

The swimming capacity of juvenile Murray cod (*Maccullochella peelii*): an ambush predator endemic to the Murray-Darling Basin, Australia

Nick S. Whiterod^{1,2}

¹Murray-Darling Freshwater Research Centre, PO Box 991, Wodonga, VIC 3690, Australia

²Charles Sturt University, School of Environmental Sciences, PO Box 789, Albury, 2640, NSW Australia

Accepted for publication August 29, 2012

Abstract – This study documented the swimming capacity of a large ambush predator, Murray cod *Maccullochella peelii*, endemic to the Murray-Darling Basin, Australia. It was evident that the species is a swimming generalist, maintaining moderate ability across all aspects of the swimming capacity parameters that were investigated. For instance, the species was capable of prolonged swimming performance (critical swimming speed, U_{crit} : absolute, 0.26–0.60 m·s⁻¹, relative, 1.15–2.20 BL s⁻¹) that was inferior to active fish species, but comparable with other ambush predators. The species had low energetic demands, maintaining a low mass-specific standard (21.3–140.3 mg·h⁻¹ kg⁻¹) and maximum active metabolic rate (75.5–563.8 mg·h⁻¹ kg⁻¹), which lead to a small scope for activity (maximum active metabolic rate–standard metabolic rate; 1.4–5.9). They were reasonably efficient swimmers (absolute and relative optimal swimming speed, 0.17–0.61 m·s⁻¹ and 0.77–1.93 BL·s⁻¹, respectively) and capable of repeat bouts of prolonged performance (recovery ratio = 0.99). Allometric changes in aspects of swimming capacity were realised with body mass, whereas broad swimming capacity was maintained across a wide range of temperatures. The swimming capacity demonstrated by *M. peelii* reflects a sit-and-wait foraging strategy that seeks to conserve energy characteristic of ambush predators, but with distinct features (e.g., lack of fast-start ability) that may reflect their evolution in some of the world's most hydrologically and thermally variable rivers.

Key words: Swimming capacity; body mass; temperature; ambush predator; *Maccullochella peelii*

Introduction

The swimming capacity of freshwater fish defines how they avoid predators and unfavourable conditions, seek and defend habitat, find and capture prey and undertake movement (Videler 1993). It encompasses the repeatability of prolonged (20 s–200 min), and burst (<20 s) performance, the energetic cost required to propel the fish through the water, and swimming efficiency (Beamish 1978). Such is the importance of swimming capacity, many researchers view it as a major determinant of ecological success and evolutionary fitness (Plaut 2001).

Freshwater fish show a wide range of swimming capacities, but often specialise in cruising, fast-starts, manoeuvrability or maintain generalist abilities (Webb 1984b). The majority of swimming capacity

assessments have focused solely on cruising specialists (see Beamish 1978; Hammer 1995; Videler 1993; Wolter & Arlinghaus 2003), and highlight efficient, prolonged swimming, strongly influenced by body mass and temperature (Beamish 1978; Boisclair & Tang 1993). Comparatively little, however, is known of the swimming capacity of ambush predators (Beamish 1978; Zeng et al. 2009), despite them playing important roles in many freshwater environments around the world, often regulating fish communities through trophic cascading, resource competition and behaviour alteration (cf. Moyle & Cech 2004).

Ambush predators are characterised by a sit-and-wait foraging strategy, where long periods of inactivity are interspersed with rapid high-energy predatory strikes (Webb 1984a). Consequently, typical ambush predators, such as Northern pike *Esox lucius* possess low

Whiterod

standard and active metabolic rates (Armstrong et al. 1992), and are capable of rapid burst performance (i.e., fast-start specialists), often at the expense of prolonged swimming performance (Harper & Blake 1990; Webb 1984a). Yet, many aspects of the swimming capacity of ambush predators, particularly those preferring warm-water habitats, have not been investigated, such as recovery ability, optimal swimming speed and minimum cost of transport. This information may shed light on their ecological function in the freshwater environments in which they have evolved (cf. Videler 1993).

Murray cod *Maccullochella peelii* Mitchell is a large (up to 113.6 kg), long-lived (up to 48 years) and slow-growing warm-water ambush predator endemic to the rivers of the Murray-Darling Basin (MDB) in south-eastern Australia (Lintermans 2007). *M. peelii* are apex predators and are likely to play an important role in the functioning of MDB rivers through top-down regulation of prey resources (Ebner 2006). Consistent with typical ambush predators, it is largely sedentary (Jones & Stuart 2007; Koehn et al. 2009), maintains a low standard metabolic rate (Clark et al. 2005), and is an opportunistic feeder (Baumgartner 2007; Ebner 2006). A proportion of adults have been shown to undertake upstream (up to 130 km) movements in late winter and early spring (Koehn et al. 2009), but juveniles appear to be less mobile (Jones & Stuart 2007) and only capable of moderate burst performance (Lyon 1999; Ryan et al. 2003). Yet, a more comprehensive exploration of range of aspects of prolonged swimming performance and energetics, across a range of sizes is warranted.

This study sort to provide the first assessment of the swimming capacity of *M. peelii* by investigating prolonged swimming performance (critical swimming speed and recovery ability) and energetics (standard metabolic rate, active metabolic rate, scope for activity, optimal swimming speed and minimum cost of transport) across juvenile body mass and at temperatures spanning the range experienced by the species in its natural environment. It is hypothesised that *M. peelii* will feature a moderate swimming capacity, consistent with other ambush predators, that is suited to energy conservation.

Materials and methods

Fish and holding conditions

The swimming capacity of juvenile *M. peelii* ($n = 42$) was investigated across a range of body sizes (wet mass, W , 57.6–791.9 g, total length, T_L , 160–386 mm, approximate age 1–3 years) at three temperatures (16, 20.5 and 25 °C; CSU Animal Ethics Code, #06/116). Fish were sourced from native fish hatcher-

ies in the southern MDB, and experiments were conducted at the Adaptational and Evolutionary Respiratory Physiology (AERP) Laboratory at La Trobe University (Bundoora, Victoria) and the Murray-Darling Freshwater Research Centre (MDFRC) Laboratory (Wodonga, Victoria). Fish were acclimated in well-aerated tanks, temperature was changed at 1 °C·day⁻¹ until it reached the experimental temperature and fish were acclimated for at least 7 days (see Ohlberger et al. 2007). Daily checks confirmed that oxygen concentration was maintained above 85% saturation (>6.0 mg O₂ l⁻¹) throughout the acclimation and experimentation period. A 12L: 12D photoperiod was maintained, and fish were fed an excess of food (chironomids, fish or pellets) twice daily.

