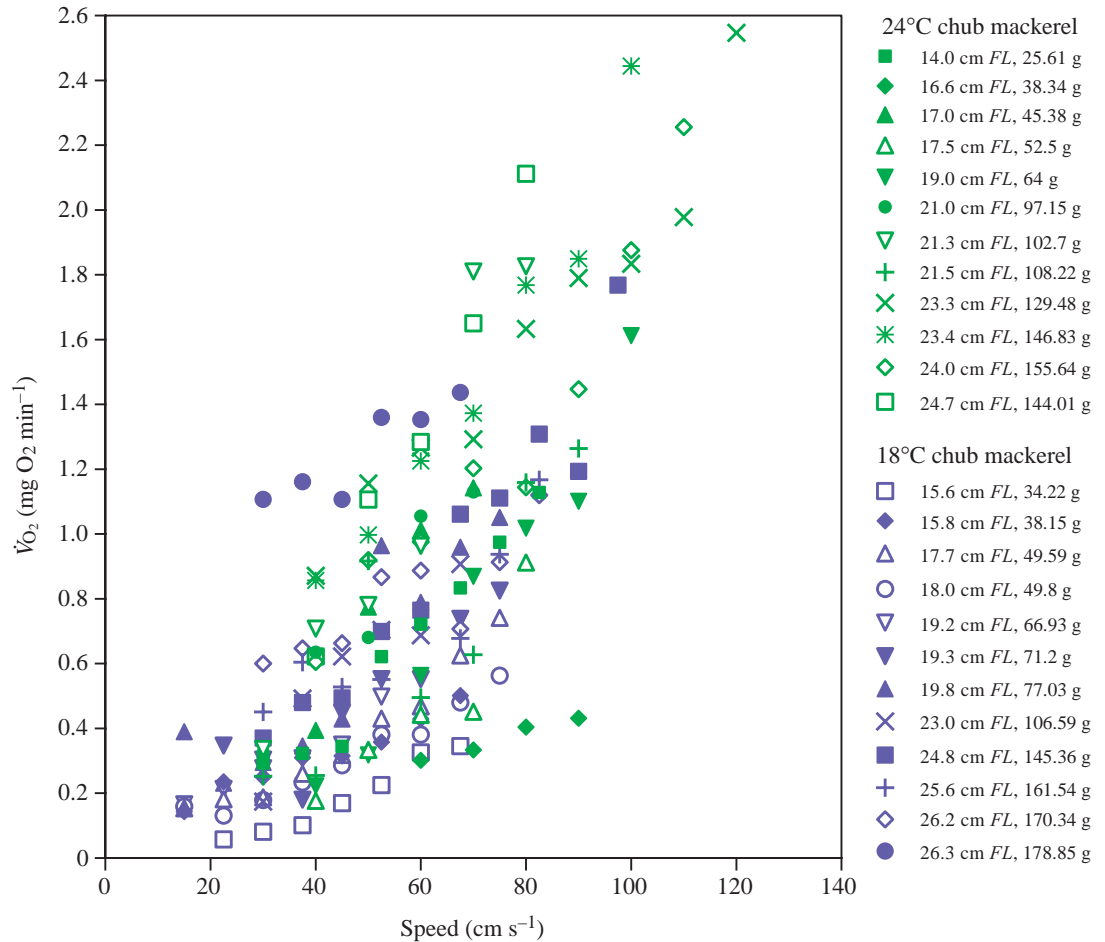
The y-intercept of each linear regression and the coefficient  $a$  of the exponential regression ( $y = a \times 10^{bx}$ ) can be used as estimates of the rate of oxygen consumption at zero speed (standard metabolic rate) for each individual.

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

$FL$ , fork length;  $U_{\text{max,c}}$ , maximum continuous swimming speed (see text);  $\text{COT}_{\text{net}}$ , net cost of transport.

For the regressions, the rate of oxygen consumption,  $y$ , is in  $\text{mg O}_2 \text{ min}^{-1}$  and swimming speed,  $x$ , is in  $\text{cm s}^{-1}$ .

Fig. 2. Rate of oxygen consumption ( $\dot{V}_{O_2}$ ) versus swimming speed for all individual chub mackerel at 18 °C (blue symbols) and 24 °C (green symbols). The fork length ( $FL$ ) and mass of each individual are indicated. The best-fitting regressions for each individual at 18 °C are presented in Table 1, and those for each individual at 24 °C are given in Sepulveda and Dickson (2000).



equation for chub mackerel at 24 °C as a baseline with which the corresponding regression for the 18 °C mackerel was compared. Each variable was tested for the effects of temperature, speed and fish size, in terms of both mass and fork length, all possible two-way and three-way interactions and a four-way interaction term.

Unless indicated, values are presented as means  $\pm$  S.D.

## Results

### Maximum sustainable swimming speed

At a given fish size,  $U_{max,c}$  was significantly greater at 24 than at 18 °C ( $P=0.001$ , ANCOVA) (Fig. 1). The  $U_{max,c}$  values ranged from 52.5 to 97.5  $cm s^{-1}$  at 18 °C and from 70 to 120  $cm s^{-1}$  at 24 °C. For both temperatures,  $U_{max,c}$  (in  $cm s^{-1}$ ) increased significantly with  $FL$  (Fig. 1) and with mass (Table 1). The effect of fish size on  $U_{max,c}$  did not differ significantly between the two temperatures (ANCOVA).

### Swimming energetics

In the chub mackerel at both temperatures, the rate of oxygen consumption ( $\dot{V}_{O_2}$  in  $mg O_2 min^{-1}$ ) increased significantly with both fish mass and swimming speed. At a given speed and fish size,  $\dot{V}_{O_2}$  was significantly higher at 24 than at 18 °C (Fig. 2). These findings are best represented by

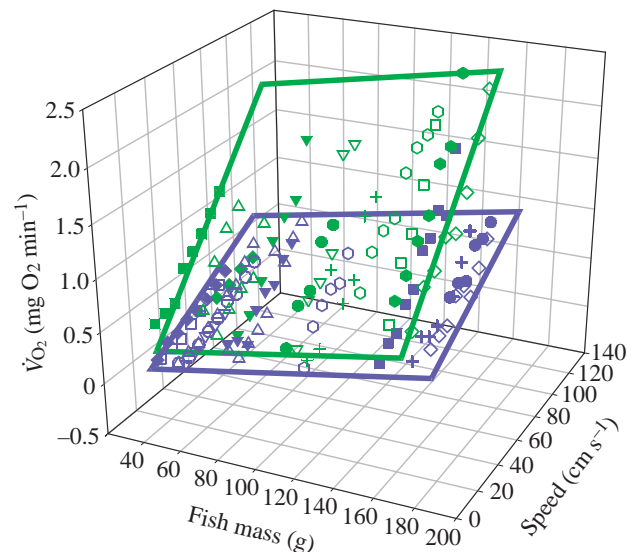


Fig. 3. Rate of oxygen consumption ( $\dot{V}_{O_2}$ ) at 18 °C (blue plane and symbols) and 24 °C (green plane and symbols) as a function of both swimming speed and fish mass for all individuals studied. The maximum and minimum values of speed and mass at 18 and 24 °C were used to solve the multiple regression equations for  $\dot{V}_{O_2}$  (Table 2) for the four corners of each plane. At a given speed and mass,  $\dot{V}_{O_2}$  is significantly higher at 24 than at 18 °C, and the rate of increase in  $\dot{V}_{O_2}$  with speed is greater at 24 °C (ANCOVA,  $P<0.0001$ ).

