Factorial Aerobic Scope Is Independent of Temperature and Primarily Modulated by Heart Rate in Exercising Murray Cod (*Maccullochella peelii peelii*)

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Accepted 7/6/2004; Electronically Published 5/3/2005

ABSTRACT

Several previous reports, often from studies utilising heavily instrumented animals, have indicated that for teleosts, the increase in cardiac output ($\dot{V}_b$) during exercise is mainly the result of an increase in cardiac stroke volume (V_S) rather than in heart rate (f_H). More recently, this contention has been questioned following studies on animals carrying less instrumentation, though the debate continues. In an attempt to shed more light on the situation, we examined the heart rates and oxygen consumption rates ($\dot{M}o_2$; normalised to a mass of 1 kg, given as $\dot{M}o_{2\,kg}$) of six Murray cod (*Maccullochella peelii peelii*; mean mass ± SE = 1.81 ± 0.14 kg) equipped with implanted f_H and body temperature data loggers. Data were determined during exposure to varying temperatures and swimming speeds to encompass the majority of the biological scope of this species. An increase in body temperature (T_b) from 14°C to 29°C resulted in linear increases in $\dot{M}o_{2\,kg}$ (26.67–41.78 μmol min^{-1} kg^{-1}) and f_H (22.3–60.8 beats min^{-1}) during routine exercise but a decrease in the oxygen pulse (the amount of oxygen extracted per heartbeat; 1.28–0.74 μmol beat^{-1} kg^{-1}). During maximum exercise, the factorial increase in $\dot{M}o_{2\,kg}$ was calculated to be 3.7 at all temperatures and was the result of temperature-independent 2.2- and 1.7-fold increases in f_H and oxygen pulse, respectively. The constant factorial increases in f_H and oxygen pulse suggest that the cardiovascular variables of the Murray cod have temperature-independent maximum gains that contribute to maximal oxygen transport during exercise. At the expense of a larger factorial aerobic scope at an optimal temperature, as has been reported for species of salmon and trout, it is possible that the Murray cod has evolved a lower, but temperature-independent, factorial aerobic scope as an adaptation to the largely fluctuating and unpredictable thermal climate of southeastern Australia.

Introduction

For all vertebrates, the Fick principle for oxygen convection by blood describes the rate of oxygen uptake ($\dot{M}o_2$) as a function of cardiac output ($\dot{V}_b$) and tissue oxygen extraction ($C_aO_2 - C_{\bar{v}}O_2$), where C_aO_2 is the oxygen content of arterial blood and $C_{\bar{v}}O_2$ is the oxygen content of mixed venous blood. This is formalised by the equation

$$\dot{M}o_2 = \dot{V}_b \times (C_aO_2 - C_{\bar{v}}O_2). \quad (1)$$

As cardiac output is the product of heart rate (f_H) and stroke volume (V_S), the equation can also be written as

$$\dot{M}o_2 = f_H \times V_S \times (C_aO_2 - C_{\bar{v}}O_2). \quad (2)$$

The product of V_S and $(C_aO_2 - C_{\bar{v}}O_2)$ and of $\dot{M}o_2/f_H$ is known as the oxygen pulse, so by calculating the oxygen pulse from $\dot{M}o_2$ and f_H, it is possible to determine the relative contributions of f_H and of $V_S(C_aO_2 - C_{\bar{v}}O_2)$ to the increased delivery of oxygen to the metabolising tissues during exercise. Thus, if f_H rather than oxygen pulse primarily contributes to the change in $\dot{M}o_2$, then f_H and not V_S is the primary cause of the modulation in $\dot{V}_b$.

A number of studies, primarily restricted to the salmonids, have suggested that teleosts modulate $\dot{V}_b$, and hence aerobic scope, during increased activity primarily through changes in

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Physiological and Biochemical Zoology 78(3):347–355. 2005. 1522-2152/2005/7803-4043$15.00

V_S rather than f_H (Stevens and Randall 1967; Kiceniuk and Jones 1977; Farrell 1991; Kolok and Farrell 1994). Many such studies used fish that were heavily instrumented and were most likely surgically stressed due to insufficient recovery periods, and the influence of postoperative stress has been recently reported to alter the relationship between cardiovascular variables in rainbow trout (*Oncorhynchus mykiss*), chinook salmon (*Oncorhynchus tshawytscha*; Thorarensen et al. 1996 and references within), yellowfin tuna (*Thunnus albacares*; Korsmeyer et al. 1997), and Atlantic cod (*Gadus morhua*; Webber et al. 1998).

