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Cardiorespiratory physiology and swimming energetics of a high-energy-demand teleost, the yellowtail kingfish (*Seriola lalandi*)

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Summary

This study utilizes a swimming respirometer to investigate the effects of exercise and temperature on cardiorespiratory function of an active teleost, the yellowtail kingfish (*Seriola lalandi*). The standard aerobic metabolic rate (SMR) of *S. lalandi* (mean body mass 2.1 kg) ranges from 1.55 mg min^{-1} kg^{-1} at 20°C to 3.31 mg min^{-1} kg^{-1} at 25°C. This 2.1-fold increase in SMR with temperature is associated with a 1.5-fold increase in heart rate from 77 to 117 beats min^{-1}, while cardiac stroke volume remains constant at 0.38 ml beat^{-1} kg^{-1} and the difference in oxygen content between arterial and mixed venous blood [($C\mathrm{a}_{\mathrm{O_2}}$–$C\bar{\mathrm{v}}_{\mathrm{O_2}}$)] increases marginally from 0.06 to 0.08 mg ml^{-1}. During maximal aerobic exercise (2.3 *BL* s^{-1}) at both temperatures, however, increases in cardiac output are limited to about 1.3-fold, and increases in oxygen consumption rates (up to 10.93 mg min^{-1} kg^{-1} at 20°C and 13.32 mg min^{-1} kg^{-1} at 25°C) are mediated primarily through augmentation of ($C\mathrm{a}_{\mathrm{O_2}}$–$C\bar{\mathrm{v}}_{\mathrm{O_2}}$) to 0.29 mg ml^{-1} at 20°C and 0.25 mg ml^{-1} at 25°C. It seems, therefore, that the heart of *S. lalandi* routinely works close to its maximum capacity at a given temperature, and changes in aerobic metabolism due to exercise are greatly reliant on high blood oxygen-carrying capacity and ($C\mathrm{a}_{\mathrm{O_2}}$–$C\bar{\mathrm{v}}_{\mathrm{O_2}}$). Gross aerobic cost of transport (GCOT) is 0.06 mg kg^{-1} *BL*$^{-1}$ at 20°C and 0.09 mg kg^{-1} *BL*$^{-1}$ at 25°C at the optimal swimming velocities (U_{opt}) of 1.2 *BL* s^{-1} and 1.7 *BL* s^{-1}, respectively. These values are comparable with those reported for salmon and tuna, implying that the interspecific diversity in locomotor mode (e.g. sub-carangiform, carangiform and thunniform) is not concomitant with similar diversity in swimming efficiency. A low GCOT is maintained as swimming velocity increases above U_{opt}, which may partly result from energy savings associated with the progressive transition from opercular ventilation to ram ventilation.

Key words: cardiac output, cardiac stroke volume, heart rate, aerobic metabolism, rate of oxygen consumption, teleost, temperature, tissue oxygen extraction.

Introduction

Metabolic studies of highly active teleost fishes are inherently difficult due to their pelagic life history and often large body mass (M_{b}). Nevertheless, progressive technological advances have permitted the study of several (usually juvenile) high performance species (Brett, 1965; Brett and Glass, 1973; Sepulveda and Dickson, 2000; Dickson et al., 2002; Lee, C. G. et al., 2003; Dabrowski et al., 2004), including the exceptionally active tunas (Dewar and Graham, 1994; Korsmeyer et al., 1997a; Korsmeyer et al., 1997b). Current data imply that high-energy-demand fish, particularly the tunas, have an enhanced standard aerobic metabolic rate (SMR) when compared with more sedentary species, presumably to support energetically expensive morphological and physiological adaptations and allow an increased aerobic metabolic scope (Brill and Bushnell, 1991; Korsmeyer and Dewar, 2001; Graham and Dickson, 2004).

While we are beginning to obtain a better understanding of the basic metabolic requirements of high-energy-demand teleosts, the necessity to instrument animals for circulatory measurements has resulted in a limited understanding of the cardiorespiratory adaptations that allow such an enhanced metabolic capacity. Aerobic metabolic rate, as indicated by the rate of oxygen consumption ($\dot{M}_{\mathrm{O_2}}$), may be enhanced at the circulatory level by augmentation of any of the variables contributing to the Fick equation:

$$\dot{M}_{\mathrm{O_2}} = \dot{V}_{\mathrm{b}} \times (C\mathrm{a}_{\mathrm{O_2}} - C\bar{\mathrm{v}}_{\mathrm{O_2}}) , \quad (1)$$

where $\dot{V}_{\mathrm{b}}$ is cardiac output [the product of heart rate (f_{H}) and cardiac stroke volume (V_{S})], and ($C\mathrm{a}_{\mathrm{O_2}}$–$C\bar{\mathrm{v}}_{\mathrm{O_2}}$) is the difference in oxygen content between arterial ($C\mathrm{a}_{\mathrm{O_2}}$) and mixed venous ($C\bar{\mathrm{v}}_{\mathrm{O_2}}$) blood (a measure of tissue oxygen extraction). The initial indication was that, unlike other vertebrates, teleost fish modulate $\dot{V}_{\mathrm{b}}$ primarily through changes in V_{S} rather than f_{H} (Stevens and Randall, 1967; Kiceniuk and Jones, 1977; Farrell and Jones, 1992), although

the reverse is true for some species, particularly those considered to be of high energy demand (Axelsson et al., 1992; Korsmeyer et al., 1997a; Altimiras and Larsen, 2000; Cooke et al., 2002; Graham and Dickson, 2004; Clark et al., 2005). Some high performance species possess an enhanced blood oxygen-carrying capacity owing to higher levels of haemoglobin, which acts to augment (Ca_{O_2}–$C\bar{v}_{O_2}$) such that extraordinary increases in $\dot{V}_b$ are not necessary to attain maximum levels of $\dot{M}_{O_2}$ (Brill and Bushnell, 2001; Graham and Dickson, 2004). Nevertheless, many teleosts utilize similar proportional increases in $\dot{V}_b$ and (Ca_{O_2}–$C\bar{v}_{O_2}$) to satisfy an increase in $\dot{M}_{O_2}$ with exercise (Brill and Bushnell, 1991; Bushnell and Jones, 1994; Korsmeyer et al., 1997b).

The genus *Seriola* (amberfishes, amberjacks, and yellowtails) has a circumglobal distribution and comprises several species of highly active predatory marine fish, which may exceed 2 m in length and M_b of around 80 kg (Gillanders et al., 2001; Poortenaar et al., 2001). Members of this genus utilize a carangiform swimming mode, are facultative ram-ventilators, and share many specialized morphological adaptations with the tunas, including a fusiform body shape to reduce drag, fin grooves to increase streamlining, a high-aspect-ratio tail with a narrow caudal peduncle, and finlets along the trailing edges of the body (Dewar and Graham, 1994). The limited cardiorespiratory data that exist for the *Seriola* genus have been obtained exclusively from studies on *S. quinqueradiata* (commonly referred to as 'yellowtail'), which is an inhabitant of the northwestern Pacific Ocean. This species has been reported to have a SMR greater than most other high performance fishes and approaching that of the tunas (Yamamoto et al., 1981; Korsmeyer and Dewar, 2001), although these data may have been affected by stress due to heavy instrumentation and confinement to a small static respirometer. Interestingly, the published resting f_H value of this species at 25°C is approximately 90 beats min^{-1} (Ishimatsu et al., 1990; Lee, K. S. et al., 2003a), which is quite high for a resting teleost, and may reflect a high maximum f_H considering that a twofold increase during exercise is not uncommon (Bushnell and Jones, 1994; Korsmeyer et al., 1997a; Altimiras and Larsen, 2000; Clark et al., 2005).