Swimming respirometers

Swimming experiments were conducted in three purpose built intermittent flow Steffensen-type swimming respirometers (35, 87 and 137 L), capable of accommodating various sized fish (Steffensen et al. 1984). The three respirometers were similarly constructed: PVC pipe with clear acrylic swimming sections and flow rectifiers with a darkened upstream end. Flow velocity within each respirometer was regulated by a calibrated propeller and power supply (35 L and 87 L driven by a electric trolling motor connected to a Manson power supply [Manson; www.manson.com.hk]); 137 L employed a 245-mm diameter propeller connected to a Baldor VPT 34550 motor (The ABB Group; www.baldor.com) and ranged between 0.02–0.42 m·s⁻¹ (35 L), 0.02–0.46 m·s⁻¹ (87 L) and 0–1.22 m·s⁻¹ (137 L). Temperature and oxygen saturation were measured continuously (1 s response time) using calibrated oxygen and temperature electrodes (35 L - Loligo Systems and 87 L - HACH LDOTM HQ10; 137 L-HACH LDOTM sc100, accuracy of ±0.1 mg·l⁻¹. Loligo Systems; www.loligo systems.com and Hach; www.hach.com) and logged to a computer for processing.

Experimental procedure

The swimming experiments followed the repeat critical swimming speed (U_{crit}) protocol (Jain et al. 1998, 1997). Individual fish were weighed (W , nearest 0.1 g) and measured for total length (TL, nearest 1 mm) and then, introduced into an appropriately sized respirometer with a flow velocity of 0.3 BL·s⁻¹ (body lengths s⁻¹). Following a 30-min acclimation period, fish were given a practice swim, where flow velocity was increased by 0.2 BL·s⁻¹ every 2 min until fatigue, to estimate U_{crit} and familiarise fish to the respirometer (Jain et al. 1997). Fish were then left to recover overnight at 0.3 BL·s⁻¹ and generally

settled on the bottom of respirometer. The next day, the first U_{crit} trial was undertaken with flow velocity increased from acclimation ($0.3 \text{ BL}\cdot\text{s}^{-1}$) at $0.2 \text{ BL}\cdot\text{s}^{-1}$ increments every 20 min. At each flow velocity, the respirometer was sealed, and decline in oxygen concentration was measured (15 min measuring, 2 min flushing, 3 min waiting). Flow velocity was increased incrementally until the fish became fatigued (i.e., drifted downstream and collapsed against the back screen). At this point, the U_{crit} was ceased and flow velocity was immediately decreased to $0.3 \text{ BL}\cdot\text{s}^{-1}$ for the duration of the 1.5 h recovery period (Lee et al. 2003a). A second U_{crit} test and recovery period were then conducted.

After the second recovery period, fish were removed and morphological characteristics were determined (see below). Following this, the oxygen concentration was measured (over 30 min) in the empty respirometer to account for bacterial respiration, which was always negligible (<5% total metabolism). For all swimming experiments, the solid blocking effect (cross-sectional area of fish/cross-sectional area of respirometer) was always $\leq 10\%$, and no flow velocity correction was necessary (Bell & Terhune 1970).

For each measurement period, the mass-specific rate of active metabolic rate (M_A , $\text{mg O}_2 \text{ h}^{-1}\cdot\text{kg}^{-1}$) was calculated from the slope of the linear regression of the decline in oxygen concentration:

$$M_A = (s \cdot V_R \cdot \alpha) \cdot W^{-1} \quad (1)$$

where, s is the slope of the linear regression (% saturation per h), V_R is the volume of the respirometer minus the volume of the fish (L), α is the solubility of oxygen in water at the experimental temperature and salinity ($\text{mg O}_2 \cdot \text{l}^{-1}$) and W is the body mass of the fish (kg). Only measurements from significant oxygen concentration slopes ($P = 0.05$) were used.

Data analysis

Swimming performance

Swimming performance was assessed using both relative ($\text{BL}\cdot\text{s}^{-1}$) and absolute ($\text{m}\cdot\text{s}^{-1}$) U_{crit} protocol (Brett 1964):

$$U_{crit} = U_p + (T_p \cdot T_i^{-1}) \cdot U_i \quad (2)$$

where, U_p is the velocity at which the fish last swam for the full period, U_i the flow velocity increment, T_p is the elapsed time (min) from the last flow velocity increment to exhaustion and T_i is the time between

flow velocity increments. The ability of fish to recover following prolonged swimming and repeat performance was expressed as a recovery ratio (RR), representing the ratio of between the U_{crit} from the first (U_{crit1}) and second swimming trials (U_{crit2}). A $RR = 1$ indicating U_{crit} performance was identical for both swimming trials (Jain et al. 1998).

Swimming energetics

For each fish, the relationship between mass-specific M_A ($\text{mg O}_2 \text{ h}^{-1}\cdot\text{kg}^{-1}$) and relative U_{crit} ($\text{BL}\cdot\text{s}^{-1}$) was best described by a power function (Videler 1993):

$$M_A = M_S + \gamma U^\beta \quad (3)$$

where, M_A is defined by the standard metabolic rate (M_S , $\text{mg O}_2 \text{ h}^{-1}\cdot\text{kg}^{-1}$) and the constants, γ and β . The M_A at U_{crit} is a suitable measure of maximum active metabolic rate (M_{Amax} , $\text{mg O}_2 \text{ h}^{-1}\cdot\text{kg}^{-1}$; Enders et al. 2006) and was estimated by inserting the U_{crit} determined from equation 2 into equation 3. For each fish, the scope for activity (SFA) was described simply as the ratio of M_{Amax} and M_S (Fry 1957). Differentiation of equation 3 with respect to swimming speed (U) and zero setting gives the energetically optimal swimming speed (U_{opt} , $\text{BL}\cdot\text{s}^{-1}$), the swimming speed associated with the minimum energetic costs per unit distance. U_{opt} represents the swimming speed where the ratio of the M_A to swimming speed reaches a minimum (Videler 1993):

$$U_{opt} = [M_S / (\beta - 1) \cdot \gamma]^{1/\beta} \quad (4)$$

The energy expenditure during swimming reaches a minimum at U_{opt} (indicating the minimum cost of transport, COT_{min}) and equates to the minimum energy needed by a fish to swim one unit distance (Videler 1993):