The contention that $\dot{V}_b$ in teleosts is modulated primarily through changes in V_S is not supported by studies on species such as northern pike (*Esox lucius*; Armstrong 1986, 1998), Atlantic salmon (*Salmo salar*; Lucas 1994), and, more recently, species of trout (Altimiras and Larsen 2000; Brodeur et al. 2001; Beaumont et al. 2003). It is more likely, therefore, that cardiac frequency modulation is more prominent among teleosts during increases in $\dot{M}o_2$, as it is in other vertebrates, than many previous studies imply. Our study used implantable f_H data loggers and swimming respirometry to examine f_H and $\dot{M}o_2$ in the Murray cod (*Maccullochella peelii peelii* [Mitchell]), which is predominantly a sedentary, sit-and-wait predator and belongs to a hitherto unstudied family of teleosts (family Percichthyidae).

We wished, therefore, to determine if changes in aerobic scope were mainly correlated with changes in f_H or oxygen pulse; if the former were true, then $\dot{V}_b$ must be modulated primarily by increases in f_H. Further, because temperature is known to influence the cardiometabolic parameters of ectotherms (e.g., Satchell 1991; Korsmeyer et al. 1997; Butler et al. 2002), the relationship between f_H and $\dot{M}o_2$ was examined over a range of acute temperature changes similar to those observed in some natural environments of this species in southeastern Australia.

Material and Methods

Animals

Data were obtained from a total of six Murray cod with a mean body mass, M_b ($\pm$SE of the mean), of 1.81 $\pm$ 0.14 kg and a mean length of 485 $\pm$ 9 mm (Animal Ethics Code 99/42L). All animals were obtained from the Department of Primary Industries, Marine and Freshwater Resources Institute (MAFRI) hatchery at Snobs Creek, Victoria, Australia, where they had been raised indoors. Fish were kept individually in 1,000-L tanks through which there was a continual turnover of filtered freshwater obtained from the nearby creek (>95% oxygen saturation; average daily temperature range 21°–26°C).

Surgery

Fish were anaesthetised using approximately 0.25 mL L^{-1} alfaxalone (Alfaxan-CD, Jurox, New South Wales) before surgery, and exposure was continued throughout. Fish were weighed, measured, and positioned upside down between two foam pads on an operating table. The skin and underlying tissue layers of the abdomen were opened along a 3–4-cm incision along the ventral midline. Sterilised f_H and body temperature (T_b) data loggers (HRTDL; see Woakes et al. 1995 for construction details) were implanted so that one electrode (length 70 mm) was positioned close to the heart and the other (length 30 mm) was along the side of the HRTDL in the abdominal cavity. The body of the HRTDL (40 mm × 30 mm × 15 mm) was fixed in place with one or two sutures of surgical silk (Ethicon, Norderstedt, Germany) through the body wall. Correct positioning of the HRTDL could be determined through the use of a radio receiver that detected short-pulse low-power radio frequency transmissions emitted by the HRTDL on each QRS wave of the electrocardiogram. The muscle layer and skin were individually closed with nondissolvable surgical suture, and the wound was swabbed with iodine antiseptic after surgery. Loggers recorded f_H and T_b every 5-s and 30-s period, respectively, and the time at which the HRTDL was implanted was noted to the nearest minute.

Following surgery, fish were placed in a small recovery tank to regain full consciousness (approximately 20 min) before being released into a 1,000-L holding tank. Water in the holding tank was treated with 5 g L^{-1} salt and 2 mg L^{-1} methylene blue as a prophylactic treatment to aid recovery of the fish. After 24 h, salt and methylene blue were flushed from the holding tank by the introduction of a continuous flow of freshwater (7.5–10 L min^{-1}) that was maintained throughout the remainder of the experiment. All fish survived the procedure. The fish were fed every other day and given 14 d to recover before experiments. Fish were not fed for a 2-d period before they were used for experiments, to allow full gut evacuation (B. Ingram, unpublished data); hence, we avoided incorporating the influence of specific dynamic action into the measurements.

Swim Flume Apparatus

Measurements of $\dot{M}o_2$ were determined in a purpose-built closed-system swimming flume with a water volume of 39 L. Fish were introduced into the flume through an opening at the top of the swimming chamber that was afterward sealed with a screw cap. The fish were restricted to the transparent swimming chamber (diameter 150 mm) by a removable mesh grill (10 × 10-mm grid) positioned at either end of the chamber, and the anterior end of the swimming chamber was equipped with narrow tubes to assist in achieving a uniform flow. The chamber was completely covered with black sheeting except for a 15-mm gap at the dorsal end that was used to monitor the well-being of the fish.

