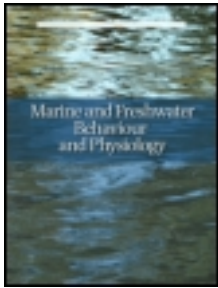


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Marine and Freshwater Behaviour and Physiology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/gmfw20>

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Published online: 17 Jul 2013.

To cite this article: Marine and Freshwater Behaviour and Physiology (2013): Refining the activity component of a juvenile fish bioenergetics model to account for swimming costs, Marine and Freshwater Behaviour and Physiology, DOI: 10.1080/10236244.2013.819155

To link to this article: <http://dx.doi.org/10.1080/10236244.2013.819155>

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Refining the activity component of a juvenile fish bioenergetics model to account for swimming costs

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(Received 26 October 2012; final version received 6 June 2013)

We develop a swimming costs model that accounts for the influence of flow velocity and body weight on the net active metabolic rate of Murray cod (*Maccullochella peelii*). Laboratory trials indicated that swimming costs increased with flow velocity (exponent = 2.36) and declined allometrically with body weight (exponent = -0.27). The newly derived swimming costs model provided a more dynamic estimate of Murray cod energy consumption, which explained 74% of variation in the swimming costs. This new model was compared to traditional bioenergetics models (fixed proportion and optimal swimming speed) to determine swimming costs in a variable temperature (6.4–26.1 °C) and flow velocity (0.06–0.46 m s⁻¹) regime downstream of a large hypolimnetic-releasing impoundment on a major Australian river. Incorporating species-specific swimming cost models, such as the one developed here, into bioenergetics modelling allows the exploration of the impact of flow velocity in lotic systems on the growth responses of freshwater fish.

Keywords: activity component; bioenergetics model; swimming costs; Murray Cod; *Maccullochella peelii*

Introduction

Fish bioenergetics models describe the allocation of consumed energy into metabolic demand (standard metabolism [M_S], active metabolism [M_A], digestive metabolism [M_D]), wastes (W) and growth (G) (Kitchell et al. 1977). These models have been developed for an increasing number of fish species (Hartman & Kitchell 2008) to investigate their habitat use (Ciannelli et al. 1998), predator–prey relationships (Vatland et al. 2008), the role of fish in nutrient cycling (Bunnell et al. 2005), the impacts of invading species (Ruzycki et al. 2003) and impacts of climate change (Petersen & Kitchell 2001) in lentic systems. The models also represent a theoretical basis to assess the impacts imposed by the regulation of lotic systems, particularly the alteration of discharge and temperature regimes downstream of hypolimnetic-releasing impoundments (Bevelheimer 2002; Murchie et al. 2008). Whilst adverse bioenergetic responses have been attributed to altered temperature regimes (Bevelheimer 2002; Petersen & Paukert 2005), few studies have investigated the influence of flow velocity changes on the bioenergetics of freshwater fish.

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Metabolic scope (net active metabolic rate, net M_A) defines the energetic bounds within which aerobically fuelled activity is possible (Fry 1957; Claireaux & Legardère 1999). In fish, this metabolic scope predominately accounts the energy required to propel the fish through the water or hold its position against the prevailing flow velocity. In bioenergetics terms, these swimming costs can represent a large and variable component (0–40%) of the energy budget of many freshwater fishes, often explaining observed differences in the allocation of energy to growth (Boisclair & Leggett 1989; Videler 1993; Hölker & Breckling 2002). During the application of bioenergetics models to lentic systems, net M_A is represented by an activity component, which is defined using an activity multiplier (ACT), which is typically set as either a fixed proportion of M_S (e.g. $ACT=1$) or varying consistently with body weight and temperature (Kitchell et al. 1977). Others define the activity component in relation to optimal swimming speed (Rice et al. 1983; Stewart et al. 1983) or food consumption (Kerr 1982). In lotic systems, the activity component of many bioenergetics models is unlikely to effectively represent the energy used during swimming in fluctuating flow velocity environments (Boisclair 2004). It follows that bioenergetics models that more accurately reflect swimming costs by incorporating flow velocity into calculations will produce a more accurate estimate of overall activity, particularly where flow velocity fluctuates across temporal and spatial scales.