$$COT_{min} = M_{Aopt} \cdot U_{opt}^{-1} \quad (5)$$

where, the minimum cost of transport (COT_{min} , converted to $\text{J}\cdot\text{m}^{-1}\cdot\text{kg}^{-1}$) is the active metabolic rate (M_{Aopt} , $\text{mg}\cdot\text{h}^{-1}\cdot\text{kg}^{-1}$) at U_{opt} (converted to $\text{m}\cdot\text{h}^{-1}$). To achieve these estimates, M_A values ($\text{mg}\cdot\text{h}^{-1}\cdot\text{kg}^{-1}$) were converted to energetic units ($\text{J}^{-1}\cdot\text{m}^{-1}\cdot\text{kg}^{-1}$) using a standard oxycaloric equivalent of $14.2 \text{ J}\cdot\text{mg}\cdot\text{O}_2^{-1}$ (Hepher 1988).

Morphology

The streamline nature of the body shape of all fish was explored using a fineness ratio (FR): total length

Whiterod

divided by the square root of maximum depth and maximum breadth (Blake 1983). The morphology of the caudal peduncle was quantified using a depth factor (*CPDF*): depth of caudal peduncle divided by maximum depth of the body (Webb & Weihs 1986).

Statistics

The prolonged performance from the first and second swim trials was compared using a paired student's *t*-test, and where differences were not significant, average U_{crit} (from both trials) was estimated. To explore the relationships between swimming capacity variables and body mass and temperature, multivariate non-linear regression was used. Standard relationships were used to inform model development: body mass generally influences parameters allometrically (aW^b) or linearly ($a+bW$) (Beamish 1978), whereas variables change according to exponential (e^{cT}), linear ($a+bW$) and parabolic ($a + bT + cT^2$) relationships with temperature (Angilletta et al. 2002; Beamish 1978; Lee et al. 2003b). Subsequently, a total of 6 combinations [(1) $aW^b \cdot e^{cT}$; (2) $a + bW \cdot e^{cT}$; (3) $aW^b \cdot cT + dT^2$; (4) $a+bW \cdot cT + dT^2$; (5) $aW^b \cdot c + dT$; and (6) $a+bW + cT$] were investigated during the regression analysis.

All models were tested for the significance of single parameter estimates, and models containing non-significant estimates were removed. The remaining models were evaluated using the Akaike information criteria (AIC; Akaike 1974):

$$AIC = 2k + n \cdot \ln(RSS \cdot n^{-1}) \quad (6)$$

where, k is the number of parameters, n is the number of individual data points (in the present study,

$n = 42$) and RSS is the residual sum of squares. The regression model with the lowest AIC (most negative value) was deemed most appropriate and robust (Akaike 1974). All parameter estimates are mean \pm standard error, and the significance level for regression models was set at $P = 0.05$. All statistical analyses were performed using Sigmaplot 11 (Systat Software Inc.; www.sigmaplot.com).

Results

Maccullochella peelii always swam using body caudal fin (BCF) propulsion, and often employed burst-and-coast swimming at higher flow velocities (i.e., typically >80–90% of U_{crit}). For each fish, U_{crit} did not vary significantly between the first and second swim trials (*t*-test, d.f. = 41, $P > 0.05$) and mean relative prolonged swimming performance ranged from 1.15 to 2.20 BL s^{-1} and absolute prolonged swimming performance between 0.26 and 0.60 $m \cdot s^{-1}$ (Fig. 1a,b). Multivariate regression analysis revealed that relative U_{crit} declined with body mass (*t*-test, d.f. = 41, $P < 0.001$) and increased exponentially with temperature (*t*-test, d.f. = 41, $P < 0.001$), leading to a significant combined model (ANOVA *F*-tests, d.f. = 39, $P < 0.001$, $r^2 = 0.40$; Table 1). In absolute terms, U_{crit} increased with body mass (*t*-test, d.f. = 41, $P < 0.05$) and temperature (*t*-test, $n = 42$, $P < 0.001$), leading to a significant combined model (ANOVA, d.f. = 39, $P < 0.001$, $r^2 = 0.70$) explaining 70.0 % of the variation. The recovery ratio (*RR*), ranged from 0.81 to 1.13, but did not vary significantly with body mass or temperature ($P > 0.05$ for all ANOVA *F*-tests), leading to a mean *RR* for all fish of 0.99 (± 0.01).

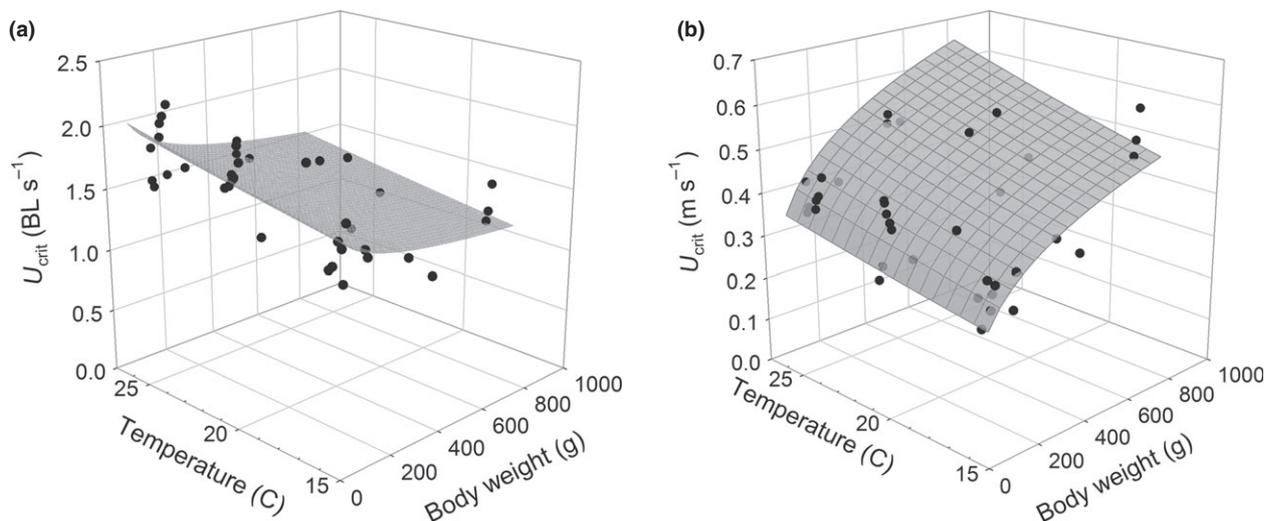


Fig. 1. Relationship between the (a) relative ($BL \cdot s^{-1}$), and (b) absolute ($m \cdot s^{-1}$) critical swimming speed of juvenile *M. peelii* and body weight (g), and temperature ($^{\circ}C$). See Table 1 for model details for each parameter.