The flow of water through the flume was generated using a closed-system pool pump (model PACR 300, Davey, Scoresby, Victoria), and the flow of water through the swimming chamber

Table 1: Polynomial regression relationships of mass-independent rate of oxygen consumption ($\dot{M}o_{2\,kg}$, μmol min^{-1} kg^{-1}) and heart rate (f_H, beats min^{-1}) against water speed (body lengths s^{-1}) for Murray cod at established mean temperatures (temperature range indicated)

y, T_b (°C)	N	n	a	b	c	r^2	Rest[a]
$\dot{M}o_{2\,kg}$:							
Mean 16.1 ± .5 (14°–20°C)	6	19	1.270	.927	−.356	.71	18.62
Mean 22.0 ± .3 (21°–24°C)	6	18	1.334	1.079	−.446	.82	21.56
Mean 27.2 ± .3 (25°–29°C)	5[b]	24	1.427	.785	−.266	.75	26.70
f_H:							
Mean 16.1 ± .5 (14°–20°C)	6	19	1.259	.746	−.363	.63	18.2
Mean 22.0 ± .3 (21°–24°C)	6	18	1.504	.574	−.248	.50	31.9
Mean 27.2 ± .3 (25°–29°C)	5[b]	24	1.607	.556	−.189	.75	40.4

Note. Equations were calculated using data obtained over a speed range of 0.18–1.45 body lengths per second, though the maximum swimming speed for 14°–20°C was 1.12 body lengths s^{-1}. Regression equations of the form $\log y = a + bU + cU^2$, where U is water speed (body lengths per second); n denotes the number of data points forming the regression.

[a] Predicted value at zero water speed at the mean T_b (see text). Units as described in table title.

[b] One individual was not measured at a warm temperature due to malfunctioning heating equipment.

could be altered by use of a three-way valve that allowed water to bypass the chamber. The water flow rate through the swimming chamber was calibrated with a flow probe (model OSS-PC1) that determined flow over a 30-s period according to the number of revolutions of a 50-mm propeller positioned in the centre of the swimming chamber. A maximum water speed of 0.50 m s^{-1} was achieved through the empty swimming chamber when the bypass was completely closed.

Water temperature and oxygen saturation in the flume were continuously monitored using a calibrated oxygen and temperature electrode (model 600XLM, Yellow Springs Industries [YSI], Yellow Springs, OH; employs a rapid pulse system that removes flow dependence and thus does not create a boundary layer at the membrane surface) positioned inside the flume. Data were logged at one sample per 10 s to a computer using Ecowatch software (EcoWin, Yellow Springs, OH). An empty chamber was regularly used as a blank as a precaution to ensure that microbial respiration was not altering $\dot{M}o_2$ measurements, though the reduction in oxygen saturation of the water passing through the chamber was in all cases negligible.

Protocol

Rate of oxygen consumption and f_H measurements were obtained for all six fish at three water temperatures (except for one individual, for which measurements were performed only at two temperatures due to malfunctioning heating equipment). Between measurements, the flume was continuously flushed with oxygenated water from the holding tank at the desired experimental temperature (the temperature of the water was established at least 18 h before experimentation), and fish remained predominantly quiescent when they were not swimming against high water flows. During each 10–12-min $\dot{M}o_2$ measurement, the flume was sealed, with care taken to remove any obvious bubbles from the system. Measurements were ceased and the flume reopened to freshwater before oxygen saturation in the flume fell to 75%.

Fish were introduced to the flume and given 30 min to acclimate, and then the speed was increased incrementally until the fish began to lose position; the speed was then reduced to a speed at which the fish could hold station, and the $\dot{M}o_2$ measurement commenced. The maximum swimming speed ranged, depending primarily on temperature, between 0.32 and 0.50 m s^{-1}. It was our intention not to quantify maximum swimming speed but to ensure that the fish were swimming at maximum sustainable aerobic speeds; maximum aerobic contributions previously have been shown to occur at 80%–90% of maximum swimming speed in salmonids and at 30%–50% in cyprinids (Jones 1982).