three-dimensional, multivariate plots of  $\dot{V}_{O_2}$  as a function of both fish mass and speed at the two temperatures (Fig. 3; Table 2). The multivariate ANCOVA indicated significant effects of temperature, speed and fish mass on  $\dot{V}_{O_2}$ , as well as a significant interaction between speed and temperature (for all,  $P < 0.0001$ ). There was a greater rate of increase in  $\dot{V}_{O_2}$  with speed at 24 than at 18 °C (Fig. 3; Table 2). When the effects of speed and mass are taken into account, there was no significant effect of  $FL$  on  $\dot{V}_{O_2}$  ( $P = 0.18$ ).

At a given fish size, the incremental cost of swimming or net cost of transport ( $COT_{net}$ ), which is proportional to the slope of the  $\dot{V}_{O_2}$  versus swimming speed regression for each individual (Fig. 2), was significantly greater at 24 than at 18 °C ( $P = 0.02$ , ANCOVA) (Fig. 4). This is reflected in the significant speed  $\times$  temperature interaction term in the multivariate analysis for  $\dot{V}_{O_2}$ . At both temperatures, mass-specific  $COT_{net}$  decreased with fish  $FL$  (Fig. 4) and with fish mass (Table 1) but, when the effect of  $FL$  was accounted for, there was no significant effect of fish mass on  $COT_{net}$  (ANCOVA).

The mass-specific SMRs, estimated from the coefficient  $a$  in the exponential  $\dot{V}_{O_2}$  versus swimming speed curves (the  $y$ -intercept of the  $\log \dot{V}_{O_2}$  versus swimming speed regression) for each individual (Fig. 2), ranged from 38.6 to 290.2  $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$  (mean  $126.4 \pm 67.2 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ ,  $N = 12$ ) at 18 °C and from 53.2 to 280.0  $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$  (mean  $143.2 \pm 80.3 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ ,  $N = 12$ ) at 24 °C. There was a significant effect of mass on SMR when expressed as  $\text{mg O}_2 \text{ min}^{-1}$  ( $P < 0.001$ ), but not when expressed as  $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ . There was no significant effect of temperature on the relationship between SMR ( $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ ) and fish mass (ANCOVA) or on the mean mass-specific SMR ( $t$ -test).

#### Swimming kinematics

When the effects of fish size were accounted for, tail-beat frequency increased significantly with speed at both temperatures ( $P < 0.0001$ ) at the same rate (Table 2; Fig. 5). When the effects of speed were taken into account, there was a significant effect of  $FL$  on tail-beat frequency ( $P < 0.0001$ )

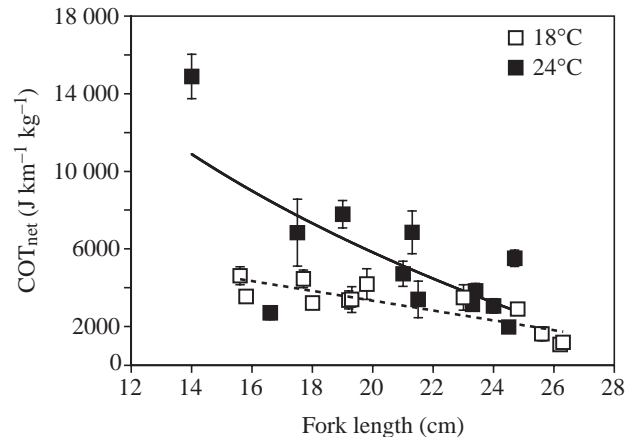


Fig. 4. The mass-specific net cost of transport ( $COT_{net}$ ) for chub mackerel at 18 °C (open squares) and 24 °C (filled squares) as a function of fish fork length ( $FL$ ). The lines are the best-fitting equations:  $COT_{net} = -253FL + 8387$ ,  $r^2 = 0.72$ ,  $N = 12$ ,  $P < 0.001$ , at 18 °C (dashed line);  $COT_{net} = -31383 \log FL + 46734$ ,  $r^2 = 0.48$ ,  $N = 12$ ,  $P < 0.02$ , at 24 °C (solid line). At a given fish size,  $COT_{net}$  was greater at 24 than at 18 °C (ANCOVA;  $P = 0.02$ ), even if the highest point for the 14.0 cm  $FL$  mackerel at 24 °C is omitted. Values are means  $\pm$  S.E.M.

(Table 2; Fig. 5). The rate of decrease in tail-beat frequency with  $FL$  did not vary with temperature (Fig. 5). When the effects of speed and fork length were accounted for, neither mass nor temperature had a significant effect on tail-beat frequency. Thus, at both temperatures, chub mackerel of a given size use the same tail-beat frequency to swim at a given speed.

The effects of fish size, swimming speed and temperature on tail-beat amplitude, expressed both in absolute units (cm) and relative to fish size (as a percentage of  $FL$ , %  $FL$ ), were examined. In both mackerel groups, tail-beat amplitude (in both cm and %  $FL$ ) increased significantly with speed ( $P < 0.0001$ ) and tail-beat amplitude (in cm) increased with  $FL$  ( $P < 0.0001$ ) (Table 2; Fig. 6). The rates of increase in tail-beat amplitude with speed and with  $FL$  were not affected by temperature (Fig. 6). When speed and fork length were

Table 2. Equations for the three-dimensional planes or lines representing the final models of the repeated-measures multiple regression analysis for  $\dot{V}_{O_2}$  and each kinematic variable as a function of swimming speed, fish fork length and fish mass