Given these previous findings for *Seriola*, it appears that members of this genus may have enhanced aerobic metabolic capacities and may prove to be useful models for the study of exercise physiology in high-energy-demand teleosts. The present study utilizes a temperate species, *S. lalandi* (commonly referred to as 'yellowtail kingfish'), to investigate cardiorespiratory function at rest and while exercising in a custom-built swimming respirometer. Several hypotheses relating to high-energy-demand teleosts are tested, specifically that *S. lalandi* has (1) an exceptionally high SMR, (2) an enhanced aerobic metabolic scope, (3) a substantial contribution from f_H to attain the required $\dot{M}_{O_2}$, and (4) a low cost of transport resulting from specialized adaptations presumed to increase swimming efficiency.

Materials and methods

Animals

Ten yellowtail kingfish *Seriola lalandi* (Valenciennes 1833) were studied between 10 November 2005 and 10 January 2006. Fish eggs were originally purchased from Clean Seas Aquaculture (Arno Bay, South Australia) in February 2004 and transported to the South Australian Research and Development Institute where they were hatched. The larvae were weaned in larval tanks, and eventually relocated to a 40 000 l holding tank where they were raised on commercial pellets (Skretting, Cambridge, Tasmania) to a body mass of approximately 2 kg. The holding tank was of ample volume and had a mild circular flow, which allowed the fish to form schools and cruise at their desired swimming velocities during this rearing period. At least 3 days prior to commencing experiments, the fish were moved to 1000 l indoor tanks at the same water temperature to which they were exposed outdoors (approximately 20°C), and on a 13 h:11 h light:dark cycle that resembled day length patterns for this time of year. Fish were fed once per day, but were fasted for at least 30 h prior to use in experiments, to eliminate the influence of specific dynamic action on the measurements. All experiments were conducted under project number S-024-2005 with the approval of the University of Adelaide Animal Ethics Committee.

Swimming respirometer

Measurements of $\dot{M}_{O_2}$ at different swimming velocities were performed in a constant temperature room using an upright Brett-type swimming respirometer (water volume 137 l), which was constructed at La Trobe University in Melbourne, Australia. The respirometer was constructed from Perspex™ tubing (250 mm internal diameter) and the fish was restricted to an 850 mm long transparent working section at the top. The entire respirometer sat within an aerated waterbath (length 1500 mm, width 300 mm, height 1200 mm; replaced with fresh seawater at 2 l min^{-1}), which provided thermal stability and a source of oxygenated water to flush the respirometer between measurements. Water velocity through the respirometer was regulated by a 245 mm diameter propeller, which was positioned at one end of the respirometer and connected *via* a stainless steel shaft to a computer-driven DC motor (Baldor, VPT 34550; interfaced with 0–10 V external Penta Drive Regenerative speed controller) mounted above the waterbath. Voltage to the motor was calibrated against water velocity through the center of the working section using a flow meter (model OSS-PC1, Hydrological Services, Australia), and the maximum attainable water velocity was 1.22 m s^{-1}. A submersible pump with a one-way valve, positioned at the bottom of the respirometer, provided the only interface between the water in the respirometer and that in the waterbath, and computer control of the submersible pump (using a voltage output from PowerLab; see below) allowed the respirometer to be automatically flushed and sealed continuously at predefined intervals. The volume of water pumped into the respirometer by the submersible pump was released through a pipe at the top of the respirometer that extended above the water line of the

waterbath. Water temperature and oxygen saturation in the respirometer were continuously monitored using a calibrated sensor (sc100 LDO, Hach, USA), and outputs from this, and a measure of the voltage supplied to the propeller motor and submersible flushing pump, were collected at 100 Hz (PowerLab/4SP and Chart software, ADInstruments, Sydney, Australia).

Instrumentation

Ventilation rate

Concurrently with measuring $\dot{M}_{O_2}$, it was of interest to determine how opercular ventilation rate (f_G) changed with swimming speed in this facultative ram-ventilating species. Therefore, before being introduced into the respirometer, each fish (N=6; M_b ± s.e.m.=1.90±0.12 kg; length=543±8 mm) underwent the following procedure in order to measure the electromyographic (EMG) signal produced from the opercular muscles. A fish was caught by dip net and placed in a tub (length 1500 mm, width 700 mm, height 700 mm) containing 100 l seawater and 1 ml l^{-1} of anaesthetic (2-phenoxyethanol, Ace Chemicals, Camden Park, SA, Australia) at 20°C. When ventilation became shallow and the fish lost responsiveness to touch (~10 min), it was weighed, measured and positioned between two foam pads on an operating bench. Ventilation of the gills with aerated seawater and a lower dose of anaesthetic (0.75 ml l^{-1}) was continued throughout the procedure by way of a recirculation system and a hose positioned in the mouth of the fish.

Approximately 10 mm of insulation was stripped from the ends of two 1 m lengths of otherwise insulated stainless steel electrode wire (diameter 0.25 mm). These ends were threaded through 18 G hypodermic needles that had been positioned subcutaneously approximately 400 mm apart along the ventral midline between the two gills. The needles were then removed along the length of the wire, which left the two wire electrodes in place. Each length of electrode wire was sutured to the skin at the point of insertion, led up opposite sides of the body and secured beside the first dorsal fin. This procedure took a maximum of 7 min.

The fish was then placed in the respirometer at 20°C at a slow water velocity (0.3–0.7 BL s^{-1}). Assisted ventilation with aerated seawater was continued until the fish displayed strong opercular movements and began to right itself. The loose ends of the wire electrodes were passed through a small tube at the top of the respirometer that extended above the waterline of the waterbath. The EMG signal was amplified (BioAmp, ADInstruments, Sydney, Australia) and recorded using the PowerLab. Following swimming trials, wire electrodes were removed and the fish released into the holding tank.

Cardiac output

Four different fish (M_b=2.35±0.31 kg; length=569±26 mm), but from the same cohort as those detailed above, were available to measure cardiac output using ventral aortic flow cuffs. Fish were anaesthetized as described above. One operculum and underlying gills were held back with a piece of soft plastic, and the ventral aorta was exposed through a 10 mm incision made on the lateral wall of the isthmus at the ventral base of the first and second gill arches. The ventral aorta was freed of surrounding connective tissue and a silastic Doppler flow cuff (20 MHz, internal diameter 4–5 mm, Indus Industries, Baylor College of Medicine, Houston, TX, USA) secured around the blood vessel. The incision was closed with sutures and the leads from the cuff secured to the skin on the fringe of the opercular cavity, again near the lateral midline, and finally beside the first dorsal fin. The whole procedure was completed within 30–45 min. The fish was then placed in the respirometer at 20°C, where it received the same treatment as detailed above. The leads from the flow cuff were passed through the small tube at the top of the respirometer, connected to an Ultrasonic Flow/Dimension System (Indus Industries) and the signal collected at 100 Hz.

Following swimming trials, fish were euthanised with an overdose of anaesthetic and the flow cuff was calibrated *in situ*. An 18 G hypodermic needle was inserted into the bulbus arteriosus posterior to the flow cuff and blood was collected in a flask. Another needle was inserted into the ventral aorta just anterior to the flow cuff, then blood was circulated through the needles in an anterior direction at known flow rates using a peristaltic pump (IsmaTec SA, Glattbrugg, Switzerland). The outlet tube connected to the needle in the ventral aorta was raised by 300 mm such that the blood vessel had a back pressure of ~3 kPa. Individual calibration equations (mean r^2=0.84) were then applied to the data set for that individual, and cardiac output was calculated as ml min^{-1} kg^{-1}. Finally, the heart was excised, then the ventricle was detached, rinsed with saline, and weighed in relation to total body mass.