This protocol took account of the fact that fish metabolism was elevated when the fish was initially introduced into the flume. Upon conclusion of the maximum $\dot{M}o_2$ measurement, the flume was opened and the fish remained in the flume on a low water speed (0.02 m s^{-1}) for at least 7 h to allow cardiovascular variables to decrease and stabilise. Following this period, $\dot{M}o_2$ was determined while the fish swam at a comfortable water speed similar to that generally encountered in the holding tanks (0.06 m s^{-1}, termed "routine exercise"). The design of the flume did not allow the measurement of $\dot{M}o_2$ while the fish was at complete rest at zero water speed. Finally, $\dot{M}o_2$ measurements were determined at a speed approximately midway between the speeds used for routine and maximum exercise (0.15–0.23 m s^{-1}). Swimming speed of the fish in the flume was subsequently corrected for the solid blocking effect

of each individual fish using the method given by Jones et al. (1974).

The slope of the decline in oxygen saturation of water with time when the flume was sealed was used to calculate $\dot{M}O_2$ (given at STPD). The mean T_b and f_H for a trial were determined during the last half of the period used to determine the $\dot{M}O_2$ reading. At the end of the trial, fish were returned to their holding tanks, and the temperature of the tank water was altered by adjusting temperature-regulating elements. The desired temperature (± 2°C) was influenced by the daily temperature fluctuations of the creek water and was typically reached within 2.5 h, after which fish were given a further 18 h to acclimate before experimentation. For some individuals, $\dot{M}O_2$ measurements were determined at additional speeds and additional temperatures on a separate occasion (see Table 1). At the conclusion of experimentation, the HRTDL was removed using the same procedure as during implantation.

Data Analysis and Statistics

Following $\log_{10}$-transformation of the data, least squares regressions were used to determine the relationships between f_H and $\dot{M}O_2$ against M_b (covariate) across all temperatures for routine and maximum exercise. A test for homogeneity of slopes revealed no difference between slopes for routine and maximum exercise for each variable ($P > 0.5$). The common regression coefficient was computed (f_H, $b = 0.17$, $P = 0.740$; $\dot{M}O_2$, $b = 0.90$, $P < 0.001$), and, in the case where this was significantly different from 0, it was used to standardise all data for the covariate (see Packard and Boardman 1999 for full explanation). Corrections for the covariate ($\log M_b$ in this case) are normally made to the grand mean but, given that the data have been log transformed, proportionality across M_b is maintained and adjustments to $\dot{M}O_2$ values were therefore made to a M_b of 1 kg (denoted by $\dot{M}O_{2\,kg}$).

Least squares regressions were used to determine the relationships between $\dot{M}O_{2\,kg}$, f_H, and oxygen pulse (determined from eq. [2]) for the group data against T_b. Differences between group regressions, where appropriate, were tested with ANCOVA. Stepwise multiple linear regression was used to determine the interactions between T_b, f_H, and $\dot{M}O_{2\,kg}$. Significance was considered at $P < 0.05$. Data are presented as mean ± SE of the mean, and $\log_{10}$ is used throughout for logarithmic transformations. N = number of animals; n = number of data points.

Results

The period immediately following surgery typically was characterised by a large tachycardia. Heart rate declined rapidly during the first hour, after which the decline slowed. Stable low values were obtained approximately 24 h postsurgery. Following this, fish remained predominantly quiescent during periods of nonfeeding in the holding tanks, and T_b remained in unity with water temperature at all times. The dependence of f_H on T_b becomes clearly evident when examining f_H traces of individual fish in holding tanks when exposed to the diurnal water temperature fluctuations of Snobs Creek (Fig. 1).