Kinematic variable, $y$	Multiple regression equation
$\dot{V}_{O_2}$ at 18 °C ( $\text{mg O}_2 \text{ min}^{-1}$ )	$y = (-0.283 \pm 0.214) + (0.0096 \pm 0.0026)U + (0.0044 \pm 0.0010)M$
$\dot{V}_{O_2}$ at 24 °C ( $\text{mg O}_2 \text{ min}^{-1}$ )	$y = (-0.746 \pm 0.121) + (0.0204 \pm 0.0011)U + (0.0044 \pm 0.0010)M$
Tail-beat frequency (Hz)	$y = (5.20 \pm 0.738) + (0.047 \pm 0.002)U + (-0.165 \pm 0.034)FL$
Tail-beat amplitude (cm)	$y = (-0.611 \pm 0.511)^* + (0.012 \pm 0.002)U + (0.161 \pm 0.024)FL$
Tail-beat amplitude (% $FL$ )	$y = (13.10 \pm 0.60) + (0.056 \pm 0.008)U$
$l$ (cm)	$y = (-5.15 \pm 2.06) + (0.086 \pm 0.005)U + (0.639 \pm 0.097)FL$
$\lambda$ at 18 °C (cm)	$y = (-1.17 \pm 2.56) + (1.11 \pm 0.09)FL$
$\lambda$ at 24 °C (cm)	$y = (0.98 \pm 1.88)^* + (1.11 \pm 0.09)FL$

Standard errors ( $\pm$ S.E.M.) are given for each coefficient.

The final multiple regression equations for all variables except  $\dot{V}_{O_2}$  and  $\lambda$  were the same for chub mackerel at both 18 and 24 °C.

\*Indicates a coefficient that does not differ significantly from zero ( $P > 0.05$ ).

$FL$ , fork length (cm);  $l$ , stride length;  $\lambda$ , propulsive wavelength;  $U$ , swimming speed;  $M$ , body mass.

accounted for, there was no significant effect of mass on tail-beat amplitude (in cm or % *FL*). When expressed as a percentage of *FL*, there was no significant effect of fish size on tail-beat amplitude (Table 2), indicating that dividing tail-beat amplitude by fish length was an appropriate adjustment for size differences in both groups of chub mackerel. When the effects of speed and fork length were accounted for, there was no significant effect of temperature on tail-beat amplitude (in cm or % *FL*) (Table 2; Fig. 6).

Stride length (*l*) increased significantly with speed ( $P < 0.0001$ ) and with *FL* ( $P < 0.0001$ ) at both temperatures (Table 2; Fig. 7). When the effects of speed and *FL* were accounted for, there was no significant effect of fish mass on *l*. The slopes of the regressions of *l* versus speed and of *l* versus *FL* did not differ with temperature. When the effects of speed and fork length were accounted for, there was no significant effect of temperature on *l* (Fig. 7).

There were significant effects of temperature ( $P = 0.0024$ ) and *FL* ( $P < 0.0001$ ), but not of speed or mass, on the propulsive wavelength ( $\lambda$ ) (Table 2). Thus, the relationship between the mean  $\lambda$  for each individual and fish *FL* was compared at the two temperatures. At a given fish size, mean  $\lambda$  was significantly greater at 24 than at 18 °C (Fig. 8). The rate of increase in  $\lambda$  with *FL* was the same at both temperatures (Fig. 8).

When the data for the 24 °C chub mackerel were analyzed previously (Donley and Dickson, 2000), there were significant effects of fish *FL* on both relative stride length and relative propulsive wavelength expressed as a percentage of *FL*. This indicates that attempting to normalize stride lengths and propulsive wavelengths for fish size by dividing by *FL* introduces a different size effect to the data and, thus, may result in misleading conclusions (see Packard and Boardman, 1999). Therefore, we have not included analyses of the relative (size-specific) values of these two kinematic variables.

## Discussion

### Maximum sustainable swimming speed and swimming energetics

A 6 °C increase in temperature resulted in significant increases in  $U_{\max,c}$  and  $COT_{\text{net}}$  in *S. japonicus*. Standard metabolic rate (SMR) was expected to vary with temperature, but did not, possibly because the fish were acclimated to their respective temperatures or because of the relatively small temperature difference and the large error associated with extrapolation to obtain the SMRs. The only other comparable energetics data for mackerel are from Shadwick and Steffensen (2000), who estimated SMR at 14–15 °C for *S. japonicus* using procedures similar to those in the present study. Their values (90–120 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> for 145–199 g fish) fall within the range that we measured for similar-sized fish (85–290 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> for 145–179 g fish at 18 °C and 95–177 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> for 144–156 g fish at 24 °C). Thus, when estimated by extrapolation to zero speed, there seems to

be little measurable change in SMR between 14 and 24 °C for *S. japonicus* when fish are acclimated to the respective measurement temperature.

Sepulveda and Dickson (2000) showed that, at 24 °C, the SMR for *S. japonicus* was lower than that for similar-sized kawakawa tuna, but the SMR values measured in the present study are similar to or somewhat higher than those reported for other active teleosts of similar size at similar temperatures. For example, SMRs of 73 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> were measured in menhaden (303 ± 38 g) acclimated to and measured at 15 °C, and those (283 ± 40 g) acclimated to and measured at 20 °C had SMRs of 87 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> (Macy et al., 1999). Freadman (1979) measured an SMR of 156 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> at 15 °C in 217 g bluefish, *Pomatomus saltatrix*, and the values estimated from Fig. 3 of Brett and Glass (1973) for sockeye salmon of the same mass as the mackerel in the present study are 90–110 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> at 18 °C and 140–190 mg O<sub>2</sub> h<sup>-1</sup> kg<sup>-1</sup> at 24 °C.

Maximal sustainable speeds have been measured previously in mackerel. Atlantic mackerel *S. scombrus* (29–33 cm *FL*), swimming in a circular gantry tank and stimulated to swim at different speeds by the optomotor response, could maintain a speed of 4.1 *FL* s<sup>-1</sup> (120–137 cm s<sup>-1</sup>) for 30 min at 11.7 °C (He and Wardle, 1988). If the  $U_{\max,c}$  versus *FL* regressions in Fig. 1 are extrapolated to that size range, these values fall between the lines for 18 and 24 °C and, thus, are higher than the present study would predict. Roberts and Graham (1979) swam *S. japonicus* (34.3–39.2 cm *FL*) at maximum speeds of 3.2–4.5 *FL* s<sup>-1</sup> (125–171 cm s<sup>-1</sup>) in a swimming tunnel 12 cm in diameter at 16.1–21.8 °C. The time for which each fish swam at those speeds was not explicitly stated, but was apparently 3 min. These values fall close to the  $U_{\max,c}$  versus *FL* regression for chub mackerel at 24 °C, when extrapolated to the higher *FL* values. The maximum sustainable swimming speeds ranged from 2.75 to 3.25 *FL* s<sup>-1</sup> (70–86 cm s<sup>-1</sup>) for 24–28 cm *FL* *S. japonicus* at 14–15 °C (Shadwick and Steffensen, 2000) (R. E. Shadwick, personal communication), comparable with the values of 67.5–97.5 cm s<sup>-1</sup> (2.6–3.9 *FL* s<sup>-1</sup>) for 24.8–26.3 cm *FL* *S. japonicus* at 18 °C in the present study. Thus, the  $U_{\max,c}$  values for a given temperature and fish size in the present study appear to be somewhat lower than the only other values for *Scomber* spp. that we could find, but methodological differences could at least partially account for this.