Swimming protocol

Resting values for each individual at 20±0.5°C were obtained only following at least 24 h of recovery in the respirometer, when all measured variables had stabilized. Rates of oxygen consumption were repeatedly measured as the fish was exposed to incremental changes in water velocity. Some fish instrumented with EMG electrodes were incremented beyond their maximum sustainable swimming velocity (characterized by vigorous burst episodes and subsequent resting against the grid at the posterior end of the respirometer; typically $\geqslant$2.3 BL s^{-1}), whereas fish instrumented with flow cuffs were exposed only to sustainable velocities so as to minimize the risk of damage to the ventral aorta. Each $\dot{M}_{O_2}$ measurement was performed over a 10 min period so that oxygen saturation in the respirometer never fell below 75%, and the respirometer was flushed for 20 min between each measurement with oxygenated water from the waterbath. Fish were maintained at each swimming velocity for at least 60 min (i.e. two measurement cycles) to ensure that all variables had reached a steady state (this excludes speeds greater than 2.3 BL s^{-1} where fish were unable to maintain position for more than ~10 min). Swimming speed was corrected for the solid blocking effect of each individual using the method described elsewhere (Jones et al., 1974), which increased swimming

speed measurements by 10–24%. Several fish struggled immediately when water velocity was increased above that used to obtain resting values (i.e. 0.3–0.7 $BL\ s^{-1}$). In such circumstances, water velocity was rapidly increased to a high, yet sustainable level, to encourage a greater level of exercise, and fish were maintained at this velocity until $\dot{M}_{O_2}$ plateaued. Some individuals swam at intermediate speeds in later attempts (after a sufficient recovery period), but the number of steady state data points able to be obtained from each individual (minimum 3 velocities, maximum 6 velocities) was reliant upon how well they adjusted to swimming in the respirometer (sample sizes are indicated in tables and figures).

Water heating equipment became available towards the end of this study. Thus, to examine the effect of temperature on cardiorespiratory function, two of the fish that had been instrumented with a flow cuff were maintained at 0.3–0.7 $BL\ s^{-1}$ in the respirometer after the 20°C swimming protocol while the water was heated from 20°C to 25±0.5°C (taking approximately 3 h). Fish were given at least 2 h to acclimate to the new temperature (also to ensure complete recovery from the previous swim at 20°C), and then the same swimming protocol was performed as outlined above.

Data analysis and statistics

Rates of oxygen consumption (given as mass-specific values and at STPD) were calculated using the rate of decline in oxygen saturation in the respirometer over the final 7 min of each 10 min measurement. Calculations took account of the effect of temperature on the oxygen capacitance of the water (Dejours, 1975). The respirometer was regularly sealed without containing a fish, to determine background respiration rates and subsequently correct $\dot{M}_{O_2}$ measurements of the fish, although the reduction in oxygen saturation during these trials was in all cases negligible.

Tissue oxygen extraction was calculated by rearrangement of Eqn 1, such that $\dot{M}_{O_2}$(mg min^{-1} kg^{-1})/$\dot{V}_b$(ml^{-1} min^{-1} kg^{-1})=(Ca_{O_2}–$C\bar{v}_{O_2}$)(mg ml^{-1}). Heart rate was obtained by triggering a rate-meter linked with the output from the flow cuff, and cardiac stroke volume was calculated by dividing $\dot{V}_b$ by f_H. Gross aerobic cost of transport (GCOT) was calculated by dividing each $\dot{M}_{O_2}$ value by the swimming velocity (U) at which the measurement was obtained, and net aerobic cost of transport (NCOT) was calculated from ($\dot{M}_{O_2}$–SMR)/U.

Least-squares regressions were used where appropriate, and comparisons of slopes and elevations were performed using analysis of covariance (ANCOVA). Significance was considered at $P<0.05$. Data are presented as mean ± standard error of the mean (s.e.m.). Minimum and maximum values are denoted by the subscripts min and max, respectively. N=number of animals, n=number of data points.

Critique of methods

The automated method of controlling the respirometer and collecting data allowed for long periods of steady state swimming from undisturbed fish. Thus, although the sample size was low (N=2) for fish at 25°C, we believe that the data obtained are representative of the species in general. In support of this, the 25°C data displayed solid trends that were consistent with those obtained from fish at 20°C (Fig. 1), and these data compare favourably to values obtained from the closely related *S. quinqueradiata* at the same temperature (see Discussion). Although it was not determined if fish at 25°C were capable of sustained swimming at velocities in excess of 2.3 $BL\ s^{-1}$, similar swimming characteristics (e.g. occasional burst-and-glide episodes) were displayed by all fish around this speed, irrespective of temperature, and we believe that the acute temperature change utilized in this study has a negligible influence on maximum sustainable swimming velocity.

Results

Recovery from surgery

Following introduction to the respirometer after implantation of either EMG electrodes or a blood flow cuff, $\dot{M}_{O_2}$ values remained elevated and unstable for approximately 15 h and 19 h, respectively, before a resting plateau was reached and statistically similar values were obtained between the two groups ($P>0.4$). Nevertheless, data from all animals were included for analysis only following at least 24 h of recovery and acclimation to the respirometer.

Zero swimming velocity

Two individuals instrumented with EMG electrodes at 20°C opted to rest on the bottom of the respirometer when exposed to a slow water velocity (0.42 $BL\ s^{-1}$ on both occasions), rather than gently swimming against the water flow as did all other individuals. Consequently, the resting $\dot{M}_{O_2}$ data points from these two animals can be included in the regression as zero swimming velocity at 20°C, thus alleviating the need to extrapolate this regression to the vertical axis, as was the case with all other variables at both temperatures (Fig. 1, Table 1). It should be noted that these two individuals were in perfect health and swam just as well as all other fish when water velocity was increased.

The rate of oxygen consumption at 0 $BL\ s^{-1}$ (i.e. SMR) increased 2.1-fold (Q_{10}=4.5) from 1.55 mg min^{-1} kg^{-1} at 20°C to 3.31 mg min^{-1} kg^{-1} at 25°C (Fig. 1A, Table 2). The increase in $\dot{M}_{O_2}$ with temperature was mediated primarily through a significant 1.5-fold increase in $\dot{V}_b$ ($P<0.01$), which itself was governed solely by an increase in f_H while V_S remained statistically unchanged. The blood convection requirement ($\dot{V}_b/\dot{M}_{O_2}$) decreased with an increase in temperature and, correspondingly, (Ca_{O_2}–$C\bar{v}_{O_2}$) increased by a similar proportion (Fig. 1, Table 2). Opercular ventilation rate (f_G) at 20°C was 72.2±3.8 strokes min^{-1} at 0 $BL\ s^{-1}$ (Fig. 2B).