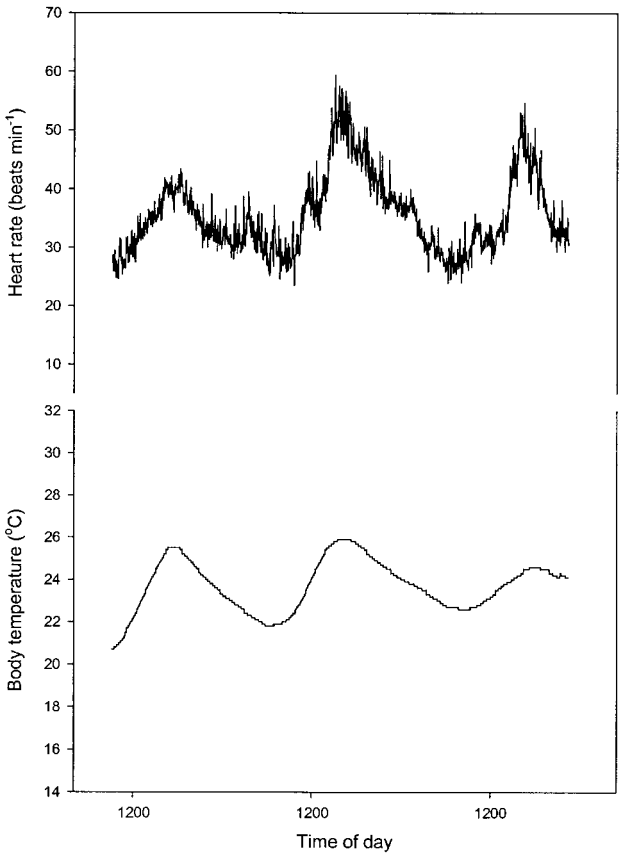

Figure 1. Diurnal fluctuations of heart rate (f_H) and body temperature (T_b) of unfed Murray cod while exposed to natural fluctuations in water temperature. We observed that body temperature remained in unity with water temperature at all times, and f_H displayed a clear dependence on T_b.

During swimming experiments, both f_H and $\dot{M}O_{2\,kg}$ increased with water speed at all temperatures throughout the range of 14°–29°C. Heart rate and $\dot{M}O_{2\,kg}$ during exercise were best related to swimming speed and temperature in accordance with the polynomial regression equations given in Table 1. Fish below approximately 20°C were not able to sustain swimming speeds in excess of 1.12 body lengths s^{-1}, whereas above 20°C, some fish were able to maintain a maximum swimming speed of up to 1.45 body lengths s^{-1} for the duration of the swimming experiment (approximately 10–12 min).

An increase in T_b resulted in significant increases both in $\dot{M}O_{2\,kg}$ (Fig. 2*a*) and f_H (Fig. 2*b*) and a significant decrease in oxygen pulse (Fig. 2*c*) regardless of activity state. Regression

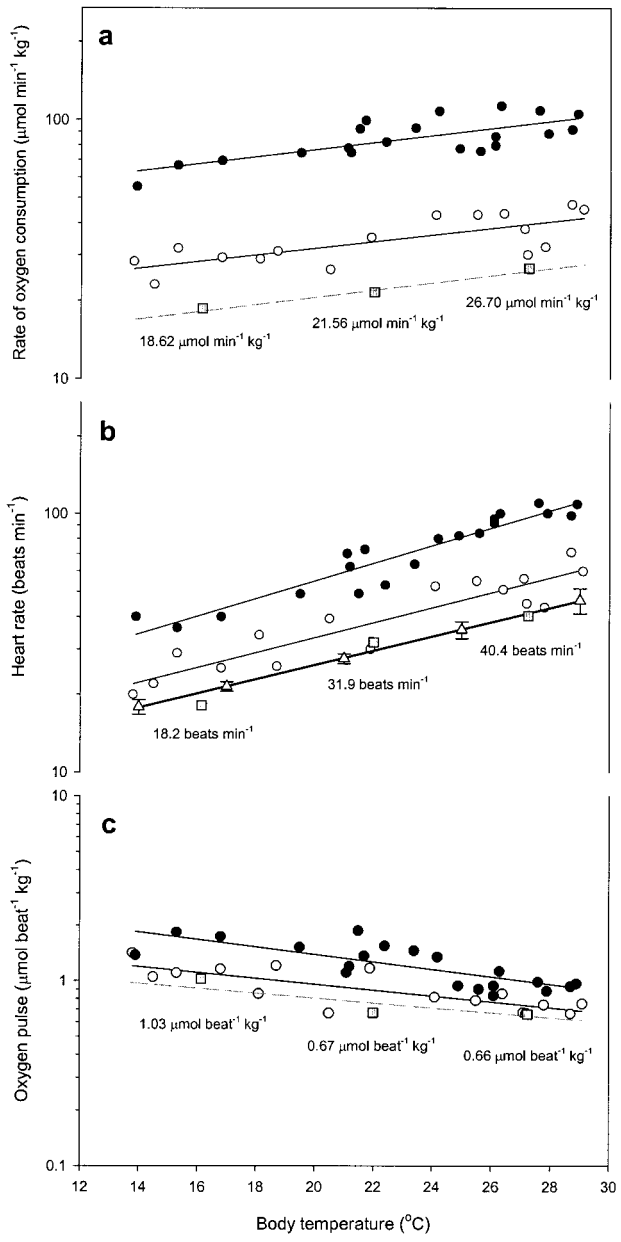

Figure 2. Relationship of (*a*) mass-independent rate of oxygen consumption ($\dot{M}o_{2\,kg}$), (*b*) heart rate (f_H), and (*c*) oxygen pulse with body temperature (T_b) for Murray cod. The regressions of all three variables displayed statistically similar slopes at routine exercise (*open circles* and *solid line*) and maximum exercise (*solid circles* and *solid line*; $P > 0.05$), and all regressions for maximum exercise had significantly elevated intercepts compared with those for routine exercise. Also indicated for f_H are values (*triangles*; mean ± SE) and the associated regression line (*bold line*) determined for animals fasted for 2 d and resting in holding tanks. Regression equations are given in Table 2. Further, for each variable the values predicted for zero water speed, calculated using regression equations in Table 1, are indicated (*squares*), and the associated regression lines (*dashed lines*) are shown for $\dot{M}o_{2\,kg}$ and oxygen pulse.