The globally critically endangered Murray cod (*Maccullochella peelii*) is a large (nowadays up to 1.4 m total length) ambush predator occupying the main channel demersal habitats associated with woody structure in the rivers of the Murray–Darling Basin (MDB), Australia (Jones & Stuart 2007; Koehn 2009a, b; Koehn et al. 2009). Once commercially harvested, declines in distribution and abundance of this species have coincided with river regulation, habitat destruction and overfishing (Lintermans 2007). The species appears susceptible to regulated discharge (and hence flow velocity) and temperature regimes within rivers below impoundments in the MDB (2004). One possible mechanism for this susceptibility relates to the regulated flow velocity regimes, which may considerably increase the swimming costs and alter the bioenergetics of this low-energy species (Whiterod 2010) with a broad, but moderate, swimming capacity (Whiterod 2013). Whilst river regulation has been implicated in the decline of the species (cf. Sherman et al. 2007), the bioenergetic constraints imposed by the altered flow velocity and temperature regimes remain unresolved.

In the present study, we explored the allometric effects of body weight and the influence of flow velocity and temperature on the swimming costs of juvenile Murray cod. Specifically, we sought to: (1) develop a swimming costs model for Murray cod; and (2) demonstrate the performance of this model in relation to traditional methods to estimate the activity component of bioenergetics models using field data collected from fluctuating flow velocity environments.

Materials and methods

Swimming capacity experiments

The swimming capacity of juvenile Murray cod ($n=42$) was investigated across a range of body weights (57.6–791.9 g) at temperatures between 15.7 and 26.5 °C (CSU Animal Ethics Code, #06/116). 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 seven days (see Ohlberger et al. 2007). Experiments were conducted in three purpose-built intermittent flow Steffensen-type swimming respirometers (35, 87

and 137L), capable of accommodating various sized fish (Steffensen et al. 1984). The three respirometers were similarly constructed: PVC pipe with clear acrylic swimming sections, flow rectifiers with a darkened upstream end. Flow velocity within each respirometer were regulated by a calibrated propeller and power supply (35 and 87L) driven by an electric trolling motor connected to a Manson power supply (Manson; www.manson.com.hk); 137L employed a 245 mm diameter propeller connected to a Baldor VPT 34550 motor (The ABB Group; www.baldor.com) and ranged between 0.02 and 0.42 m s^{-1} (35L), 0.02–0.46 m s^{-1} (87L) and 0–1.22 m s^{-1} (137L).

Temperature and oxygen saturations were measured continuously (1-s response time) using calibrated oxygen and temperature electrodes (35L – Loligo Systems and 87L – HACH LDO™ HQ10; 137L – HACH LDO™ sc100, accuracy of $\pm 0.1 \text{ mg L}^{-1}$, Loligo Systems; www.loligosystems.com and Hach; www.hach.com) and logged to a computer for processing. Individual fish were weighed (W , to 0.1 g) and measured for total length (T_L , to 1 mm), then introduced into an appropriately sized respirometer with a flow velocity of 0.3 BL s^{-1} (body lengths second⁻¹).

Following a practice swim and overnight acclimation (0.3 BL s^{-1}), the weight-specific rate of oxygen consumption, (M_A , $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$ at STPD and standardised to a 1 kg fish) was calculated from the slope of the linear regression of the decline in oxygen concentration, averaged from two replicate critical swimming speed (U_{crit}) trials (with 1.5 h recovery period in between) using 0.2 BL s^{-1} increments every 20 min (15 min measuring, 2 min flushing, 3 min waiting):

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

where s is the slope of the linear regression (h^{-1}), 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 ($\text{mg O}_2 \text{ L}^{-1}$) and W is the body weight of the fish (kg). 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 across the three respirometers, the solid blocking effect (cross sectional area of fish/cross sectional area of respirometer) was always $\leq 10\%$ (mean solid blocking effect, 35L = $8.6 \pm 0.3\%$; 87L = $6.3 \pm 0.2\%$; 137L = $5.7 \pm 0.3\%$) and no flow velocity correction was necessary (Bell & Terhune 1970). Individual fish were not used in more than one swimming trial. Only oxygen concentration slopes with an r^2 (the coefficient of determination) > 0.95 were used.