Effects of exercise

At 20°C, $\dot{M}_{O_2}$ increased exponentially with swimming velocity up to approximately 2.3 $BL\ s^{-1}$, after which $\dot{M}_{O_2}$ plateaued ($\dot{M}_{O_2max}$) and swimming often became more erratic and interspersed with burst episodes. For this reason, it was considered hazardous to expose fish instrumented with flow

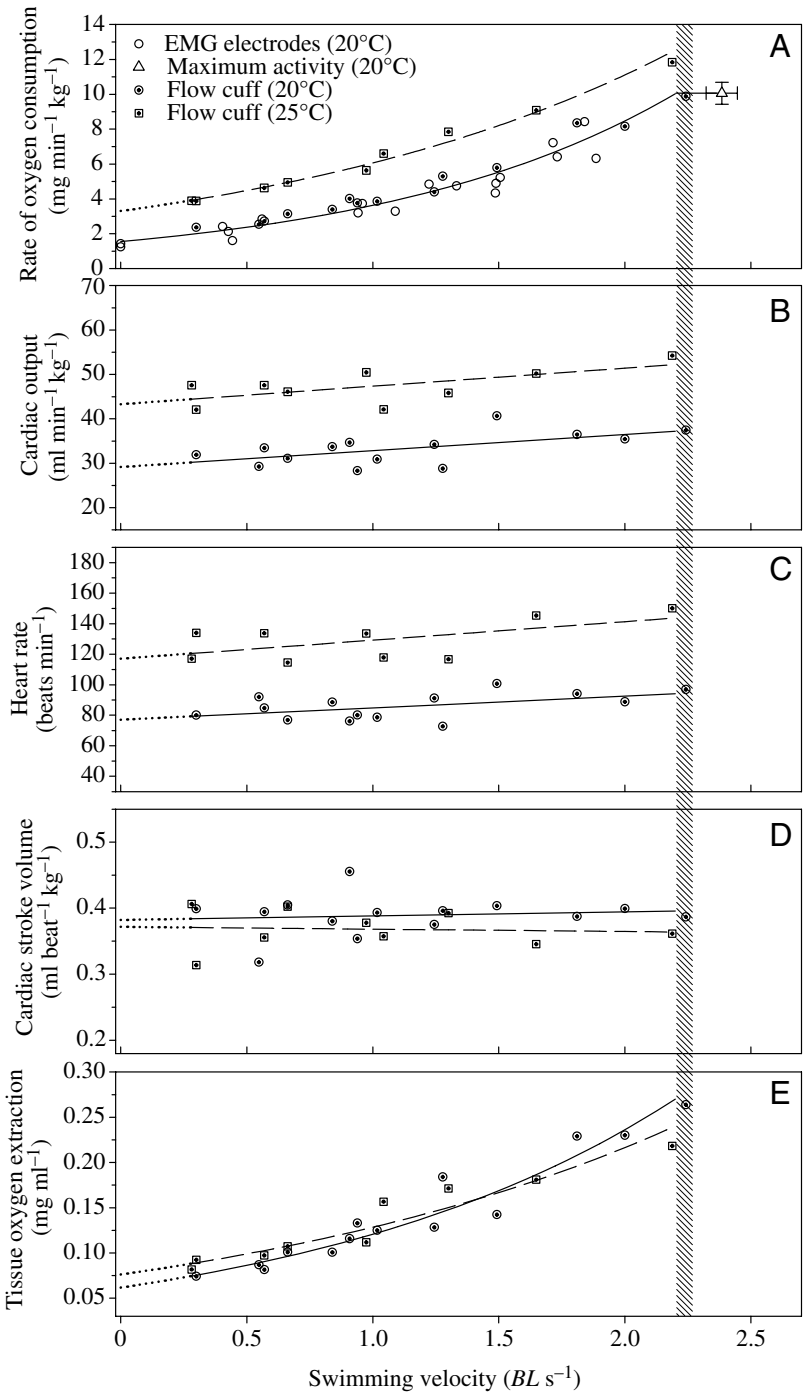

Fig. 1. (A) Rate of oxygen consumption ($\dot{M}_{O_2}$), (B) cardiac output ($\dot{V}_b$), (C) heart rate (f_H), (D) cardiac stroke volume (V_S), and (E) tissue oxygen extraction [(Ca_{O_2}–$C\bar{v}_{O_2}$)] as a function of swimming velocity for *Seriola lalandi*. The triangle, circles and bold regression lines represent animals at 20°C [(A) N=10; (B–E) N=4], while squares and broken regression lines represent animals at 25°C (N=2). Open symbols are from animals instrumented with EMG electrodes, whereas symbols containing crosses are from animals instrumented with a blood flow cuff. The hatched vertical line represents the approximate maximum sustainable swimming velocity (U_{max}), about 2.3 BL s^{-1}. Given the lack of steady state swimming at speeds greater than 2.3 BL s^{-1}, $\dot{M}_{O_2}$ data from four animals that swam for short periods at velocities in excess of this value were pooled and are presented in A as mean ± s.e.m. (open triangle). Dotted lines are extrapolations of regression lines to the vertical axis. Regression equations are given in Table 1.

cuffs to swimming velocities greater than 2.3 BL s^{-1}, so data at speeds above this are exclusively from animals instrumented with EMG electrodes at 20°C (Fig. 1A). Fish at 25°C displayed a similar exponential pattern of increasing $\dot{M}_{O_2}$ with swimming velocity; however, this was elevated in comparison with fish at 20°C (P<0.01). Although it was not determined if fish at 25°C were capable of sustained swimming at velocities in excess of 2.3 BL s^{-1}, behavioural observations indicated that this was unlikely and, consequently, the maximum sustainable swimming velocity (U_{max}) is considered herein to be 2.3 BL s^{-1} at both temperatures.

The absolute aerobic scope ($\dot{M}_{O2max}$–SMR) remained essentially unchanged across temperature at approximately 9.5 mg min^{-1} kg^{-1}, hence the factorial aerobic scope ($\dot{M}_{O2max}$/SMR) decreased substantially from 7.0 at 20°C to 4.0 at 25°C (Table 2). At both temperatures, a slight (~1.3-fold) linear increase in f_H was solely responsible for the linear rise in $\dot{V}_b$ with exercise, although this increase was insufficient (as indicated by a large drop in $\dot{V}_b/\dot{M}_{O_2}$), and a substantial exponential increase in (Ca_{O_2}–$C\bar{v}_{O_2}$) (up 4.7-fold at 20°C, up 3.3-fold at 25°C) was necessary to obtain the required level of $\dot{M}_{O_2}$ (Fig. 1, Table 2). A multiple linear regression analysis

Table 1. *Regression equations describing the relationship between measured cardiorespiratory variables and swimming velocity (U)*

y	Temperature (°C)	N	n	a	b	LL_a	UL_a	S_b	r^2	P
Exponential regressions										
$\dot{M}_{O_2}$ (mg min^{-1} kg^{-1})	20*	10	32	1.55	0.85	1.48	1.63	0.04	0.94	<0.01
	25	2	9	3.31	0.61	3.21	3.42	0.03	0.99	<0.01
(Ca_{O_2}–$C\bar{v}_{O_2}$) (mg ml^{-1})	20	4	14	0.06	0.67	0.06	0.07	0.05	0.93	<0.01
	25	2	9	0.08	0.52	0.07	0.08	0.06	0.92	<0.01

y	Temperature (°C)	N	n	a	b	S_a	S_b	S_{YX}	r^2	P
Linear regressions										
$\dot{V}_b$ (ml min^{-1} kg^{-1})	20	4	14	29.17	3.67	1.78	1.41	2.94	0.36	0.02
	25	2	9	43.31	4.07	2.06	1.77	3.19	0.43	0.05
f_H (beats min^{-1})	20	4	14	77.06	7.76	4.61	3.66	7.64	0.27	0.05
	25	2	9	117.14	12.14	7.45	6.41	11.52	0.34	0.10
V_S (ml beat^{-1} kg^{-1})	20	4	14	0.38	0.01	0.02	0.02	0.03	0.01	0.69
	25	2	9	0.37	0.00	0.02	0.02	0.03	0.01	0.84

Relationships were determined over a velocity range of approximately 0.3–2.3 *BL* s^{-1}; * velocity range 0–2.3 *BL* s^{-1}.