Table 1. Summary of multivariate regression analysis exploring the influence of body weight and temperature on each of the parameters of (*M. peelii*) swimming capacity.

Parameter	Notation (units)	Best model	Estimate			Model outputs		
			a (\pm SE)	b (\pm SE)	c (\pm SE)	r^2	F	P
Absolute critical swimming speed	U_{crit} (m·s ⁻¹)	$aW^b \cdot e^{(c \cdot T)}$	0.07 (\pm 0.01)	0.24 (\pm 0.03)	0.02 (\pm 0.01)	0.70	43.11	<0.001
Relative critical swimming speed	U_{crit} (BL s ⁻¹)	$aW^b \cdot e^{(c \cdot T)}$	1.91 (\pm 0.40)	-0.10 (\pm 0.03)	-0.02 (\pm 0.01)	0.40	12.41	<0.001
Recovery ratio	RR	-	0.99 (\pm 0.01)	-	-	-	-	>0.05
Standard metabolic rate	M_S (mg·h ⁻¹ ·kg ⁻¹)	$aW^b \cdot e^{(c \cdot T)}$	261.25 (\pm 81.38)	-0.32 (\pm 0.05)	0.02 (\pm 0.01)	0.65	32.52	<0.001
Maximum active metabolic rate	M_{Amax} (mg·h ⁻¹ ·kg ⁻¹)	$aW^b \cdot e^{(c \cdot T)}$	1087.29 (\pm 471.22)	-0.47 (\pm 0.07)	0.05 (\pm 0.01)	0.70	41.15	<0.001
Scope for activity	SFA (-)	$aW^b \cdot e^{(c \cdot T)}$	4.16	-0.15	0.02	-	-	-
Absolute optimal swimming speed	U_{opt} (m·s ⁻¹)	$aW^b \cdot e^{(c \cdot T)}$	0.03 (\pm 0.02)	0.35 (\pm 0.06)	0.01 (\pm 0.01)	0.54	19.63	<0.001
Relative optimal swimming speed	U_{opt} (BL s ⁻¹)	-	1.11 (\pm 0.04)	-	-	-	-	>0.05
Minimum cost of transport	COT_{min} (mg·m ⁻¹ ·kg ⁻¹)	aW^b	37.95 (\pm 13.39)	-0.57 (\pm 0.07)	-	0.72	87.30	<0.001
Fineness ratio	FR (-)	aW^b	7.76 (\pm 0.54)	-0.05 (\pm 0.01)	-	0.31	15.74	<0.001
Caudal peduncle depth factor	CPDF (-)	-	0.45 (\pm 0.01)	-	-	-	-	-

The standard metabolic rate (M_S) of *M. peelii* ranged between 21.3 and 140.3 mg·h⁻¹·kg⁻¹, whereas active metabolic rate (M_{Amax}) varied from 75.5 to 563.8 mg·h⁻¹·kg⁻¹ (Fig. 2). Both M_S and M_{Amax} declined allometrically with body mass (M_S , *t*-test, d.f. = 41, $P < 0.001$; M_{Amax} , *t*-test, d.f. = 41, $P < 0.001$) and increased exponentially with temperature (M_S , *t*-test, d.f. = 41, $P < 0.05$; M_{Amax} , *t*-test, d.f. = 41, $P < 0.001$). The combined models for M_S and M_{Amax} explained 70.2% and 65.0 % of the variation, respectively (M_S , ANOVA *F*-test, d.f. = 39, $P < 0.001$; M_{Amax} , ANOVA *F*-test, d.f. = 39, $P < 0.001$). The scope

for activity (SFA) determined from the modelled metabolic rates ranged between 1.4 and 5.9, declining with body mass and increasing exponentially with temperature (Fig. 3).

In terms of swimming efficiency, the absolute and relative optimal swimming speed (U_{opt}) ranged from 0.17 to 0.61 m·s⁻¹ and 0.77 to 1.93 BL·s⁻¹, respectively (Fig. 4). Relative U_{opt} did not vary significantly with either body mass or temperature (average, 1.11 \pm 0.04 BL·s⁻¹), and therefore, no combined model was performed ($P > 0.05$ for all ANOVA *F*-tests). Conversely, changes in body mass

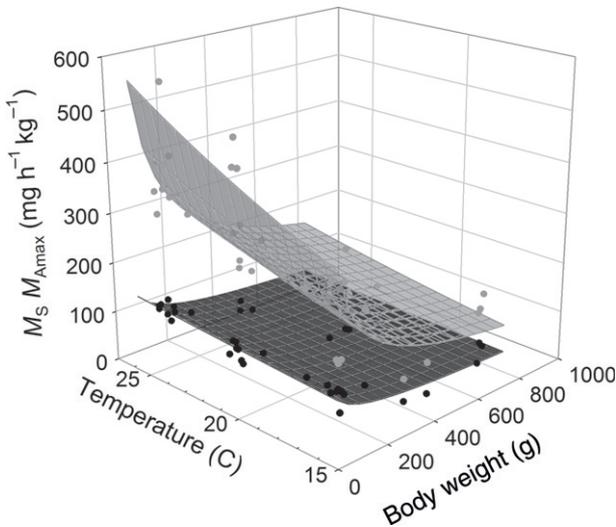


Fig. 2. Relationship between the weight-specific standard (mg O₂ h⁻¹·kg⁻¹, ●) and maximum active metabolic rate (mg O₂ h⁻¹·kg⁻¹, ○) of juvenile *M. peelii*, and body weight (g) and temperature (°C). See Table 1 for model details for each parameter.