Developing the swimming costs model

For each fish, the standard metabolic rate was determined from rearrangement of the power relationship between M_A ($\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$) and relative U_{crit} (BL s^{-1}) and solving for zero flow (Videler 1993):

$$M_A = M_S + \gamma U^\beta \quad (2)$$

where M_A is defined by the standard metabolic rate (M_S , $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$) and the constants, γ and β . The weight-specific swimming costs (net M_A) of Murray cod were calculated by subtracting the standard metabolic rate (M_S , $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$) from the active metabolic rate (M_A , $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$) and then converting into units of $\text{g g}^{-1} \text{ d}^{-1}$ consistent with the Wisconsin-type bioenergetics model (Hanson et al. 1997).

$$\text{net } M_A = M_A - M_S \quad (3)$$

Multivariate non-linear regression was then used to investigate the effects of body weight (W , g), flow velocity (U , BL s^{-1}) and temperature (T , °C) on net M_A . Previously determined relationships for the species (for M_S and M_A) were used to inform model development for net M_A : body weight has an allometric influence (aW^b), exponential increases are realised with temperature (e^{dT}) (Whiterod 2013) and a power function has been shown to best describe the influence of flow velocity (U^c) (see Beamish 1978; Videler 1993). The significance of single parameter estimates were individually tested (using the t -test), and if non-significant, the parameter was removed. Parameter estimates are mean \pm standard error and $\alpha=0.05$. All statistical analyses were performed using Sigmaplot 11 (Systat Software Inc., Chicago, USA).

Incorporating into bioenergetics model

The present study utilised the Wisconsin-type bioenergetics model framework (Hanson et al. 1997), which has been successfully applied to a diverse range of applications for over 40 fish species (Hartman & Kitchell 2008). The simplicity of the model application allows for the ability to isolate individual model components, such as swimming costs, to generate meaningful and broadly applicable conclusions. Specifically, the developed (1) swimming costs model was compared to the (2) fixed proportion (Kitchell et al. 1977) and the (3) optimal swimming speed (Stewart et al. 1983) methods of calculating activity using the net M_A and the activity multiplier (ACT) of the bioenergetics model (Hanson et al. 1997):

$$ACT = (M_S + \text{net } M_A) M_S^{-1} \quad (4)$$

Specifically, model estimates (net M_A and ACT) were compared with estimates obtained using a fixed proportion activity multiplier appropriate for Murray cod ($ACT_{FP}=2$), the net M_A at optimal swimming speed (M_{Aopt} of 1.11 BL s^{-1}) and M_S ($0.0063W^{-0.315}e^{0.022T}$, with units $g\ g^{-1}d^{-1}$) of Murray cod from Whiterod (2012).

The three methods were compared using mean daily discharge ($m^3\ s^{-1}$) and temperature (°C) data obtained between July 2008 and June 2009 from a site (Doctor's Point, 146°94'E, 36.11'S) on the River Murray, directly downstream of the large hypolimnetic-releasing Hume Dam, Australia (PINNEENA database, NSW Office of Water). Additionally, information on the cross-sectional profile and stage height (m) were used to estimate cross-sectional area (m^2) to convert mean daily discharge into depth-averaged flow velocity ($m\ s^{-1}$). As Murray cod mainly occupy the main channel demersal habitats (Koehn 2009a, b), we characterised the flow velocity that Murray cod may experience in these habitats, by calculating the mean flow velocity in the bottom 10% of the water column, relative to depth-averaged flow velocity, using the typical logarithmic vertical flow velocity profile for rivers (Rantz 1982). This approach yielded bottom flow velocities that were 0.648 times that of depth-averaged estimates. For the simulation period, discharge ranged from 9.3 to 149.8 $m^3\ s^{-1}$ and cross-sectional area from 80.4 to 192.2 m^2 . For each method, we ran a 365-day simulation, assuming a starting weight of 100 g (198 mm TL), and a conservative daily growth rate of 0.35% d^{-1} determined from estimated growth rates of Murray cod (1–5 years old) across the MDB (Rowland 1998).