Exponential regression equations expressed as $y=ae^{bU}$; linear regression equations expressed as $y=a+bU$. S_a=s.e.m. of a; S_b=s.e.m. of b; S_{YX}=s.e.m. of estimate; error intervals for a in exponential equations were asymmetric, thus lower limits (LL) and upper limits (UL) are given. P values were determined by ANOVA.

revealed that (Ca_{O_2}–$C\bar{v}_{O_2}$) accounted for 79% of the variability in $\dot{M}_{O_2}$ (r^2=0.79). The addition of f_H (r^2=0.98) and V_S (r^2=0.99) strengthened the relationship, while the addition of water temperature had no effect. Opercular ventilation rate at 20°C increased linearly with water speed until it reached 88.5 strokes min^{-1} at approximately 1 *BL* s^{-1}, after which the rate and amplitude of the opercular stroke declined rapidly as the fish became progressively more reliant on ram ventilation (Fig. 2B).

Aerobic cost of transport

The gross aerobic cost of transport (GCOT) was always higher at 25°C, but at both temperatures changed in a somewhat shallow U-shaped relationship with swimming velocity (Fig. 2D). Nevertheless, minimum values of GCOT ($GCOT_{min}$) occurred at the optimal swimming velocities (U_{opt}) of 1.2 *BL* s^{-1} at 20°C and 1.7 *BL* s^{-1} at 25°C. Interestingly, $GCOT_{min}$ was at the point when f_G was at approximately 50% of its maximum attainable value, and it could be suggested that the energy saved from the transition from one method of ventilation to the other is at least partially causal to the plateaued relationship displayed between GCOT and swimming velocity above U_{opt}. Some of the variation in GCOT with temperature is likely attributable to the effect of temperature on SMR, although, even when accounting for SMR by calculating the net aerobic cost of transport (NCOT),

Table 2. *Cardiorespiratory variables of S. lalandi at zero and maximum swimming velocities*

	U (*BL* s^{-1})					
	20°C			25°C		
Variable	0	2.3	Factorial change	0	2.3	Factorial change
$\dot{M}_{O_2}$ (mg min^{-1} kg^{-1})	1.55	10.93	7.0	3.31*	13.32*	4.0
$\dot{V}_b$ (ml min^{-1} kg^{-1})	29.2	37.6	1.3	43.3*	52.7*	1.2
f_H (beats min^{-1})	77.1	94.9	1.2	117.1*	145.1*	1.2
V_S (ml beat^{-1} kg^{-1})	0.38	0.40	1.0	0.37	0.36	1.0
(Ca_{O_2}–$C\bar{v}_{O_2}$) (mg ml^{-1})	0.06	0.29	4.7	0.08	0.25	3.3
$\dot{V}_b/\dot{M}_{O_2}$ (ml mg^{-1})	18.8	3.4	–5.5	13.1*	4.0	–3.3

Maximum swimming velocity (U_{max})=2.3 *BL* s^{-1}.

Values calculated from regression equations in Table 1; for N and error values, see Table 1. U_{max} was taken to be 2.3 *BL* s^{-1} at both temperatures (see text). *Significantly different from the corresponding measurement at 20°C (P<0.05).

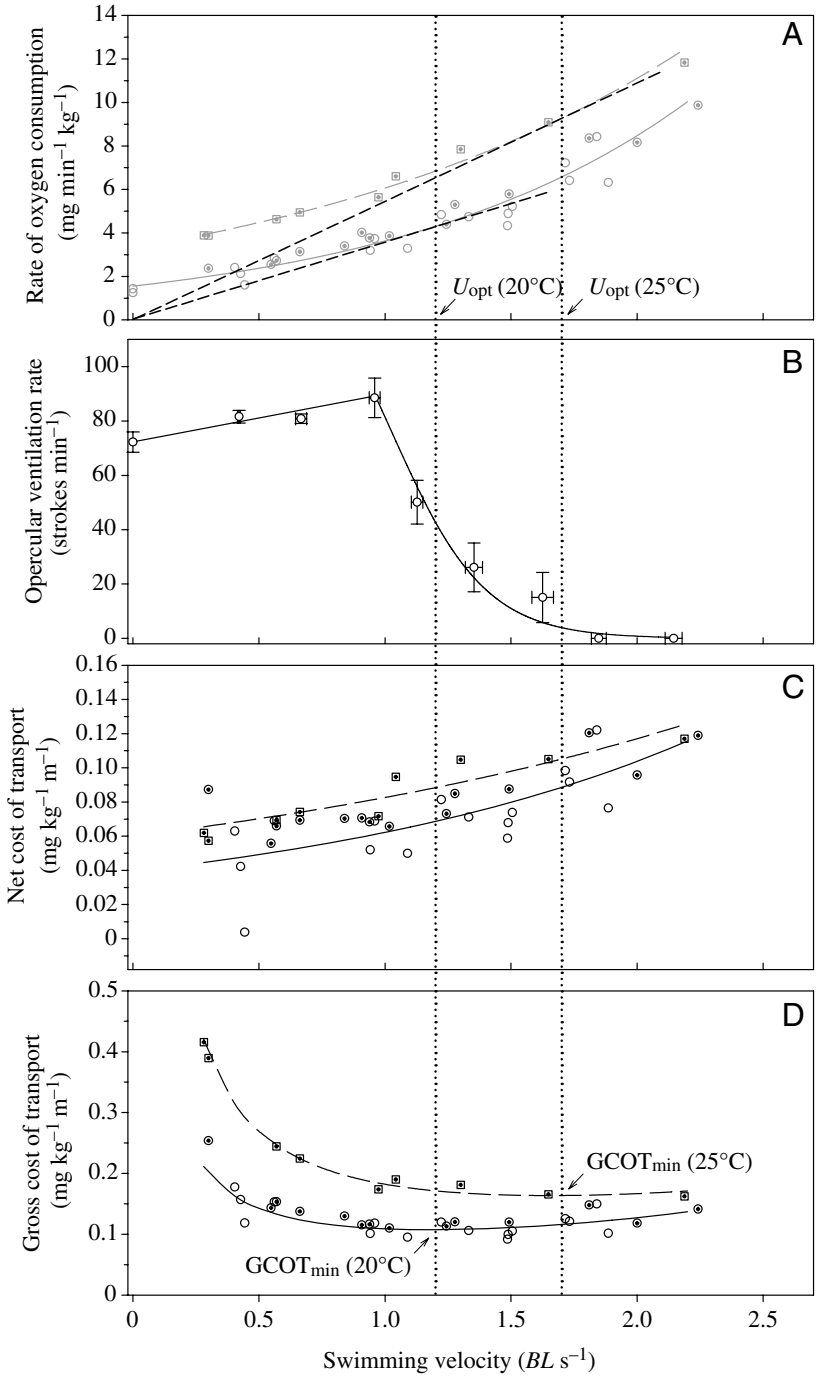

Fig. 2. Relationship of (A) rate of oxygen consumption ($\dot{M}_{O_2}$), (B) opercular ventilation rate (f_G), (C) net aerobic cost of transport (NCOT), and (D) gross aerobic cost of transport (GCOT) as a function of swimming velocity (up to 2.3 BL s^{-1}) for *Seriola lalandi* at 20°C and 25°C (symbols as in Fig. 1). In A, the slopes at the tangent to the curves from the origin (bold broken lines) are equal to the optimum swimming velocity (U_{opt}), which occurs where GCOT is at a minimum (GCOT$_{min}$) (illustrated by vertical dotted lines). In B, data have been binned into increments of 0.25 BL s^{-1} and symbols represent means ± s.e.m. (N=6, n=45).

the efficiency of swimming was still greater at the cooler temperature (Fig. 2C).