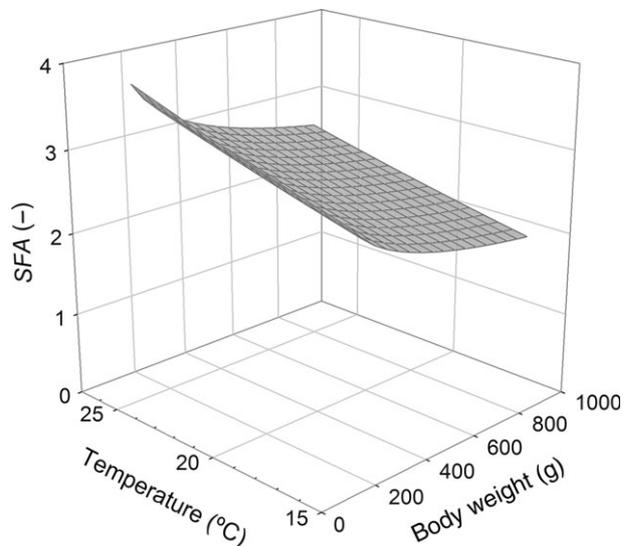


Fig. 3. Relationship between modelled scope for activity (SFA) of juvenile *M. peelii* and body weight (g), and temperature (°C). See Table 1 for model details for each parameter.

Whiterod

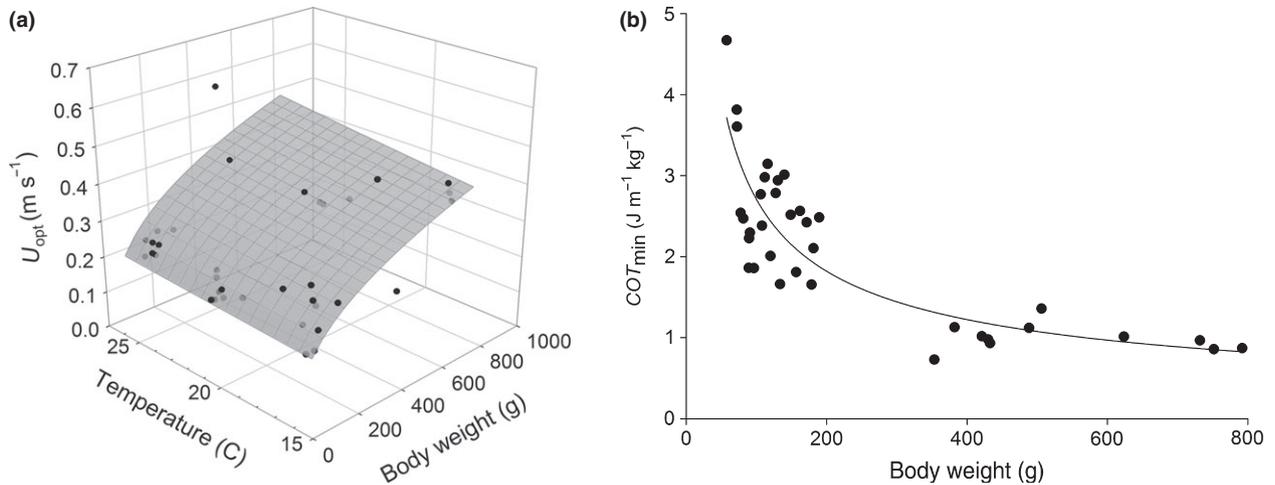


Fig. 4. Relationship between the (a) absolute optimal swimming speed ($m\ s^{-1}$) of juvenile *M. peellii*, and body weight (g), and temperature ($^{\circ}C$), and (b) minimum cost of swimming ($J\ km^{-1}\ kg^{-1}$) with body weight (g). See Table 1 for model details for each parameter.

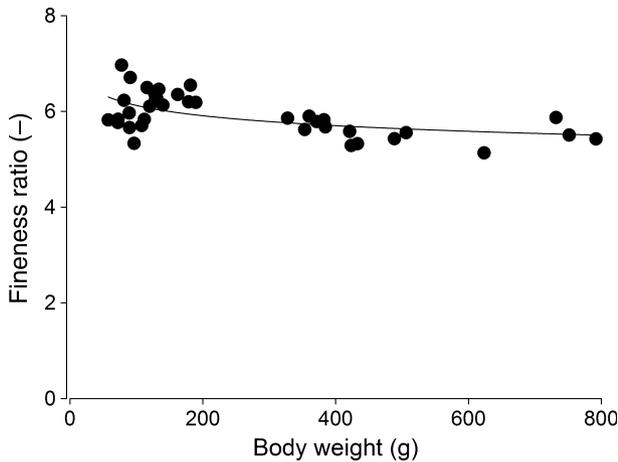


Fig. 5. Relationship between the fineness ratio (–) of juvenile *M. peellii* and body weight (g). See Table 1 for model details for each parameter.

(t -test, d.f. = 41, $P < 0.001$) and temperature (t -test, d.f. = 41, $P < 0.05$) significantly influenced absolute U_{opt} , resulting in a combined model (ANOVA F -test, $n = 42$, $P < 0.001$) explaining 54.3 % of the variation. Corresponding the minimum cost of transport (COT_{min}), values ranged from 4.67–0.73 $J\ m^{-1}\ kg^{-1}$, declining with body mass (t -test, d.f. = 40, $P < 0.001$), but was unrelated to temperature (t -test, d.f. = 41, $P = 0.23$), with a significant single allometric function best describing the relationship between COT_{min} and body mass (ANOVA F -test, d.f. = 40, $P < 0.001$, $r^2 = 0.61$; Fig. 4).

The fineness ratio (FR) of *M. peellii* ranged from 5.13 to 6.96, decreasing with body mass (ANOVA F -test, d.f. = 40, $P < 0.001$, $r^2 = 0.31$), whereas the caudal peduncle depth factor ($CPDF$, 0.36–0.56) did not change with body mass (ANOVA F -test, d.f. = 40, $P > 0.05$, average, 0.45 ± 0.01 ; Fig. 5).

Discussion

Comparative swimming capacity

Many aspects of the swimming capacity of *M. peellii* were consistent with those of typical ambush predators. For instance, the species maintained low metabolic rates, and as a consequence, have small energetic demands ($SFA = 1.4$ – 5.9) compared with more active species (up to 15.4; Brett & Glass 1973). Similarly, the moderate prolonged swimming performance of *M. peellii* was consistent (1.15 – $2.20\ BL\ s^{-1}$) with other ambush predators, tested over a similar size range, such as *E. lucius*, (0.8 – $3.2\ BL\ s^{-1}$), Burbot *Lota lota* (0.7 – $3.0\ BL\ s^{-1}$) and Southern catfish *Silurus meridionalis* (1.9 – $3.4\ BL\ s^{-1}$; Jones et al. 1974; Zeng et al. 2009), yet inferior to other freshwater fish (Videler 1993; Wolter & Arlinghaus 2003). For instance, an absolute U_{crit} ($0.48\ m\ s^{-1}$) for a 300-mm *M. peellii* is only one-third of what would be expected using the generalised freshwater fish relationship ($1.47\ m\ s^{-1}$) derived by Wolter & Arlinghaus (2003).