equations and Q_{10} values for each variable at routine exercise and maximum exercise are given in Table 2. The elevation of the regression for each variable at maximum exercise was greater than for that at routine exercise ($P < 0.05$; Table 2). The slope of the regression at routine exercise was in all cases statistically similar to that at maximum exercise ($P > 0.05$; Fig. 2), indicating a constancy of the factorial scope (given, in this instance, as the ratio of the elevations for maximum exercise to routine exercise) for each variable over the temperature range, the difference in elevation being 2.4-, 1.7-, and 1.5-fold for $\dot{M}o_{2\,kg}$, f_H, and oxygen pulse, respectively.

Interestingly, if the values of f_H are predicted for zero water speed (i.e., animals at rest) from the equations given in Table 1 they compare favourably to the values measured from undisturbed animals in holding tanks before experimentation (cf. square symbols and bold regression, Fig. 2*b*). By employing the same principle for $\dot{M}o_{2\,kg}$, values of resting $\dot{M}o_{2\,kg}$ may be predicted for zero water speed at the mean T_b's indicated in Table 1 (16.1°C, 18.62 μmol min^{-1} kg^{-1}; 22.0°C, 21.56 μmol min^{-1} kg^{-1}; 27.2°C, 26.70 μmol min^{-1} kg^{-1}); thus, a regression for resting $\dot{M}o_{2\,kg}$ (and, by calculation, oxygen pulse) can be predicted (dashed regressions; Fig. 2*a*, 2*c*). Given that proportionality remains the same between the regression of resting $\dot{M}o_{2\,kg}$ and that of maximum $\dot{M}o_{2\,kg}$ (mean slope 0.014), a factorial aerobic scope (maximum $\dot{M}o_{2\,kg}$: resting $\dot{M}o_{2\,kg}$) of 3.7 can be predicted throughout the temperature range, resulting from factorial scopes of f_H and oxygen pulse of 2.2 and 1.7, respectively.

The log-log relationship between f_H and $\dot{M}o_{2\,kg}$ for routine exercise and maximum exercise is illustrated in Figure 3. The parallel slopes of the regressions (*solid lines*) suggest a systematic contribution of both f_H and oxygen pulse from routine exercise to maximum exercise across the T_b range of 14°–29°C. Also displayed in Figure 3 are the relationships that exist between f_H and $\dot{M}o_{2\,kg}$ during exercise at three typical temperatures of 14.0°C, 20.5°C, and 29.0°C (*dashed lines*), as predicted using the group multiple regression equation that relates T_b, f_H, and $\dot{M}o_{2\,kg}$:

$$\log \dot{M}o_{2\,kg} = -6.75 + 1.2 \times \log f_H + 1{,}895.5 \times (1/T_b), \quad (3)$$

where T_b is in degrees Kelvin and $n = 58$. Although $\log f_H$ was the most prominent contributor to the prediction of $\dot{M}o_{2\,kg}$ ($r^2 = 0.56$), stepwise regression revealed that the addition of $1/T_b$ significantly strengthened the relationship ($r^2 = 0.67$).

Discussion

The main disadvantage of surgical implantation of the HRTDL is that, due to the invasive nature of the surgery, there may be a considerable period of postoperative stress, during which time

Table 2: Linear regression relationships of mass-independent rate of oxygen consumption ($\dot{M}o_{2\,kg}$, μmol min^{-1} kg^{-1}), heart rate (f_H, beats min^{-1}), and oxygen pulse (μmol beat^{-1} kg^{-1}) versus T_b at routine exercise and maximum exercise for Murray cod

y	n	a	b	S_a	S_b	S_{YX}	r^2	Q_{10}
$\dot{M}o_{2\,kg}$:								
Routine exercise	17	1.244*	.013	.070	.003	.064	.56	1.35
Maximum exercise	20	1.611	.014	.069	.003	.055	.55	1.38
f_H:								
Rest	25	.870*	.027	.049	.002	.064	.86	1.86
Routine exercise	17	.943*	.029	.075	.003	.069	.85	1.95
Maximum exercise	20	1.061	.034	.063	.003	.050	.90	2.19
Oxygen pulse:								
Routine exercise	17	.332*	−.016	.076	.003	.070	.61	.69
Maximum exercise	20	.578	−.020	.093	.004	.075	.59	.63