Discussion

Many physiological parameters of high performance fish are not well defined due to the logistical constraints in working with them, so a great deal is still to be learnt of the adaptive mechanisms that allow these species to exploit the open oceans. The present study exposed *S. lalandi* to changes in swimming velocity and temperature in order to investigate several generalizations relating to the cardiorespiratory physiology of high-energy-demand teleosts. It was hypothesized that *S. lalandi* would have a high SMR, an enhanced aerobic metabolic scope mediated largely through increases in f_H, and a low cost of transport resulting from morphological adaptations to reduce hydrodynamic resistance.

Standard metabolic rate

Standard metabolic rate is defined as the resting and fasting metabolism at a given temperature and is theoretically the minimum sustainable metabolic rate (Dejours, 1975;

Korsmeyer and Dewar, 2001). Measurements of SMR in active species of fish are often difficult, if not impossible, because many fish maintain a routine swimming velocity. Nevertheless, several studies have estimated SMR of high-energy-demand species using fish immobilised by neuromuscular or spinal block, or by extrapolating $\dot{M}_{O_2}$ and swimming velocity relationships to zero swimming speed (Brill, 1987; Graham et al., 1989; Dewar and Graham, 1994; Clark et al., 2005). The present study lends support to the latter method in that the regression used to predict SMR at 20°C gives a value only 6% different when including or excluding the two data points obtained at zero swimming velocity (Fig. 1A).

The mass-specific SMR of *S. lalandi* at 20°C (1.55 mg min^{-1} kg^{-1}) is lower than that reported previously for the closely related *S. quinqueradiata* at a similar temperature (2.45 mg min^{-1} kg^{-1}) (Yamamoto et al., 1981). It seems, however, that SMR of the *Seriola* genus is somewhat enhanced in comparison with that of many other active species, and it thus approaches values reported for tunas (Fig. 3A). Interestingly, if data from all species are standardised to 25°C assuming a Q_{10} of 2.5, the difference between SMR of tunas and other active teleosts becomes much less evident with increasing M_b (Fig. 3B). Nevertheless, given that members of the *Seriola* genus share many adaptations with the tunas, but presumably lack the same thermoregulatory capacity (Dewar et al., 1994), these data provide further evidence that fishes can have a high SMR without the elevated tissue temperatures associated with regional endothermy (Korsmeyer and Dewar, 2001; Sepulveda et al., 2003).

The temperature sensitivity of SMR determined for *S. lalandi* between 20°C and 25°C (Q_{10}=4.5) is greater than typically documented for biological rate processes (Q_{10}=2–3) (Schmidt-Nielsen, 1990), although similar findings have been reported [Q_{10}=6.8 for SMR in the bat ray *Myliobatus californica*, following an acute temperature change (Hopkins and Cech, 1994)]. It is plausible that the acute nature of the temperature change used in the present study was causal to the large temperature sensitivity, thus a longer period of acclimation to 25°C may have resulted in a depression in SMR (O'Steen and Bennett, 2003; MacNutt et al., 2004). Nevertheless, the time course used here (from 20°C to 25°C in ~3 h) was chosen to simulate ecologically relevant changes in temperature that may be experienced during relatively rapid horizontal or vertical migrations, and the enhanced temperature sensitivity of SMR may be of functional significance in such circumstances.

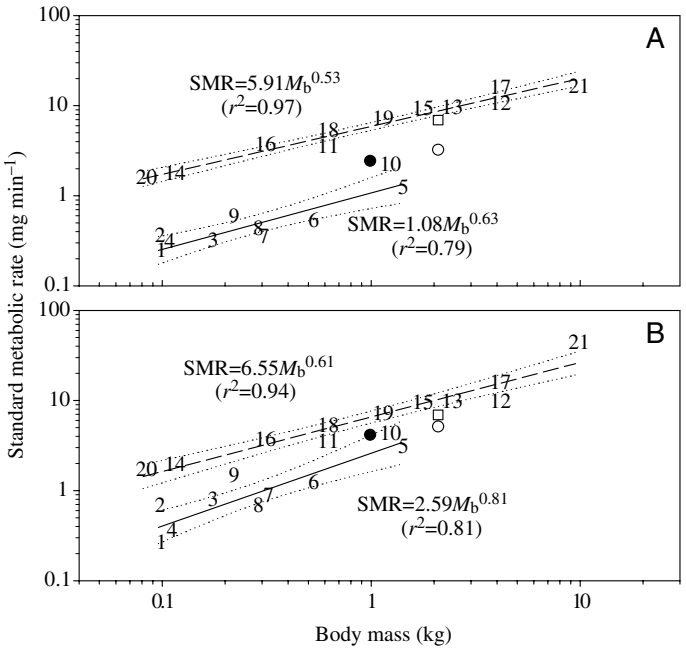

Fig. 3. Interspecific comparison for teleosts of standard metabolic rate (SMR) *versus* body mass (M_b) at (A) the temperature at which the measurement was made, and (B) 25°C (corrected using Q_{10}=2.5). Numbers 1–10 and bold regression lines represent non-tuna species considered to be of high performance; numbers 11–21 and broken regression lines represent species of tuna (dotted lines indicate 95% confidence intervals for each regression). 1–3, mackerel *Scomer japonicus* measured at [1]24°C (Sepulveda and Dickson, 2000), [2]18°C (Dickson et al., 2002) and [3]15°C (Shadwick and Steffensen, 2000); 4–5, salmon *Oncorhynchus nerka* measured at [4]24°C (Brett and Glass, 1973) and [5]15°C (Brett, 1965); 6–7, rainbow trout *Oncorhynchus mykiss* measured at [6–7]15°C (Bushnell et al., 1984; Brill, 1987); 8, menhaden *Brevoortia tyrannus* measured at 20°C (Macy et al., 1999); 9, bluefish *Pomatomus saltatrix* measured at 15°C (Freadman, 1979); 10, bonito *Sarda chiliensis* measured at 18°C (Sepulveda et al., 2003); 11–14, yellowfin *Thunnus albacares* measured at [11–13]25°C (Brill, 1987; Dewar and Graham, 1994) and [14]24°C (Sepulveda and Dickson, 2000); 15–17, skipjack *Katsuwonus pelamis* measured at [15–17]25°C (Brill, 1979; Dewar and Graham, 1994); 18–20, kawakawa *Euthynnus affinis* measured at [18–19]25°C (Brill, 1987) and [20]24°C (Sepulveda and Dickson, 2000); 21, albacore *Thunnus alalunga* measured at 15°C (Graham et al., 1989). Closed circle represents *Seriola quinqueradiata* measured at 19°C (Yamamoto et al., 1981), and open symbols represent data for *Seriola lalandi* from the present study measured at 20°C (open circle) and 25°C (open square). For comparative purposes, data for species of *Seriola* were not included in formulating the regressions.