There is limited information available on the swimming efficiency (U_{opt} and COT_{min}), nor on the recovery ratio, for ambush predators. The present study indicates that *M. peellii* have lower swimming efficiency than most active freshwater fish species: swimming optimally slower (U_{opt}) whilst incurring consistently greater energetic costs (COT_{min}), compared with other freshwater fish (Videler 1993). However, the magnitude of its relative U_{opt} is within the theoretically determined range (1 – $2\ BL\ s^{-1}$) for efficient swimming (Weihs 1973), suggesting moderate efficiency. These efficiencies are, in part, attributed to a degree of streamlineness with a FR (5.13–6.96) within the range for optimal swimming in

freshwater fish (i.e., $FR = 2-7$) and close to the optimal levels (approximately 4.5; Blake 1983). The recovery ability of *M. peelii* ($RR \sim 1$) appears similar to active species, although these studies used shorter recovery periods (45 min; Jain et al. 1998; Lee et al. 2003a) and suggests that repeatability of prolonged performance may be a feature of the swimming capacity of ambush predators.

An intriguing feature of the swimming capacity of *M. peelii* is the apparent lack of fast-start ability (Lyon 1999; Ryan et al. 2003). Juvenile stages of notable ambush predators, such as *E. lucius*, achieve burst performance of $3.97 \text{ m}\cdot\text{s}^{-1}$ (Harper & Blake 1990), yet *M. peelii* reaches considerably lower burst speeds ($1.40 \text{ m}\cdot\text{s}^{-1}$), a level more consistent with active species (Lyon 1999; Ryan et al. 2003). It is evident that *M. peelii* possess morphological features (number of vertebrae and deep body) that are not well suited to fast-start performance (Lyon 1999). Additional morphological deficiencies such as a small caudal peduncle relative to the height of its caudal fin ($CPCF$ approximately 0.4–0.5, with $CPDF$ of typical ambush predators close to 1; Webb & Weihs 1986) that limit the production of the thrust necessary for fast-starts were highlighted in the present study. Clearer insight into the burst performance of *M. peelii* could be gained from further experimentation across body mass and temperature and with complementary morphological and physiological investigation.

Influence of body mass and temperature

The swimming capacity of juvenile *M. peelii* was strongly influenced by body mass, with increases in body mass significantly improving absolute U_{crit} performance and swimming efficiency (absolute U_{opt} and COT_{min}), but reducing relative performance and efficiency. These patterns reflect ontogenetic changes in the competing influence of physiological and morphological trade-offs between thrust and drag during swimming (Beamish 1978). Faster and more efficient absolute swimming by larger individuals suggests that the trade-off becomes more favourable with size, with improvements in thrust sufficient to overcome any increases in drag imposed by a larger frontal area (Webb 1975).

In relative terms, however, declines in the trade-off ensure that smaller *M. peelii* are capable of faster performance and can swim optimally faster with lower energetic cost than larger individuals. Mass-specific M_S and M_{Amax} declined allometrically with body mass, but not consistently, ensuring declines in SFA with body mass. This suggests that whilst smaller individuals have greater relative metabolic costs, they have more metabolic energy available for important

swimming activities than larger *M. peelii*. Interestingly, the recovery ability of *M. peelii* did not change with body mass, despite the expectation of improved recovery of larger individuals (Lee et al. 2003a).

The basis of the physiological and morphological changes in the absolute and relative thrust-drag trade-off is unclear for *M. peelii*. In other freshwater fish, changes in thrust and drag have been linked to physiological (propulsive systems, muscle type and power) and morphological (surface roughness and streamlining) considerations (Webb 1975; Webb & Weihs 1986). From the present study, it is evident that streamlining (as revealed by declines in FR towards the optimal ratio of 4.5) is important as a means to minimise drag as *M. peelii* grow but further investigations could shed light on these issues.

With increases in temperature, exponential increases (temperature exponents, 0.01–0.05) occurred across most aspects of *M. peelii* swimming capacity. *Maccullochella peelii* swim absolutely faster and more efficiently at higher temperatures within the range tested; presumably a reflection of greater metabolic capacity to produce thrust (Beamish 1978). Furthermore, M_S and M_{Amax} increased exponentially with temperature, resulting in greater metabolic capacity, as expressed by the SFA at higher temperatures (2.4 at 16 °C to 3.0 at 25 °C for a 500 g fish). Clark et al. (2005), however, reported a constant SFA for larger individuals (approximately 1800 g) across a wider range of temperatures (15–29 °C). The nature of the discrepancy remains unclear, but may reflect the different body sizes explored.

Several aspects of the swimming capacity of *M. peelii* showed insensitivity to temperature. For instance, measures of swimming efficiency (relative U_{opt} and COT_{min}) did not change with temperature, and, as in other species, may reflect adaptation to thermally fluctuating environments (Claireaux et al. 2006; Ohlberger et al. 2007). Furthermore, improved recovery at higher temperatures, due to greater metabolic capacity to clear excess postoxygen consumption ($EPOC$), was expected (Jain & Farrell 2003), yet the RR of *M. peelii* remained constant (approximately 1). The temperature insensitivity of their recovery ability may indicate that the period of recovery (1.5 h) at all temperatures was sufficient to allow metabolic recovery necessary to repeat prolonged performance, or it could represent another adaptation to variable temperatures. An understanding of the $EPOC$ and repeat swimming ability following shorter recovery periods would be insightful (Lee et al. 2003a).

In general, *M. peelii* maintain swimming capacity across a wide range of temperatures, apparently lacking greater performance at specific temperatures (cf. Huey & Hertz 1984). Whilst this does suggest

Whiterod

physiological adaptation to thermally fluctuating environments (Clark et al. 2005), the greatest swimming capacity of many species often corresponds with the species' preferred temperature (Ohlberger et al. 2008; Ojanguren and Brana, 2000). Juvenile *M. peelii* prefer temperatures of 29 °C (Ryan et al. 2003), which may represent the optimal temperature for its swimming capacity. This could be resolved through exploration of aspects of its swimming capacity at this preferred temperature.