The  $U_{\max,c}$  values measured in *S. japonicus* are similar to those reported for other active teleost fishes of similar size at similar temperatures. Sepulveda and Dickson (2000) showed that, at 24 °C, the  $U_{\max,c}$  for *S. japonicus* did not differ significantly from that measured in similar-sized kawakawa tuna. We have measured  $U_{\max,c}$  values of 74–118 cm s<sup>-1</sup> at 27 °C for 19.1–26.0 cm green jack *Caranx caballus* in the same respirometer system (K. A. Dickson, M. W. Hansen, J. M. Donley and J. A. Hoskinson, unpublished results). At 13.5 °C, 25.3 cm herring, *Clupea harengus*, could maintain a speed of 121 cm s<sup>-1</sup> for 30 min and, at 14.4 °C, 25.5 cm saithe, *Pollachius virens*, could maintain a speed of 98 cm s<sup>-1</sup> for

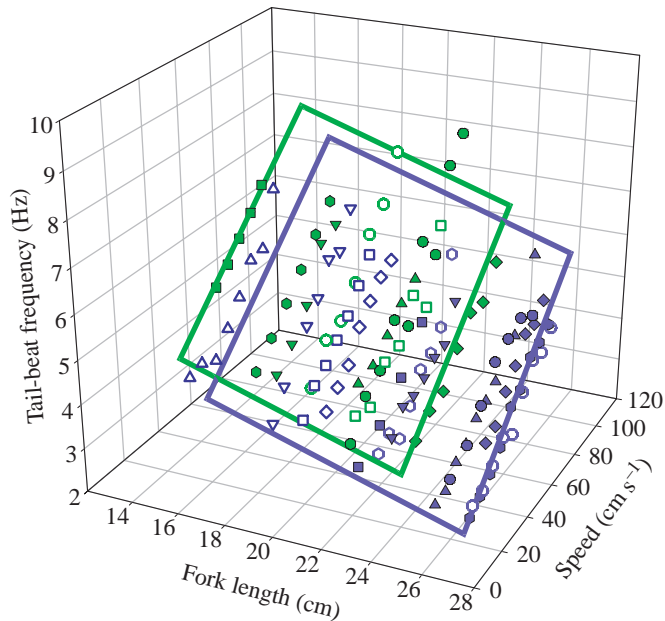


Fig. 5. The dependence of tail-beat frequency on both swimming speed and fish fork length (*FL*) in chub mackerel at 18 °C (blue plane and symbols) and 24 °C (green plane and symbols). Each symbol indicates the tail-beat frequency *versus* speed data for one individual. The maximum and minimum values of speed and *FL* at 18 and 24 °C were used to solve the multiple regression equation for tail-beat frequency (Table 2) for the four corners of each plane. There was no significant effect of temperature on the relationship between tail-beat frequency and speed and *FL* (ANCOVA,  $P>0.05$ ).

30 min (He and Wardle, 1988). Sockeye salmon (18.5 cm) maintained a speed of 77.4 cm s<sup>-1</sup> for 60 min at 15 °C but only 69.4 cm s<sup>-1</sup> for 60 min at 24 °C (Brett and Glass, 1973). On the basis of the speed at which the fast, glycolytic muscle fibers are first recruited, as determined from electromyographic recordings, the  $U_{max,c}$  at 24 °C for 18.48±0.32 cm striped bass was 2.82±0.32 body lengths s<sup>-1</sup> or approximately 52 cm s<sup>-1</sup> (Sisson and Sidell, 1987), and the  $U_{max,c}$  at 20 °C for 20–25 cm scup was 80–81 cm s<sup>-1</sup> (Rome et al., 1992; Swank and Rome, 2000). Only the values for the striped bass and the sockeye salmon at 24 °C are lower than comparable values for *S. japonicus* from the present study.

The fact that the chub mackerel can achieve a higher  $U_{max,c}$  at 24 than at 18 °C is probably due to greater muscle fiber contraction rate and power output at the higher temperature, as has been found in isolated slow, oxidative muscle fibers of

Fig. 7. The increase in stride length (*l*) with both swimming speed and fish fork length (*FL*) in chub mackerel at 18 °C (blue plane and symbols) and 24 °C (green plane and symbols). Each symbol indicates the *l versus* speed data for one individual. The maximum and minimum values of speed and *FL* at 18 and 24 °C were used to solve the multiple regression equation for stride length (Table 2) for the four corners of each plane. There was no significant effect of temperature on the relationship between *l* and speed and *FL* (ANCOVA,  $P>0.05$ ).

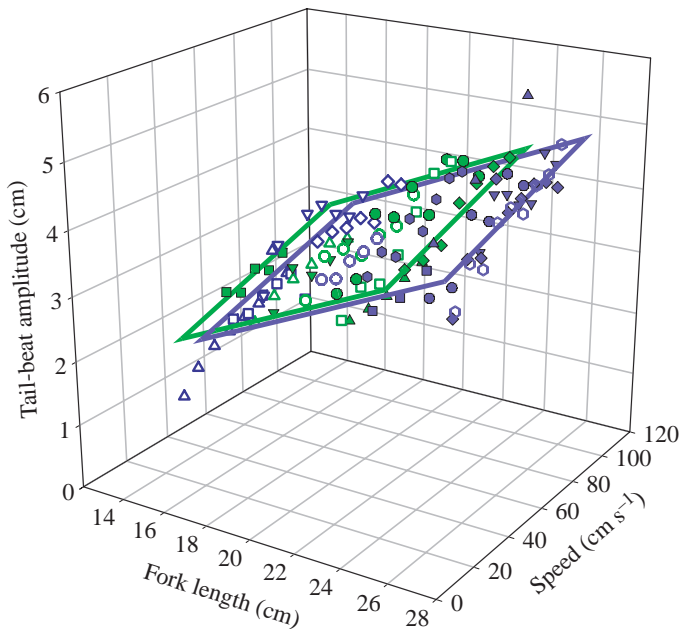
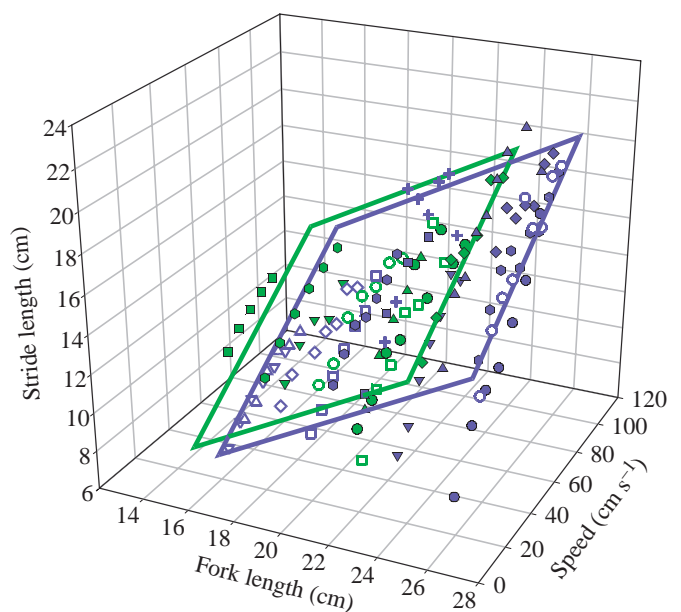