Aerobic metabolic scope

It has been widely theorised that the high SMR for pelagic species of fish supports the biochemical and anatomical framework, enabling heightened rate processes and expansion of their aerobic metabolic scope (Dewar and Graham, 1994). Maximum values of $\dot{M}_{O_2}$ determined for *S. lalandi* (Fig. 1; Table 2) are in the upper range of other active fish such as salmon (typically <14 mg min^{-1} kg^{-1}) (Brett, 1965; Lee, C. G. et al., 2003), yet they are well below the $\dot{M}_{O_2max}$ predicted for tunas [27–45 mg min^{-1} kg^{-1} (Brill and Bushnell, 1991; Brill and Bushnell, 2001)]. The absolute aerobic scope of *S. lalandi* remained at approximately 9.5 mg min^{-1} kg^{-1} across the temperature range and, subsequently, the factorial aerobic scope decreased 1.8-fold with increasing temperature (Table 2). This contrasts with several other species of teleosts, for which an increase in temperature is associated with an

increase in the absolute aerobic scope (Webber et al., 1998; Claireaux et al., 2000; Clark et al., 2005). It is possible that *S. lalandi* has a bell-shaped relationship between absolute aerobic scope and water temperature, such as that reported for species of salmon and trout (Dickson and Kramer, 1971; Brett and Glass, 1973; Taylor et al., 1996; Farrell, 2002; Lee, C. G. et al., 2003), yet this may only be determined with further experimentation at multiple temperatures. Nevertheless, the data presented for *S. lalandi* indicate that SMR comprises a smaller proportion of the absolute aerobic scope when the fish is at 20°C as opposed to 25°C, such that a greater fraction of the metabolic scope is available for other aerobic processes (e.g. swimming, digesting) when at the cooler temperature. This may prove beneficial during vertical migrations into deeper, cooler water, such as may occur when diving to obtain prey.

Circulatory contributions to $\dot{M}_{O_2}$

In teleost fish, the ventricle is composed either entirely of spongy (also referred to as trabecular) myocardium or, generally in the case of high performance species, of an inner spongy myocardium surrounded by an outer compact myocardium (Santer and Greer Walker, 1980; Farrell and Jones, 1992). It may be suggested that the outer compact myocardium acts to reduce compliance of the heart such that high-energy-demand fish have a limited ability to modulate V_S. In agreement with this, the temperature-related increase in SMR of *S. lalandi* was modulated primarily by an increase in f_H, while V_S and (Ca_{O_2}–$C\bar{v}_{O_2}$) remained essentially unchanged (Fig. 1; Table 2). In comparison with other active teleosts, $\dot{V}_b$ at zero swimming velocity was within the typically reported range, yet this was the product of a high f_H and a relatively small V_S (Table 3). The majority of the cardiorespiratory variables determined for *S. lalandi* at zero swimming velocity are within the ranges reported for the only other studied *Seriola* species, *S. quinqueradiata* (Table 3). A notable exception is that f_H of *S. lalandi* at 25°C is somewhat higher than documented values for *S. quinqueradiata* at this temperature, and this is possibly due to the fact that *S. quinqueradiata* inhabits more tropical waters and in all studies was acclimated to the experimental temperature for at least 3 days prior to measurements.

In contrast to the primary use of f_H to attain the increase in SMR with temperature, the increase in $\dot{M}_{O_2}$ during exercise was modulated primarily through an increase in (Ca_{O_2}–$C\bar{v}_{O_2}$), while f_H increased only moderately and V_S remained unchanged (Fig. 1). Thus, obtaining extremely high values of $\dot{M}_{O_2max}$, such as those seen in tuna, may be dependent upon a similar (Ca_{O_2}–$C\bar{v}_{O_2}$) to *S. lalandi*, but with an increased ability to raise f_H during exercise. Although the negligible scope in V_S would categorise *S. lalandi* as a cardiac frequency modulator, a limited capacity for increasing $\dot{V}_b$, in comparison with several other active species (e.g. Gallaugher et al., 2001; Beaumont et al., 2003; Blank et al., 2004), implies that highly regulated blood flows are of secondary importance to an enhanced blood oxygen-carrying capacity and tissue oxygen extraction. In support of this, *S. quinqueradiata* has haematocrit and haemoglobin concentrations comparable with those of the tunas

Table 3. *Comparison of variables for Seriola with those of the most extensively studied active teleost, rainbow trout, and the exceptionally high performance teleosts, the tunas*

Variable	*Seriola*[a]				Rainbow trout	Tunas
Activity level	Rest		Rest		Rest	Routine
Temperature (°C)	~20	(20)	25	(25)	10–15	25
Body mass (kg)	1.0–1.4	(~2.0)	~1.0	(1.9)	0.4–1.5	~1.0–2.0
$\dot{M}_{O_2}$ (mg min^{-1} kg^{-1})	2.5	(1.6)	–	(3.3)	0.8	12.9–16.2
Ca_{O_2} (mg ml^{-1})	0.16–0.17	–	0.14	–	0.15	0.18–0.20
$C\bar{v}_{O_2}$ (mg ml^{-1})	0.10	–	–	–	0.10	0.12–0.14
(Ca_{O_2}–$C\bar{v}_{O_2}$) (mg ml^{-1})	0.07	(0.06)	–	(0.08)	0.05	0.06–0.07
Haematocrit (%)	21–29	–	23–33	–	23–33	27–38
Haemoglobin (g dl^{-1})	7–11	–	–	–	6–9	11–13
$\dot{V}_b$ (ml min^{-1} kg^{-1})	25–50	(29)	35–70	(43)	17–37	115–132
f_H (beats min^{-1})	71–86	(77)	81–100	(117)	38	62–97
V_S (ml beat^{-1} kg^{-1})	0.35–0.55	(0.38)	–	(0.37)	0.46	1.10–1.30
$\dot{V}_b/\dot{M}_{O_2}$ (ml mg^{-1})	15.5	(18.8)	–	(13.1)	22.5	7.1–10.2
Ventricle mass (% body mass)	0.11	(0.08)	–	–	0.08–0.13	0.29–0.38
f_G (strokes min^{-1})	76.8	(72.2)	80–95	–	55–100	–

For abbreviations, see List of symbols and abbreviations.

[a]Values given in parentheses are from the present study for *S. lalandi*, whereas all other values are for *S. quinqueradiata* [~20°C data compiled from (Yamamoto et al., 1981; Yamamoto, 1991; Lee, K. S. et al., 2003b); 25°C data compiled from (Ishimatsu et al., 1990; Ishimatsu et al., 1997; Lee, K. S. et al., 2003a)]; data for rainbow trout were compiled from (Holeton and Randall, 1967; Randall et al., 1967; Stevens and Randall, 1967; Kiceniuk and Jones, 1977; Brill and Bushnell, 1991; Farrell and Jones, 1992; Gallaugher et al., 1995; Altimiras and Larsen, 2000; Brill and Bushnell, 2001); data for tunas (skipjack and yellowtail) were compiled from (Bushnell et al., 1990; Brill and Bushnell, 1991; Jones et al., 1993; Bushnell and Jones, 1994; Dewar and Graham, 1994; Korsmeyer et al., 1997a; Korsmeyer et al., 1997b; Brill and Bushnell, 2001).

(Table 3), and increases in both of these variables are causal to a 1.3-fold increase in Ca_{O_2} with chasing stress (Yamamoto, 1991). Furthermore, it is likely that a large Bohr effect ($\Delta\log P_{50}/\Delta pH$=–0.74) assists in unloading of oxygen at the tissues (Lee, K. S. et al., 2003a; Lee, K. S. et al., 2003b). If the oxygen content data determined by Yamamoto et al. (Yamamoto et al., 1981) for *S. quinqueradiata* at 20°C (Table 3) are also representative of *S. lalandi* at this temperature, it may be predicted that Ca_{O_2} must increase by at least 1.9-fold (such that Ca_{O_2}=0.33 mg ml^{-1}, $C\bar{v}_{O_2}$=0 mg ml^{-1}) to allow the 4.7-fold increase in (Ca_{O_2}–$C\bar{v}_{O_2}$) that occurs during exercise. Such changes in Ca_{O_2} and $C\bar{v}_{O_2}$ are impossible, which indicates that *S. quinqueradiata* differs markedly from *S. lalandi* in terms of tissue oxygen extraction during exercise, or that the values of (Ca_{O_2}–$C\bar{v}_{O_2}$) determined by Yamamoto et al. were overestimated (Yamamoto et al., 1981), possibly due to experimental stress. Knowledge of the gas exchange characteristics of the blood of *S. lalandi* is necessary to answer this question.