Note. Regressions were determined across a temperature range of approximately 14°–29°C. Q_{10} values for each variable are also presented. Regression equations of the form $\log y = a + bT_b$; n denotes the number of data points forming the regression. $N = 6$; Q_{10} values were determined from the slopes of the regressions according to the equation $Q_{10} = 10^{(b \times 10)}$.

* Significantly lower than intercept of regression for maximum exercise ($P < 0.05$); for each variable there were no significant differences in the slopes of the regressions between rest, routine exercise, and maximum exercise ($P > 0.05$); S_a = SE of a; S_b = SE of b; S_{YX} = SE of estimate.

data obtained need to be treated with caution (Lucas et al. 1993). Indeed, observations from our study indicate that recovery periods less than approximately 24 h are insufficient to obtain resting f_H values for Murray cod, a finding that is supported by results obtained for several other fish species (Houston et al. 1973; Webber et al. 1998; Altimiras and Larsen 2000). In contrast, studies on some species have reported that postinstrumentation recovery periods of only 12 h are sufficient (e.g., Priede and Young 1977; Lucas et al. 1991). Nevertheless, f_H data from our study for fish in holding tanks were used only after 14 d of recovery; thus, we are confident that postoperative stress did not influence the results of this study. Further, we are confident that the large ranges of T_b, f_H, and $\dot{M}o_2$ investigated in this study encompass the majority of the biological scope for the species, given the knowledge of thermal habitat and activity of this species in the natural environment (Rowland 1989, 1998; Koehn et al. 1993).

Heart rate of ectothermic animals is often temperature dependent because of increased membrane permeability of the pacemaker fibres and change in the vagal tone (Satchell 1991). Indeed, the increase in $\dot{M}o_{2\,kg}$ with T_b for Murray cod was associated with an increase in f_H and a slight, yet significant, decrease in oxygen pulse. A similar inverse relationship as that for oxygen pulse and temperature has been reported for V_S and temperature of yellowfin tuna ($Q_{10} = 0.8$; Korsmeyer et al. 1997) and rainbow trout ($Q_{10} = 0.7$; reworked data from Farrell et al. 1996) and is thought to be the result of a reduction in both filling time and force of contraction at higher temperatures (Farrell and Jones 1992).

It is interesting to note for the Murray cod that temperature offsets the linear regression that describes the relationship between f_H and $\dot{M}o_2$ at various levels of exercise (Fig. 3, *dashed lines*). A similar occurrence has been reported for the Atlantic cod (Claireaux et al. 1995), though in that study, despite relatively strong correlations between f_H and $\dot{M}o_2$, the small change in f_H observed during exercise led the authors to dismiss it as a major contributor to increased cardiac delivery in Atlantic cod. In contrast, reports for pike (Armstrong 1986) and Atlantic salmon (Lucas 1994) at various exercise states indicate that an increase in temperature simply extends the same regression line between f_H and $\dot{M}o_2$ with maintenance of the intercept. Nevertheless, there have been conflicting reports for teleosts regarding the relative contributions of f_H and V_S to increases in $\dot{V}_b$ and $\dot{M}o_2$ during exercise (Stevens and Randall 1967; Randall 1968; Kiceniuk and Jones 1977; Farrell 1991; Farrell and Jones 1992; Lucas 1994; Cooke et al. 2002; Beaumont et al. 2003). Even intraspecific reports regarding the percentage contribution of f_H to $\dot{M}o_2$ have been highly variable for many teleosts, exemplified by the broad range found for rainbow trout—between 8.7% (Stevens and Randall 1967) and 49.7% (Priede and Tytler 1977).