Fig. 6. The increase in tail-beat amplitude with both swimming speed and fish fork length (*FL*) in chub mackerel at 18 °C (blue plane and symbols) and 24 °C (green plane and symbols). Each symbol indicates the tail-beat amplitude *versus* speed data for one individual. The maximum and minimum values of speed and *FL* at 18 and 24 °C were used to solve the multiple regression equation for tail-beat amplitude (cm) (Table 2) for the four corners of each plane. There was no significant effect of temperature on the relationship between tail-beat amplitude and speed and *FL* (ANCOVA,  $P>0.05$ ).

other scombrids (Johnston and Brill, 1984; Altringham and Block, 1997) and other teleosts (e.g. Rome and Swank, 1992; Rome et al., 2000). Because of the effect of temperature on power output, the lower the temperature, the lower the speed at which the fast, glycolytic muscle fibers are first recruited and, thus, the lower the  $U_{max,c}$ , since that is the maximum





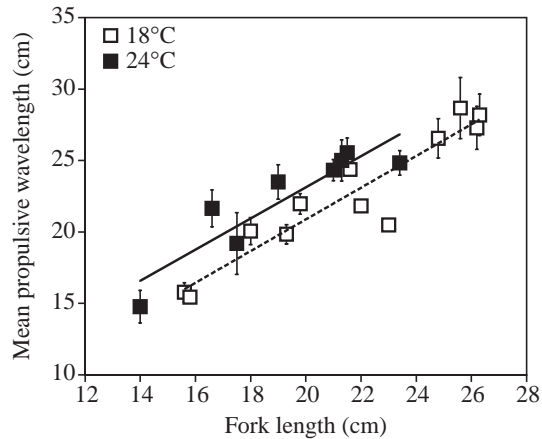


Fig. 8. Mean propulsive wavelength ( $\lambda$ ) versus fork length ( $FL$ ) for individual chub mackerel at 18°C (open squares) and 24°C (filled squares). Because there was no significant effect of speed on  $\lambda$ , the mean of the propulsive wavelengths at all swimming speeds was calculated for each individual. Error bars represent  $\pm 1$  S.E.M. The lines are the best-fitting linear regressions:  $\lambda = 1.11FL - 1.32$ ,  $r^2 = 0.89$ ,  $N = 9$ ,  $P < 0.001$ , at 18°C (dashed line);  $\lambda = 1.09FL + 1.32$ ,  $r^2 = 0.83$ ,  $N = 12$ ,  $P < 0.001$ , at 24°C (solid line). Mean  $\lambda$  increases with  $FL$  at the same rate at the two temperatures but, at a given  $FL$ ,  $\lambda$  is significantly greater at 24 than at 18°C (ANCOVA,  $P = 0.0024$ ).

speed powered only by the aerobic muscle fibers. This is the 'compression of recruitment order theory' of Rome et al. (1984) (see also Sisson and Sidell, 1987; Rome, 1990, 1995). However, if more slow, oxidative muscle fibers are contracting at a given speed at 18 than at 24°C,  $COT_{net}$  would be expected to be higher at 18°C, not lower.

The total energetic cost ( $\dot{V}O_2$ ) at each speed was higher at 24 than at 18°C, and the difference between the two planes along the y-axis in Fig. 3 represents the magnitude of the effect of temperature on a combination of locomotor and support costs. This difference was not affected by fish mass but did increase with swimming speed at the higher temperature, as indicated by steeper slopes for the  $\dot{V}O_2$  versus speed regressions (i.e. the  $COT_{net}$  values). The higher  $COT_{net}$  may be a consequence of the fact that mackerel reached higher speeds at 24 than at 18°C, since the amount of muscle contractile power required to swim should increase exponentially with speed. However, if the data points for the higher speeds ( $\geq 100$  cm s $^{-1}$ ) at 24°C are excluded, the slopes of the  $\dot{V}O_2$  versus speed regressions decrease somewhat, but are still greater at 24 than at 18°C, suggesting that other factors contribute to this difference.

The  $\dot{V}O_2$  at each speed could be higher at 24°C because of higher swimming support costs, such as a higher cardiac output and blood flow to the slow, oxidative locomotor muscle to compensate for the lower  $O_2$  solubility at the higher temperature. Other energetic expenditures, such as those for ion regulation and osmoregulation, could also be higher at the higher temperature. In addition, the mackerel at 24°C may have been more stressed than those at 18°C, or post-feeding specific dynamic action may have contributed more to  $\dot{V}O_2$  at 24°C because of the different lengths of the initial adjustment

period in the respirometer (4h for the 24°C-acclimated mackerel versus 12–19h for the 18°C-acclimated mackerel). Unfortunately, we were unable to quantify any of these costs or to separate the effects of temperature on the direct costs of swimming (production of propulsive force by myotomal muscle) from these other potential energetic demands.

There are other possible reasons why total  $\dot{V}O_2$  and  $COT_{net}$  are greater at the higher temperature. First, slow, oxidative muscle fiber contraction at a given speed could be less efficient at 24 than at 18°C in the chub mackerel. There are few studies of muscle fiber contraction efficiency in fishes, and none that we know of that has investigated the effect of temperature. In individual human slow, oxidative muscle fibers, the thermodynamic efficiency of contraction increased with an increase in temperature (He et al., 2000). In frog muscle, there was little change in the mechanical efficiency of contraction with temperature (Rall and Woledge, 1990), and we could find no studies of vertebrate skeletal muscle showing a decrease in efficiency with an increase in temperature. Nevertheless, in the mackerel in the present study, a change in muscle fiber characteristics leading to an increase in efficiency could have occurred during the acclimation period at 18°C, as suggested for scup by Swank and Rome (2001). In other teleosts acclimated to low temperatures, the amount of slow, oxidative myotomal muscle increased [e.g. in carp (Sidell, 1980), striped bass (Jones and Sidell, 1982) and rainbow trout (Taylor et al., 1996)], and cyprinid fishes can alter their muscle contractile properties to compensate for low temperature (for reviews, see Sidell and Moerland, 1989; Rome, 1995), as can scup (Swank and Rome, 2001). However, we did not measure any of these variables, so we cannot determine whether any temperature-compensatory adjustments occurred.