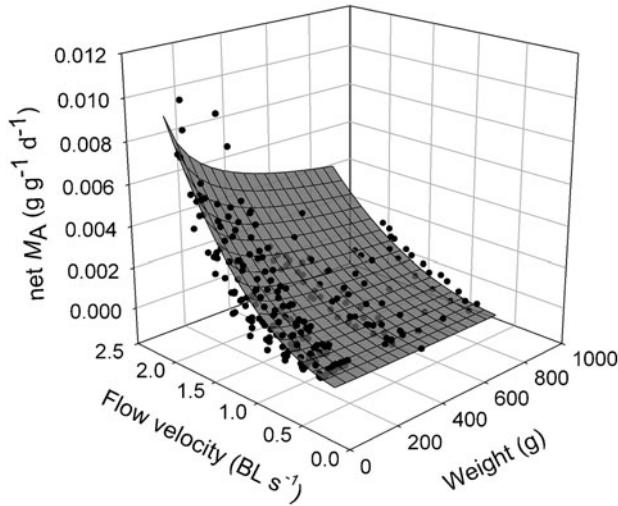


Figure 1. Relationship between the weight-specific swimming costs ($\text{g g}^{-1} \text{d}^{-1}$) of Murray cod, body weight (g) and flow velocity (BL s^{-1}).

Results

The weight-specific swimming costs (net M_A) of Murray cod ranged from 0.00001 to $0.01017 \text{ g g}^{-1} \text{d}^{-1}$, varying significantly with flow velocity ($t=18.90$, $p<0.001$) and body weight ($t=-5.77$, $p<0.001$), but not temperature ($t=0.92$, $p<0.36$, Figure 1). The resulting model including terms for flow velocity (U , $c=2.36\pm 0.12$) and body weight (W , $a=0.004\pm 0.001$, $b=-0.27\pm 0.05$), accounted for 74% of the variation in the net M_A of Murray cod:

$$\text{net } M_A = 0.0035W^{-0.26} U^{2.36} \quad (5)$$

Over the 365-day simulation period (July 08–June 09), the mean flow velocity in the bottom 10% of the water column within the River Murray directly downstream of Hume Dam ranged from 0.06 to 0.46 m s^{-1} (or 0.30 – 2.32 BL s^{-1} for starting simulation weight of 100 g and 198 mm TL , Figure 2). Mean daily temperature increased steadily from a minimum (6.4°C) in late July to a maximum (26.1°C) in February before declining.

Swimming costs determined by the model mirrored the prevailing flow velocity and net M_A ranged from 0.00003 to $0.00426 \text{ g g}^{-1} \text{d}^{-1}$, Figure 3). In contrast, net M_A estimates determined from the fixed proportion and optimal swimming speed methods were considerably less variable (net $M_{A(\text{FP})}=0.0012$ – $0.0020 \text{ g g}^{-1} \text{d}^{-1}$; net $M_{A(\text{opt})}=0.00078$ – $0.0010 \text{ g g}^{-1} \text{d}^{-1}$). Similarly, the activity multiplier (ACT) determined from the swimming costs model (1.02 – 3.14) was more variable than other methods ($ACT_{\text{FP}}=2$; $ACT_{(\text{opt})}=2.07$ – 2.60). Mean ACT estimates across the simulation period were similar ($ACT=2.30$; $ACT_{\text{FP}}=2$; $ACT_{(\text{opt})}=1.75$).

Discussion

Swimming costs for Murray cod

The swimming costs (net M_A) of freshwater fish are strongly influenced by flow velocity, body weight and often temperature (Boisclair & Leggett 1989; Boisclair & Tang

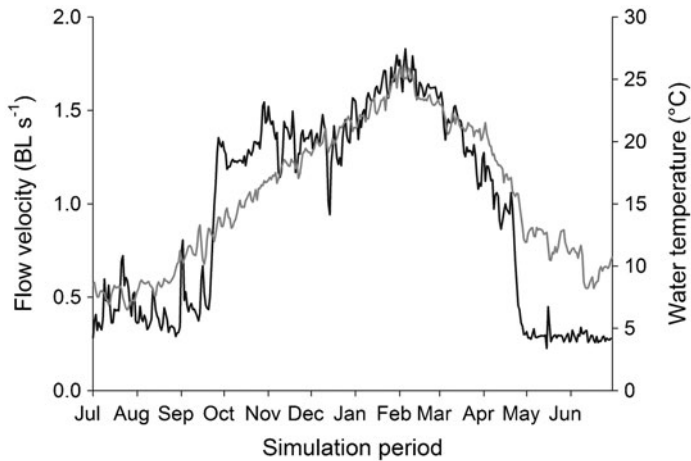


Figure 2. (a–b) Mean daily flow velocity (—, BL s^{-1}) and relative in the bottom 10% of the water column and temperature (—, $^{\circ}\text{C}$) directly downstream of Hume Dam (River Murray) between July 2008 and June 2009.