Aerobic cost of transport

Calculation of U_{opt} and $GCOT_{min}$ of high-energy-demand species is arguably of more ecological relevance than SMR or $\dot{M}_{O_2max}$. Optimum swimming velocity and $GCOT_{min}$ provide estimates of routine activity levels and energetics in the natural environment. Indeed, U_{opt} is considered a good predictor for routine swimming speeds in a range of species, suggesting that fish usually swim at speeds at which transport costs are minimal (Videler, 1993; Dewar and Graham, 1994; Tanaka et al., 2001; Lowe, 2002).

As has been found for several other teleosts (Dickson et al., 2002; Sepulveda et al., 2003), an increase in water temperature increased the aerobic cost of transport of *S. lalandi*, when calculated as either GCOT or NCOT (Fig. 2). Several theories have been proposed to explain the increase in transport costs with increasing temperature but, at present, these remain contentious (Dickson et al., 2002). Dickson et al. proposed that NCOT may be higher at warmer temperatures because of higher swimming support costs, such as higher $\dot{V}_b$ and blood flow to the oxidative locomotor muscles to compensate for the lower oxygen solubility (Dickson et al., 2002). If the same method used to derive NCOT from $\dot{M}_{O_2}$ is used to calculate the net cost of transport in terms of $\dot{V}_b$ [i.e. ($\dot{V}_b$–$\dot{V}_{b\,min}$)/U], the value is indeed higher at 25°C (0.122 ml kg^{-1} m^{-1}) than at 20°C (0.110 ml kg^{-1} m^{-1}); that is, a greater amount of blood is pumped from the heart per metre swum when *S. lalandi* is swimming at the warmer temperature. It is therefore possible that this ~10% difference is at least partly responsible for the ~20% difference in NCOT that is evident between temperatures around the optimal swimming velocities (Fig. 2C).

The U_{opt} for *S. lalandi* was higher at the warmer temperature than at the cooler temperature, which can be attributed to the thermal effects on SMR causing an increase in $GCOT_{min}$ at warmer temperatures. In comparison with the prominent U-shaped relationship that is typically documented for other species (Parsons and Sylvester, 1992; Dewar and Graham, 1994; Lee, C. G. et al., 2003), GCOT of *S. lalandi* at both temperatures followed a shallower U-shaped relationship with swimming velocity (Fig. 2D), such that increases in swimming speed above U_{opt} were associated with negligible increases in swimming cost [i.e. the oxygen required to swim 1 m remained relatively unchanged from U_{opt} to U_{max}, even though GCOT should theoretically increase exponentially with swimming velocity above $GCOT_{min}$ to overcome the exponential increase in hydrodynamic resistance (Brett, 1964; Videler and Nolet, 1990)]. It is possible that specific aerobic processes within the body (e.g. blood flow to the gut) are shut down at swimming speeds above U_{opt} in order to divert additional oxygen to the swimming musculature and reduce GCOT. Additionally, energy saved from the progressive transition from opercular ventilation to ram ventilation (Fig. 2B) may offset some of the increasing costs associated with progressively faster swimming; indeed, shifting from opercular ventilation to ram ventilation causes an 8–13% reduction in metabolic rate in rainbow trout (Steffensen, 1985). In this context, it seems that the ability to utilise ram ventilation facultatively, ensures an adequate supply of oxygen at slow swimming speeds when opercular ventilation is adopted, without resulting in

Table 4. *Comparison of swimming performance variables for S. lalandi with those of other similarly sized active teleosts*

Variable	*S. lalandi*		Sockeye salmon	Yellowfin tuna
N	10	2	12	12
Temperature (°C)	20	25	~15	25
Body mass (kg)	2.1	1.9	3.0	2.2
Body length (m)	0.56	0.55	0.63	0.51
U_{opt} (*BL* s^{-1})	1.2	1.7	1.0	2.0
$GCOT_{min}$ (mg kg^{-1} m^{-1})	0.107 (0.127)[a]	0.164 (0.130)[a]	0.135	0.158
$GCOT_{min}$ (mg kg^{-1} *BL*$^{-1}$)	0.062	0.088	0.085	0.081
NCOT at U_{opt} (mg kg^{-1} m^{-1})	0.069	0.105	0.050	0.100
NCOT at U_{opt} (mg kg^{-1} *BL*$^{-1}$)	0.039	0.058	0.032	0.051

[a]Values in parentheses were predicted using $GCOT_{min}$ (mg kg^{-1} m^{-1})=0.1525$M_b^{-0.25}$ (modified from Brett, 1964); note that this equation was formulated using data from animals at 15°C. Data for sockeye salmon are from (Lee, C. G. et al., 2003); data for yellowfin tuna are from (Dewar and Graham, 1994).

compromised streamlining and swimming efficiency at high swimming speeds when ram ventilation ensues.

The length-specific $GCOT_{min}$ determined for *S. lalandi* at 25°C compares favourably to values obtained for other high-energy-demand teleosts, including yellowfin tuna at 25°C and sockeye salmon at approximately 15°C (Table 4), although the higher U_{opt} values determined for *S. lalandi* and yellowfin tuna indicate a greater overall efficiency of these species over the salmon. In this context, it is interesting to note that the carangiform swimming mode of *S. lalandi* is comparably efficient with the thunniform swimming mode of the tunas. Thus, rather than evolving to allow more efficient swimming, thunniform locomotion may have developed as a consequence of other features such as myotomal architecture, red muscle position, and its connections with the skin and skeleton (Katz, 2002; Graham and Dickson, 2004). When considering the effect of temperature on $GCOT_{min}$ mentioned above, it is quite impressive that *S. lalandi* at 25°C swims with a greater overall efficiency than sockeye salmon at 15°C (Lee, C. G. et al., 2003). At 20°C, *S. lalandi* displayed remarkable efficiency at U_{opt}, with the $GCOT_{min}$ being substantially lower than predicted for a fish of this body mass (Table 4) (Brett, 1964), and lower than values obtained from most other species of high performance teleost (Dewar and Graham, 1994; Lee, C. G. et al., 2003). In comparison with sockeye salmon at 15°C, however, the contribution of SMR to $GCOT_{min}$ for *S. lalandi* at 20°C is relatively small, such that values of NCOT at U_{opt} are similar for the two species (Table 4).

List of symbols and abbreviations

BL	body length
Ca_{O_2}	oxygen content in arterial blood
$C\bar{v}_{O_2}$	oxygen content in mixed venous blood
EMG	electromyographic
f_G	opercular ventilation rate
f_H	heart rate
GCOT	gross aerobic cost of transport
M_b	body mass
$\dot{M}_{O_2}$	rate of oxygen consumption
NCOT	net aerobic cost of transport
SMR	standard metabolic rate
Subscripts	
max, min, opt	maximum, minimum, optimal, respectively
U	swimming velocity
$\dot{V}_b$	cardiac output
V_S	cardiac stroke volume

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