Second, at a given speed and tail-beat frequency, the slow, oxidative muscle fibers could be operating at a different point on the force/velocity or power output/stimulation frequency curves at the two temperatures (Stevens, 1979; Sisson and Sidell, 1987; Rome, 1995). In isolated slow, oxidative muscle of the eastern Pacific bonito *Sarda chiliensis*, an ectothermic scombrid species, and the yellowfin tuna *Thunnus albacares*, Altringham and Block (1997) found an increase with temperature in the frequency at which maximum power was generated. Thus, in the chub mackerel, a given tail-beat frequency could be closer to the optimal stimulation frequency at 18 than at 24°C. However, since maximum power output also increases with temperature, more power can be produced by stimulating the muscle fibers at 24°C at a sub-optimal frequency than by stimulating the muscle fibers at 18°C at their optimal frequency. Furthermore, Rome and colleagues found that, even though acclimation to 10°C improved power output at 10°C, scup produced less power from their slow, oxidative muscle at 10°C than they could at 20°C (Rome et al., 2000; Rome and Swank, 2001; Swank and Rome, 2000, 2001). To understand slow, oxidative muscle function at the different temperatures in chub mackerel, it will be necessary to combine *in vivo* measurements of muscle stimulation pattern and muscle strain along the length of the

fish with *in vitro* work loop studies, as a function of temperature.

Third, Sisson and Sidell (1987) suggested that an increase in water kinematic viscosity at a lower temperature could delay boundary layer separation, thus reducing drag and the energetic cost of swimming at a given speed at the lower temperature. Although not tested in the present study, others have shown that changes in water kinematic viscosity contribute little to temperature effects on fish swimming performance for the size of fish swimming at the speeds used here; significant effects of water viscosity have been demonstrated only with fish larvae and small juveniles at relatively low speeds, i.e. at low Reynolds numbers (Fuiman and Batty, 1997; Johnson et al., 1998). However, in the water flow regimes associated with swimming tunnels, boundary layer effects may become important. With new methods of visualizing and quantifying flow within the boundary layer of swimming fish (Anderson et al., 2001), the hypothesized effects of water temperature and kinematic viscosity on boundary layer separation could be explored.

#### *Swimming kinematics*

At both 18 and 24 °C, there were significant effects of swimming speed and fish size on tail-beat frequency, tail-beat amplitude and stride length, as expected on the basis of a number of other studies of swimming kinematics in fishes (for a review, see Donley and Dickson, 2000). The data for tail-beat frequency *versus* speed in the present study are similar to those reported previously for *S. japonicus* (26.3–32.2 cm *FL*) at 17.0–19.5 °C by Hunter and Zweifel (1971).

At a given speed and fish size, there were no significant effects of temperature on tail-beat frequency, tail-beat amplitude or stride length. This is consistent with several previous investigations with other teleost fishes in which tail-beat frequency and/or tail-beat amplitude at a given speed were not affected by temperature (Smit et al., 1974; Rome and Sosnicki, 1990; Rome et al., 1990, 1992). However, in other studies (Stevens, 1979; Sisson and Sidell, 1987), the tail-beat frequency at a given speed did vary with temperature, which was attributed to higher thrust per tail beat, greater propeller efficiency and/or lower drag at the lower temperatures. In those studies, fish were acclimated to and/or measured at temperatures representing a wider range than was used in the present study.

The only kinematic variable that was significantly affected by temperature in the chub mackerel was propulsive wavelength, which also increased significantly with *FL*, as expected, but not with fish mass or swimming speed. The increase in  $\lambda$  (=propulsive wave velocity/tail-beat frequency) with temperature is due to a higher propulsive wave velocity at 24 °C because tail-beat frequency was not significantly affected by temperature. It is not clear why  $\lambda$ , but none of the other kinematic variables measured, would vary with temperature. A faster propulsive wave velocity at 24 °C could result if temperature enhanced the rate at which action potentials within the motor neurons and muscle fibers

propagated posteriorly down the fish or if the latent period between electrical activation and muscle contraction decreased. However, in scup acclimated to and studied at both 10 and 20 °C, there was no significant effect of temperature on the speed at which electrical activity (measured by electromyography) moved posteriorly along the body or on propulsive wave velocity (Rome and Swank, 2001).

A higher  $\lambda$  at the higher temperature could result from an increase in flexural stiffness (Long et al., 1994; McHenry et al., 1995; Long and Nipper, 1996). Stiffness could be increased if the active muscles were to do more negative work at 24 than at 18 °C (McHenry et al., 1995; Long and Nipper, 1996), but there is no evidence of net negative work being produced by slow, oxidative muscle contraction in swimming chub mackerel (Shadwick et al., 1998). Furthermore, on the basis of work loop studies with isolated slow, oxidative muscle of other teleosts, including two scombrid species (Altringham and Block, 1997; Rome et al., 2000; Rome and Swank, 2001; Swank and Rome, 2000, 2001), more net positive work should be produced at the higher temperature. It should also be noted that there is considerable overlap in the propulsive wavelength data at the two temperatures in the present study (Fig. 8).

#### *Relevance to endothermy in tunas*

The positive effect of temperature on whole-animal swimming performance ( $U_{\max,c}$ ) measured in the present study is very similar in magnitude to the effect of temperature on contraction rate and power output in isolated slow oxidative myotomal muscle fibers of the two scombrid fishes studied by Altringham and Block (1997).  $U_{\max,c}$  values in the chub mackerel increased by approximately 30% with an increase of 6 °C compared with a 22–37% increase in maximal power output between 20 and 25 °C in the isolated scombrid muscle fibers. This suggests that results of such *in vitro* experiments may be used to estimate the effects of temperature on sustainable swimming speeds of fish; however, one must consider the precautions for doing so discussed by Rome (1995) and Rome et al. (2000). If the power output of slow, oxidative myotomal muscle in tunas is enhanced at higher temperatures *in vivo*, as was found by Altringham and Block (1997) *in vitro*, then increased maximal sustainable swimming speeds should result from the maintenance of elevated myotomal muscle temperatures in tunas. This hypothesis needs to be tested by comparing the maximal sustainable swimming speed of larger tunas, in which  $T_m$  is elevated more than a few degrees above the water temperature, with that of similar-sized ectothermic scombrid fishes (preferably a bonito, one of the tunas' sister group) at the same water temperature. Because this has not yet been accomplished, there has been no unequivocal test of the hypothesis that endothermy enhances sustainable swimming performance in tunas (see Sepulveda and Dickson, 2000). The present study, by measuring the effects of temperature on an ectothermic species that is closely related to the tunas, provides evidence that maintaining  $T_m \geq 6$  °C above the ambient water temperature may significantly increase

sustainable swimming speeds in tunas. The present study also suggests that the tunas would incur a higher  $COT_{net}$ .