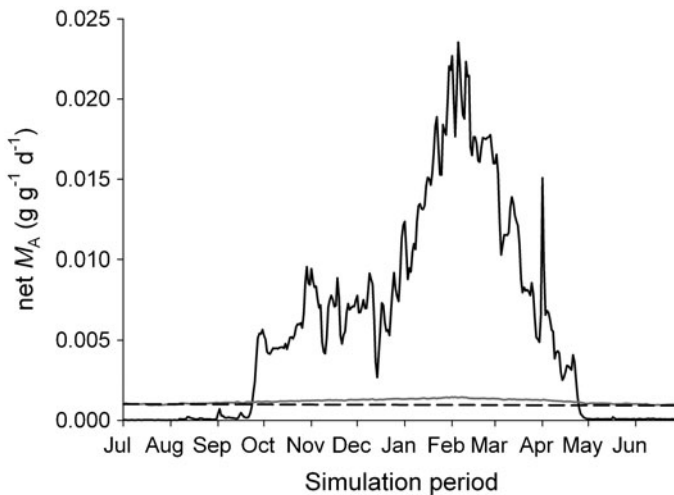


Figure 3. The influence of flow velocity and temperature directly downstream of Hume Dam (River Murray) on the swimming costs ($\text{g g}^{-1} \text{d}^{-1}$) of juvenile Murray cod. For both figures, estimates are from the present study (net M_A and ACT, —), Kitchell et al.'s (1983) fixed proportion method (net $M_{A(K)}$ and ACT_K , —) and Stewart et al. (1983) the optimal swimming speed method (net $M_{A(opt)}$ and ACT_{opt} , ----).

1993; Ohlberger et al. 2005). However, in the present study, while laboratory trials indicated that the weight-specific net M_A of juvenile Murray cod varied significantly with flow velocity and body weight, they did not vary across the range of temperatures examined. The subsequent model explained 74% of variation in the net M_A . The predictive strength of this model was comparable to net M_A models developed for multiple species (Boisclair & Tang 1993), but lower than active metabolic rate (M_A) models developed for common carp (*Cyprinus carpio*) and roach (*Rutilus rutilus*) (Ohlberger et al. 2005), perhaps reflecting the stronger link between body weight and M_S that is

incorporated in these M_A models. Taken together, body weight and flow velocity are appropriate parameters to model the weight-specific net M_A of juvenile Murray cod.

An understanding of the swimming capacity of juvenile Murray cod relative to other species is provided through exploration of the rate at which net M_A increased with each parameter (Ohlberger et al. 2007). For instance, the weight (or mass) exponent for Murray cod (-0.27 or 0.73) was not significantly different from typical scaling exponents for M_S (-0.25 to -0.2 , or 0.75 – 0.8) (Clarke & Johnston 1999) and M_A (-0.2 to -0.12 , or 0.8 – 0.88) (Videler 1993), and indicated a more gradual increase in net M_A with body weight than occurs in most species. The speed exponent (2.36), is mid-range compared to other freshwater fish (~ 2 – 3) (Videler 1993) and suggests moderately efficient swimming (cf. Whiterod 2013). Temperature exponents for fish typically range between 0.05 and 0.10 (Jobling 1994), but temperature did not influence the net M_A of Murray cod across the range of temperatures investigated. Temperature insensitivity has been observed in other species such as walleye (*Stizostedion vitreum vitreum*) and vendace (*Coregonus albula*) (Beamish 1990; Ohlberger et al. 2007), and may reflect an adaptation to thermally fluctuating environments (Clark et al. 2005; Whiterod 2013). However, investigation across the entire range of temperatures experienced in the wild and at the preferred temperature of the species (29°C : Ryan et al. 2003) would provide greater certainty of temperature insensitivity in Murray cod.