In this context, increases in swimming speed of Murray cod in our study resulted in temperature-dependent increases in $\dot{M}o_{2\,kg}$, which were regulated primarily by increases in f_H as opposed to oxygen pulse. The factorial scope of f_H found for Murray cod throughout the 14°–29°C temperature range (2.2) agrees favourably to the value of 2.4 obtained for rainbow trout at 15°C (Altimiras and Larsen 2000) and the value of 2.0 cal-

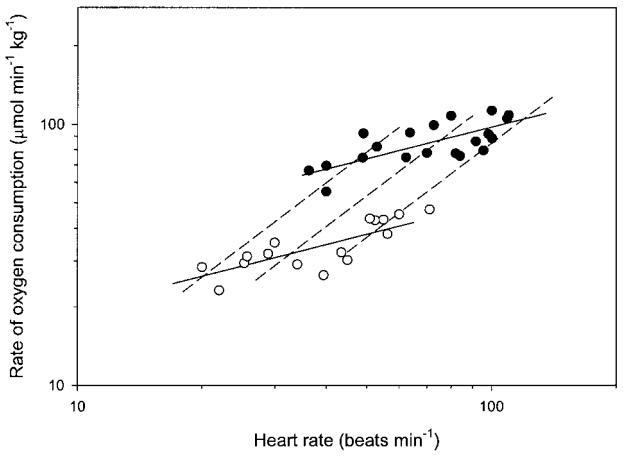

Figure 3. Log-log relationship between mass-independent rate of oxygen consumption ($\dot{M}o_{2\,kg}$) and heart rate (f_H) for Murray cod at routine exercise (*open circles*) and maximum exercise (*solid circles*). The slopes of the regressions were statistically similar ($P > 0.05$); thus they were described by a common equation that takes into account activity state: $\log \dot{M}o_{2\,kg} = 0.60 + 0.40 \times \log f_H + 0.29 \times$ state, where "state" was given a value of 1 or 2 to represent routine exercise or maximum exercise, respectively. Predicted relationships (*dashed lines*) as calculated from the group regression equation (eq. [3]) are included at 14.0°C, 21.5°C, and 29.0°C (from left to right, respectively) to illustrate the linear increase of $\log \dot{M}o_{2\,kg}$ and $\log f_H$ that occurs with exercise at different body temperatures (T_b).

culated for yellowfin tuna at 24°C (reworked data from Korsmeyer et al. 1997), though it is higher than the value of 1.6 determined for Atlantic cod at 10°C (Priede and Tytler 1977). The factorial aerobic scope of 3.7 calculated for Murray cod in our study is within the range for teleosts: greater than that determined for white crappie at 25°C (3.0; Parsons and Sylvester 1992), though approximately one-quarter of the value of 15.4 that was determined for sockeye salmon at 15°C (Brett and Glass 1973), which is hardly surprising given that Murray cod are sit-and-wait predators whereas salmon have a more active lifestyle (Korsmeyer et al. 1997).

As with any ratio, the factorial aerobic scope is particularly sensitive to changes in the denominator (minimum $\dot{M}o_2$). Therefore, conclusions resulting from interspecific comparisons of the factorial aerobic scope of the Murray cod remain tentative until measurements of minimum $\dot{M}o_2$ have been conducted. Nevertheless, it is not so much the amplitude, but rather the independence of temperature, of the factorial aerobic scope of the Murray cod that is of interest in this study. The fact that the factorial aerobic scope remained at 3.7 from 14°C to 29°C indicates that the absolute increase from rest to maximum exercise increases 3.7-fold for every given increment of temperature. Consequently, the absolute aerobic scope (maximum $\dot{M}o_2$ − resting $\dot{M}o_2$) would increase linearly with temperature and allow a greater absolute scope for activity at warmer temperatures, which is likely to be the reason why upstream migration for spawning in the natural environment occurs only after water temperature has risen to approximately 20°C (Cadwallader and Backhouse 1983; Kailola et al. 1993). In contrast are data for species of salmon (Brett and Glass 1973; Farrell 2002; Lee et al. 2003) and trout (Dickson and Kramer 1971; Taylor et al. 1996) that imply there is a small optimal temperature range within the annual operant range at which $\dot{V}_b$, and thus oxygen consumption rates, has an optimal gain from rest to maximum aerobic exercise.

The constant factorial increases in f_H and oxygen pulse determined for Murray cod suggest that the cardiovascular variables of this species have temperature-independent maximum gains that contribute to maximal oxygen transport during exercise. At the expense of a larger factorial aerobic scope at an optimal temperature, it is possible that the Murray cod has evolved a lower, but temperature-independent, factorial aerobic scope as an adaptation to the largely fluctuating and unpredictable thermal climate of southeastern Australia.

Acknowledgments

Damien O'Mahony and Justin O'Mahony are thanked for performing the surgery to implant loggers. Staff of the Marine and Freshwater Resources Institute, Snobs Creek, particularly Peter Grant, Peter Boyd, and Peter Ryder, are thanked for their hospitality and support with fish husbandry. T.D.C. was the recipient of an Australian Postgraduate Research Award.

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