However, there is an important difference between a tuna swimming in 18 °C water with its slow, oxidative locomotor muscle maintained at 24 °C and a mackerel at 24 °C. In the tuna, the heart temperature would be approximately 18 °C. Because heart rate decreases with decreasing temperature in tunas (Korsmeyer et al., 1997), cardiac output will be reduced, and perfusion of the slow, oxidative muscle fibers may also be reduced. If the rate of perfusion is not sufficient to maintain aerobic function within these muscle fibers at high contraction rates, the maximum sustainable swimming speed would be lower than that predicted on the basis of the elevated slow, oxidative muscle temperature. In fact, on the basis of swimming behavior in relation to water temperature, Brill et al. (1999) have hypothesized that the effects of temperature on cardiac function limit the thermal range of at least some tuna species. However, the higher heart mass, cardiac output, hemoglobin concentration and muscle myoglobin content of tunas compared with ectothermic scombrids and other active teleosts (for reviews, see Dickson, 1995, 1996; Brill and Bushnell, 2001) may allow the slow, oxidative locomotor muscle to maintain maximal function at its high temperature, despite being supplied by a cooler heart. Additional work is needed to understand fully how locomotor muscle physiology and cardiac function are integrated in tunas *in vivo*.

We thank J. Citanovich (captain of the R/V *Yellowfin*), G. Hunt, D. Smith and M. Hansen for helping to collect the fish used in this study, J. Hoskinson, D. Smith and M. Hansen for assistance in maintaining the fish in the laboratory, G. Hunt, T. Timpe and D. Parsons for the design and construction of the respirometer, Hexcel and Plascore, Inc. for donating supplies used in the respirometer, J. Degen for constructing the mirror used in videotaping, J. Hoskinson for assistance with videotaping and K. Messer for help with the statistical analyses. The paper was improved significantly by input from J. B. Graham, M. H. Horn, G. V. Lauder and K. Martin on the Masters theses on which the present study is based and by the comments of R. E. Shadwick and two anonymous reviewers on drafts of the manuscript. Funding was provided by CSUF intramural grants to K.A.D., student research grants from the CSUF Departmental Associations Council and Department of Biological Science, the NIH Minority Biomedical Research Support and Minority Scientist Development Programs (no. S06GM08258 and no. R25GM56820) and the National Science Foundation (no. IBN-9318065).

## 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.
- Anderson, E. J., McGillis, W. R. and Grosenbaugh, M. A. (2001). The boundary layer of swimming fish. *J. Exp. Biol.* **204**, 81–102.
- Beamish, F. W. H. (1990). Swimming metabolism and temperature in juvenile walleye, *Stizostedion vitreum vitreum*. *Environ. Biol. Fish.* **27**, 309–314.
- Block, B. A. (1991). Endothermy in fish: thermogenesis, ecology and evolution. In *Biochemistry and Molecular Biology of Fishes*, vol. 5 (ed. P. W. Hochachka and T. P. Mommsen), pp. 269–311. New York: Elsevier Science.
- 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. and Glass, N. R. (1973). Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Bd. Can.* **30**, 379–387.
- 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., 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. (2001). The cardiovascular system of tunas. In *Tunas: Physiology, Ecology and Evolution. Fish Physiology*, vol. 19 (ed. B. A. Block and E. D. Stevens), pp. 79–120. San Diego: Academic Press.
- Carey, F. G. and Lawson, K. D. (1973). Temperature regulation in free-swimming bluefin tuna. *Comp. Biochem. Physiol.* **44A**, 375–392.
- 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 mackerels and tunas. In *The Physiological Ecology of Tunas* (ed. G. D. Sharp and A. E. Dizon), pp. 7–39. New York: Academic Press.
- Collette, B. B. and Nauen, C. E. (1983). *Scombrids of the World*. F.A.O. Species Catalog, vol. 2. Rome: Food and Agricultural Organization of the United Nations. 137pp.
- 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. (1995). Unique adaptations of the metabolic biochemistry of tunas and billfishes for life in the pelagic environment. *Environ. 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.* **113A**, 39–49.
- 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.
- Freadman, M. A. (1979). Swimming energetics of striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*): gill ventilation and swimming metabolism. *J. Exp. Biol.* **83**, 217–230.
- Fuiman, L. A. and Batty, R. S. (1997). What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. *J. Exp. Biol.* **200**, 1745–1755.
- 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.
- He, Z.-H., Bottinelli, R., Pellegrino, M. A., Ferenczi, M. A. and Reggiani, C. (2000). ATP consumption and efficiency of human single muscle fibers with different myosin isoform composition. *Biophys. J.* **79**, 945–961.
- Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R. and Fournier, D. A. (1992). Physiological and behavioral thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358**, 110–112.
- Hunter, J. R. and Zweifel, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus* and other fishes. *Fish. Bull.* **69**, 253–266.
- Jayne, B. C. and Lauder, G. V. (1996). New data on axial locomotion in fishes: How speed affects diversity of kinematics and motor patterns. *Am. Zool.* **36**, 642–655.
- Johnson, T. P., Cullum, A. J. and Bennett, A. F. (1998). Partitioning the effects of temperature and kinematic viscosity on the C-start performance of adult fishes. *J. Exp. Biol.* **201**, 2045–2051.
- Johnston, I. A. and Brill, R. W. (1984). Thermal dependence of contractile properties of skinned muscle fibers from Antarctic and various warm water marine fishes including skipjack tuna (*Katsuwonus pelamis*) and kawakawa (*Euthynnus affinis*). *J. Comp. Physiol.* **155B**, 63–70.
- Jones, P. L. and Sidell, B. D. (1982). Metabolic responses of striped bass to temperature acclimation. II. Alterations in metabolic carbon sources and