Implications for bioenergetics modelling

The swimming costs of freshwater fish represent a large and variable component of its energy budget (Boisclair & Leggett 1989; Hölker & Breckling 2002). Bioenergetics modelling provides a theoretical basis suitable to explore the influence of changes in flow velocity on the swimming costs and growth dynamics of freshwater fish (Bevelhimer 2002; Murchie et al. 2008). However, few studies have accounted for the impact that flow velocity has on metabolic costs, a deficiency that stems largely from the way the activity component of bioenergetics models is currently estimated. Traditional methods (the fixed proportion and optimal swimming speed) cannot account for changes in swimming costs associated with variable flow velocities that occur in lotic systems. The simulation in the present study highlights these deficiencies, demonstrating that swimming costs and activity multiplier estimates obtained from the traditional methods were inflexible in responding to the large fluctuations in flow velocities experienced over the simulation period. In contrast, the swimming costs model developed in the present study reflects daily changes in flow velocity over the simulation period.

Short-term changes in swimming costs may have implications for interpreting the outcomes of bioenergetics modelling in environments with fluctuating flow velocity. For instance, in response to the constant high flow velocities experienced during the summer irrigation period, the swimming costs model predicted that juvenile Murray cod must expend considerably more energy compared to estimates from the Kitchell et al. (1977) and optimal swimming speed methods (24 and 73%, respectively). As a result, modelling outcomes would reflect that less energy is allocated to growth over this period. Under particularly harsh flow velocity environments, this reduction in growth may be substantial possibly leading to the energy-related mortality of individuals (see Finstad et al. 2004). In ecological terms, juvenile Murray cod may combat this increased energy expenditure (i.e. reduced scope for activity) by changing feeding habits (i.e. consuming greater amounts of food or switching to higher energy foods), seeking flow refuge or moving to more energetically profitable environments.

The swimming costs model presented here allows variation in energy expenditure imposed by prevailing flow velocities to be accounted for in bioenergetics modelling in lotic environments. This improves the value of these models as tools for exploring the growth dynamics of fish, particularly in fluctuating flow velocity environments. The enhanced model will be particularly useful when investigating the impacts of altered flow velocity and temperature regimes in lotic systems affected by hypolimnetic-releasing impoundments (Murchie et al. 2008). The present study has shown that flow velocity regimes imposed by the operation of these impoundments strongly influences the swimming costs of Murray cod. More broadly, alteration of flow velocity and temperature regimes will impact fish energy budgets by changing the magnitude of food consumption, standard and digestive metabolism and waste production (Jobling 1994). The enhanced bioenergetics model provides a framework to quantify the effects associated with these changes and enables evaluation of mitigation strategies, particularly those that focus on flow velocity.

A key challenge to implementing the swimming costs model is to characterise the flow velocity being experienced by the fish in lotic systems. It is known that Murray cod are largely sedentary and occupy main channel demersal habitats (Jones & Stuart 2007; Koehn 2009a, b; Koehn et al. 2009). In this study, we assumed that Murray cod spend the majority of its time holding station against the flow velocity prevailing in the bottom 10% of the water column. Whilst this likely provides more relevant estimates of the flow velocity experienced by Murray cod than those obtained from depth-averaged data, this estimate could be further refined through biotelemetry investigation focusing on the habitat use in Murray cod, particularly in association with woody structure (Murchie et al. 2008). Yet, the present approach is an important first step in better quantifying the impacts of short-term changes in flow velocity on fish bioenergetics.

Conclusions

We have developed a swimming costs model that explained 74% of the variation in net M_A for Murray cod for the limited range of body sizes and temperatures examined here. The swimming costs model incorporated significant relationships between net M_A and both body weight and flow velocity, but not temperature. Under conditions that prevail downstream of a large hypolimnetic-releasing impoundment, model simulations revealed more dynamic estimation of the swimming costs of Murray cod compared to traditional methods. The incorporation of the swimming costs model into bioenergetics modelling is an approach to explore the influence of flow velocity in lotic systems on the growth responses of juvenile Murray cod, and may be suitable for those wishing to carry out similar studies.

Funding

This study formed part of a PhD funded by the Mallee Catchment Management Authority, with support from the Murray–Darling Freshwater Research Centre. This manuscript was finalised with the financial support of a Charles Sturt University Writing up Award.

Acknowledgements

Thanks to the rest of the supervisory team, 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 Brian Taylor (La Trobe University) for technical assistance, and 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 Robyn Watts (CSU), Brad Sherman (CSIRO), John Koehn (ARI), the editor and two anonymous reviewers.

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