Ecological insight

It is believed that the swimming capacity of freshwater fish reflects its ecological functioning in the environment in which they have evolved (Videler 1993). It is evident that *M. peelii* possess broad and moderate ability across all aspects of its swimming capacity, and a low energy demand suited to energy conservation. This generalist swimming capacity may be explained by the river environments to which it is endemic. *M. peelii* occupies demersal main channel habitats dominated by woody structure (Jones & Stuart 2007; Koehn 2009a,b) in some of the world's most hydrologically and thermally variable rivers in the world. Consequently, swimming generalisation can be seen as a means to maximise its ability to survive and grow within these variable environments. Furthermore, the breadth of its swimming capacity may reflect the variety of swimming activities that *M. peelii* undertakes, including holding position against the prevailing flow velocity for extended periods, predatory strikes and, in the case of adults, undertaking potentially substantial upstream movements (Jones & Stuart 2007; Koehn 2009a; Koehn et al. 2009).

The strong association of *M. peelii* with woody structure may further explain their swimming capacity (Koehn 2009a). Woody structure acts to create lower flow velocity habitats compared with the middle channel of a river and lessens energy expenditure and the need for elevated prolonged performance (Crook & Robertson 1999; Koehn 2009a). Similarly, the association with woody structure provides insight into the lack of burst performance, as woody structure may render rapid bursts to capture locally abundant non-evasive food resources or escape predators unnecessary (Crook & Robertson 1999; Webb 1984a). Furthermore, many of the food resources consumed by *M. peelii* are relatively inactive, and the active components of its diet such as the native Golden perch *Macquaria ambigua* possess inferior burst performance (Lyon et al. 2008).

The present study focused on juvenile *M. peelii* as opposed to adults. Given the strong influence of body mass, it is possible that the outcomes may not reflect the swimming capacity of larger individuals of

the species. It is anticipated that larger *M. peelii* will be capable of improved absolute U_{crit} performance but with greater energetic costs compared with juveniles (Beamish 1978). Furthermore, larger individuals may be more efficient swimmers achieving greater optimal swimming speeds with lower cost of transport (Videler 1993). If confirmed, these patterns would explain the increased capacity for large-scale movement in adults (>650 mm) compared with juveniles (Jones & Stuart 2007; Koehn et al. 2009). Resolution of the swimming capacity of these larger *M. peelii* is important, but poses substantial difficulties in conducting experiments with such large animals.

Conclusions

This study provided the first comprehensive assessment of the swimming capacity of juvenile *M. peelii*. It is a generalist swimmer having evolved broad and moderate ability across all aspects of its swimming capacity. Allometric changes in aspects of swimming capacity were realised with body mass, whereas broad swimming capacity was maintained across a wide range of temperatures. The magnitude of its swimming capacity is often inferior to many freshwater fish (particularly active species), but comparable with ambush predators, although it lacks the fast-start specialisation of many other ambush predators. Furthermore, *M. peelii* have low energetic demands (standard and active metabolic rate) and were moderately efficient swimmers with sufficient ability to repeat its prolonged performance. Such a swimming capacity reflects a sit-and-wait foraging strategy that seeks to conserve energy characteristic of ambush predators, but with distinct features (e.g., lack of fast-start ability) that may reflect their evolution in some of the world's most hydrologically and thermally variable rivers.

Acknowledgements

This study formed part of a PhD funded by the Mallee Catchment Management Authority (Mallee CMA). This manuscript was finalised with the financial support of a Charles Sturt University Writing Up Award. Thanks to my supervisory team, Shaun Meredith (MDFRC), Paul Humphries (CSU), Brad Sherman (CSIRO), John Koehn (Arthur Rylah Institute) and Robyn Watts (CSU) for considerable discussion and support. I wish to thank Peter Frappell (La Trobe University) for his advice, encouragement and accessibility. I would also like to thank Brett Ingram and Marissa Bailey (Victorian Department of Primary Industries), Simon Noble (Brimin Lodge), Rowena Henry (Glencoe Fish Hatchery) and Peter Van Lierop (Alexandra Fish Farm) for supplying experimental fish. The manuscript was greatly improved by comments from Shaun Meredith and Sylvia Zukowski (MDFRC), Paul Humphries and Robyn Watts (CSU), Brad Sherman (CSIRO), John Koehn (ARI), the editor and two anonymous referees.