- distributions of fiber types in locomotory muscle. *J. Exp. Zool.* **219**, 163–171.
- Kieffer, J. D., Alsop, D. and Wood, C. M.** (1998). A respirometric analysis of fuel use during aerobic swimming at different temperatures in rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **201**, 3123–3133.
- Korsmeyer, K. E., Lai, N. C., Shadwick, R. E. and Graham, J. B.** (1997). Heart rate and stroke volume contributions to cardiac output in swimming yellowfin: responses to exercise and temperature. *J. Exp. Biol.* **200**, 1975–1986.
- Long, J. H., Jr, McHenry, M. J. and Boetticher, N. C.** (1994). Undulatory swimming: how traveling waves are produced and modulated in sunfish (*Lepomis gibbosus*). *J. Exp. Biol.* **192**, 129–145.
- Long, J. H., Jr and Nipper, K. S.** (1996). Body stiffness in undulating vertebrates. *Am. Zool.* **36**, 678–694.
- Macy III, W. K., Durbin, A. G. and Durbin, E. G.** (1999). Metabolic rate in relation to temperature and swimming speed and the cost of filter feeding in Atlantic menhaden, *Brevoortia tyrannus*. *Fish. Bull.* **97**, 282–293.
- 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.
- Marcinek, D. J., Blackwell, S. B., Dewar, H., Freund, E. V., Farwell, C., Dau, D., Seitz, A. C. and Block, B. A.** (2001). Depth and muscle temperature of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. *Mar. Biol.* **138**, 869–885.
- McHenry, M. J., Pell, C. A. and Long, J. H.** (1995). Mechanical control of swimming speed: stiffness and axial wave form in undulating fish models. *J. Exp. Biol.* **198**, 2293–2305.
- Nauen, J. C. and Lauder, G. V.** (2000). Locomotion in scombrid fishes: morphology and kinematics of the finlets of the chub mackerel *Scomber japonicus*. *J. Exp. Biol.* **203**, 2247–2259.
- Packard, G. C. and Boardman, T. J.** (1999). The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? *Comp. Biochem. Physiol.* **122A**, 37–44.
- Rall, J. A. and Woledge, R. C.** (1990). Influence of temperature on mechanics and energetics of muscle contraction. *Am. J. Physiol.* **259**, R197–R203.
- 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.** (1990). The influence of temperature on muscle recruitment and function *in vivo*. *Am. J. Physiol.* **259**, R210–R222.
- 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.
- Rome, L. C., Choi, I., Lutz, G. and Sosnicki, A. A.** (1992). The influence of temperature on muscle function in fast swimming scup. I. Shortening velocity and muscle recruitment during swimming. *J. Exp. Biol.* **163**, 259–279.
- Rome, L. C., Funke, R. P. and Alexander, R. McN.** (1990). The influence of temperature on muscle velocity and sustained performance in swimming carp. *J. Exp. Biol.* **154**, 163–178.
- Rome, L. C., Loughna, P. T. and Goldspink, G.** (1984). Muscle fiber recruitment as a function of swim speed and muscle temperature in carp. *Am. J. Physiol.* **247**, R272–R279.
- Rome, L. C. and Sosnicki, A. A.** (1990). The influence of temperature on mechanics of red muscle in carp. *J. Physiol., Lond.* **427**, 151–169.
- Rome, L. C. and Swank, D.** (1992). The influence of temperature on power output of scup red muscle during cyclical length changes. *J. Exp. Biol.* **171**, 261–281.
- Rome, L. C. and Swank, D.** (2001). The influence of thermal acclimation on power production during swimming. I. *In vivo* stimulation and length change pattern of scup red muscle. *J. Exp. Biol.* **204**, 409–418.
- Rome, L. C., Swank, D. M. and Coughlin, D. J.** (2000). The influence of temperature on power production during swimming. II. Mechanics of red muscle fibres *in vivo*. *J. Exp. Biol.* **203**, 333–345.
- Schaefer, K. M.** (1980). Synopsis of biological data on the chub mackerel, *Scomber japonicus* Houttuyn, 1782, in the Pacific Ocean. In *Synopses of Biological Data on Eight Species of Scombrids* (ed. W. H. Bayliff). Inter-American Tropical Tuna Commission Special Report No. 2, pp. 395–445. La Jolla, California: Inter-American Tropical Tuna Commission.
- 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.
- Sepulveda, C. and Dickson, K. A.** (2000). Maximum sustainable speeds and cost of swimming in juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J. Exp. Biol.* **203**, 3089–3101.
- Shadwick, R. E. and Steffensen, J. F.** (2000). The cost and efficiency of aerobic locomotion in the chub mackerel (*Scomber japonicus*). *Am. Zool.* **40**, 2108.
- Shadwick, R. E., Steffensen, J. F., Katz, S. L. and Knower, T.** (1998). Muscle dynamics in fish during steady swimming. *Am. Zool.* **38**, 755–770.
- Sidell, B. D.** (1980). Responses of goldfish (*Carassius auratus* L.) muscle to acclimation temperature: alterations in biochemistry and proportions of different fiber types. *Physiol. Zool.* **53**, 98–107.
- Sidell, B. D. and Moerland, T. S.** (1989). Effects of temperature on muscular function and locomotory performance in teleost fish. *Adv. Comp. Environ. Physiol.* **5**, 116–152.
- Sisson III, J. E. and Sidell, B. D.** (1987). Effect of thermal acclimation on muscle fiber recruitment of swimming striped bass (*Morone saxatilis*). *Physiol. Zool.* **60**, 310–320.
- Smit, H., van den Berg, R. J. and Kijne-den Hartog, I.** (1974). Some experiments on thermal acclimation in goldfish (*Carassius auratus*). *Neth. J. Zool.* **24**, 32–49.
- Stevens, E. D.** (1979). The effect of temperature on tail beat frequency of fish swimming at constant velocity. *Can. J. Zool.* **57**, 1628–1635.
- Stevens, E. D., Kanwisher, J. W. and Carey, F. G.** (2000). Muscle temperature in free-swimming giant Atlantic bluefin tuna (*Thunnus thynnus* L.). *J. Therm. Biol.* **25**, 419–423.
- Swank, D. M. and Rome, L. C.** (2000). The influence of temperature on power production during swimming. I. *In vivo* length change and stimulation pattern. *J. Exp. Biol.* **203**, 321–331.
- Swank, D. M. and Rome, L. C.** (2001). The influence of thermal acclimation on power production during swimming. II. Mechanics of scup red muscle under *in vivo* conditions. *J. Exp. Biol.* **204**, 419–430.
- Swanson, C., Young, P. S. and Cech, J. J., Jr** (1998). Swimming performance of delta smelt: maximum performance and behavioral and kinematic limitations on swimming at submaximal velocities. *J. Exp. Biol.* **201**, 333–345.
- Taylor, S., Egginton, S. and Taylor, E.** (1996). Seasonal temperature acclimatization of rainbow trout: cardiovascular and morphometric influences on maximal sustainable exercise level. *J. Exp. Biol.* **199**, 835–845.
- Videler, J. J.** (1993). *Fish Swimming*. London: Chapman & Hall.
- 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.** (1998). Swimming. In *The Physiology of Fishes*, second edition (ed. D. Evans), pp. 1–24. Boca Raton, FL: CRC Press.