References

- Akaike, H. 1974. A new look at statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.
- Angilletta, M.J.J., Niewiarowski, P.H. & Navasc, C.A. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27: 249–268.
- Armstrong, J.D., Priede, I.G. & Lucas, M.C. 1992. The link between respiratory capacity and changing metabolic demands during growth of northern pike, *Esox lucius* L. *Journal of Fish Biology* 41B: 65–75.
- Baumgartner, L.J. 2007. Diet and feeding habits of predatory fishes upstream and downstream of a low-level weir. *Journal of Fish Biology* 70: 879–894.
- Beamish, F.W.H. 1978. Swimming capacity. In: Hoar, W.S. & Randall, D.J., eds. *Fish physiology*. New York: Academic Press, pp. 101–189.
- Bell, W.H. & Terhune, L.D.B. 1970. Water tunnel design for fisheries research. *Fish Research Board of Canada Technical Report* 195: 1–69.
- Blake, R.W. 1983. *Fish locomotion*. London: Cambridge University Press.
- Boisclair, D. & Tang, M. 1993. Empirical analysis of the influence of swimming pattern on the net energetic cost of swimming in fishes. *Journal of Fish Biology* 42: 169–183.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of Fisheries Research Board of Canada* 21: 1183–1226.
- Brett, J.R. & Glass, N.R. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *Journal of Fisheries Research Board of Canada* 30: 379–387.
- Claireaux, G., Couturier, C. & Groison, A.L. 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). *Journal of Experimental Biology* 200: 3420–3428.
- Clark, T.D., Ryan, T., Ingram, B.A., Woakes, A.J., Butler, P. J. & Frappell, P.B. 2005. Factorial aerobic scope is independent of temperature and primarily modulated by heart rate in exercising Murray cod (*Maccullochella peelii peelii*). *Physiological and Biochemical Zoology* 78: 347–355.
- Crook, D.A. & Robertson, A.I. 1999. Relationships between riverine fish and woody debris: implications for lowland rivers. *Marine and Freshwater Research* 50: 941–953.
- Ebner, B. 2006. Murray cod an apex predator in the Murray River, Australia. *Ecology of Freshwater Fish* 15: 510–520.
- Enders, E.C., Boisclair, D., Boily, P. & Magnan, P. 2006. Effect of body mass and water temperature on the standard metabolic rate of juvenile yellow perch, *Perca flavescens* (Mitchill). *Environmental Biology and Fishes* 76: 399–407.
- Fry, F.E.J. 1957. The aquatic respiration of fish. In: Brown, M. S., ed. *The physiology of fishes*. New York: Academic Press.
- Hammer, C. 1995. Fatigue and exercise tests with fish. *Comparative Biochemistry and Physiology* 112A: 1–20.
- Harper, B.G. & Blake, R.W. 1990. Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*. *Journal of Experimental Biology* 150: 321–342.
- Hepher, B. 1988. *Nutrition of pond fishes*. Cambridge: Cambridge University Press.
- Huey, R.B. & Hertz, P.E. 1984. Is a jack-of-all temperatures a master of none? *Evolution* 38: 441–444.
- Jain, K.E. & Farrell, A.P. 2003. Influence of seasonal temperature on the repeat swimming performance of rainbow trout *Oncorhynchus mykiss*. *Journal of Experimental Biology* 206: 3569–3579.
- Jain, K.E., Hamilton, J.C. & Farrell, A.P. 1997. Use of a ramp velocity test to measure critical swimming speed in Rainbow trout (*Oncorhynchus mykiss*). *Comparative Biochemistry and Physiology* 117A: 441–444.
- Jain, K.E., Birtwell, I.K. & Farrell, A.P. 1998. Repeat swimming performance of mature sockeye salmon following a brief recovery period: a proposed measure of fish health and water quality. *Canadian Journal of Zoology* 76: 1488–1496.
- Jones, M.J. & Stuart, I.G. 2007. Movements and habitat use of common carp (*Cyprinus carpio*) and Murray cod (*Maccullochella peelii peelii*) juveniles in a large lowland Australian river. *Ecology of Freshwater Fish* 16: 210–220.
- Jones, D.R., Kiceniuk, J.W. & Bamford, O.S. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. *Journal of the Fisheries Research Board of Canada* 31: 1641–1647.
- Koehn, J.D. 2009a. Multi-scale habitat selection by Murray cod *Maccullochella peelii peelii* in two lowland rivers. *Journal of Fish Biology* 75: 113–129.
- Koehn, J.D. 2009b. Using radio telemetry to evaluate the depths inhabited by Murray cod (*Maccullochella peelii peelii*). *Marine and Freshwater Research* 60: 317–320.
- Koehn, J.D., McKenzie, J.A., O'Mahony, D.J., Nicol, S.J., O'Connor, J.P. & O'Connor, W.G. 2009. Movements of Murray cod (*Maccullochella peelii peelii*) in a large Australian lowland river. *Ecology of Freshwater Fish* 18: 594–602.
- Lee, C.G., Farrell, A.P., Lotto, A., Hinch, S.G. & Healey, M. C. 2003a. Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O.kisutch*) salmon following critical speed swimming. *Journal of Experimental Biology* 206: 3253–3260.
- Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S. G. & Healey, M.C. 2003b. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *Journal of Experimental Biology* 206: 3239–3251.
- Lintermans, M. 2007. *Fishes of the Murray-Darling basin: an introductory guide*. Canberra: Murray-Darling Basin Commission.
- Lyon, J.P. 1999. The effect of size on the fast-start performances of three species of native Australian fish. Honours Thesis. Wodonga: La Trobe University.
- Lyon, J.P., Ryan, T.J. & Scroggie, M.P. 2008. Effects of temperature on the fast-start swimming performance of an Australian freshwater fish. *Ecology of Freshwater Fish* 17: 184–185.
- Moyle, P.B. & Cech, J.J. 2004. *Fishes: an introduction to ichthyology*. Upper Saddle River: Prentice Hall. 726 pp.
- Ohlberger, J., Mehner, T., Staaks, G. & F., HÖLKER. 2008. Temperature-related physiological adaptations promote ecological divergence in a sympatric species pair of temperate freshwater fish, *Coregonus* spp. *Functional Ecology* 22: 501–508.

Whiterod

- Ohlberger, J., Staaks, G. & Hölker, F. 2007. Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendace (*Coregonus albula*). *Journal of Comparative Physiology B* 177: 905–916.
- Ojanguren, A.F. & Brana, F. 2000. Thermal dependence of swimming endurance in juvenile brown trout *Journal of Fish Biology* 56: 1342–1347.
- Plaut, I. 2001. Critical swimming speed: its ecological relevance. *Comparative Biochemistry and Physiology* 131A: 41–50.
- Ryan, T., Lennie, R. & Lyon, J.. 2003. Thermal rehabilitation of the southern Murray-Darling basin. Final Report to Agriculture, Forestry, Fisheries Australia MD 2001 Fish Rehab Program. Heidelberg: Arthur Rylah Institute for Environmental Research, Victorian Department of Natural Resources and Environment.
- Steffensen, J.F., Johansen, K. & Bushnell, P.G. 1984. An automated swimming respirometer. *Comparative Biochemistry and Physiology* 79A: 437–440.
- Videler, J.J. 1993. *Fish swimming*. London: Chapman and Hall. 260 pp.
- Webb, P.W. 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of Fisheries Research Board of Canada* 190: 31–159.
- Webb, P.W. 1984a. Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* 24: 107–120.
- Webb, P.W. 1984b. Form and function in fish swimming. *Scientific American* 251: 58–68.
- Webb, P.W. & Weihs, D. 1986. Functional locomotor morphology of early life stages of fishes. *Transactions of the American Fisheries Society* 115: 115–127.
- Weihs, D. 1973. Optimal fish cruising speed. *Nature* 245: 48–50.
- Wolter, C. & Arlinghaus, R. 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. *Reviews in Fish Biology and Fisheries* 13: 63–89.
- Zeng, L.Q., Cao, Z.D., Fu, S.J., Peng, J.L. & Wang, Y.X. 2009. Effect of temperature on swimming performance in juvenile southern catfish (*Silurus meridionalis*). *Comparative Biochemistry and Physiology* 153A: 125–130.