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Facilitating upstream passage of small-bodied fishes: linking the thermal dependence of swimming ability to culvert design

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Abstract. Fish passage through road culverts is poorly understood, particularly for small-bodied fishes, despite this information being integral to the restoration of waterway connectivity. We assessed the prolonged swimming performance of a small-bodied fish, empire gudgeon (*Hypseleotris compressa*; 3.2–7.7 cm total length, TL), and juvenile Australian bass (*Perca latipes*; 3.5–7.8 cm TL). Swimming trials were conducted in a hydraulic flume across a range of fixed and increasing velocities in response to acute and long-term thermal treatments. A new statistical approach (Tobit analysis) was used to relate the thermal dependence of swimming endurance to hydraulic characteristics of culverts, providing estimates of maximum water velocity allowing upstream fish passage. Reductions in water temperature of 10°C, similar to those caused by cold-water releases from dams, significantly impaired critical swimming speeds of both species. Traversable water-velocity models identified *H. compressa* as a weak swimmer, requiring very low water velocities ($\leq 0.10 \text{ m s}^{-1}$ or 2.86 body lengths (BL) s^{-1}) for unrestricted passage, whereas *P. latipes* was predicted to traverse water velocities of $\leq 0.39 \text{ m s}^{-1}$ or 12.12 BL s^{-1} . Culvert designs can be improved by limiting water velocities to accommodate weak-swimming fishes and by accounting for the thermal sensitivity of swimming performance.

Additional keywords: fish endurance, pipe culvert, thermal acclimation, thermal pollution, time to fatigue, velocity barrier.

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Introduction

Global declines in riverine fish abundance and distribution are inherently linked to reduced habitat connectivity and altered aquatic thermal regimes (Wolter and Arlinghaus 2003; Gibson *et al.* 2005; Sherman *et al.* 2007). Critical habitats have been extensively fragmented through the installation of in-stream structures (e.g. dams, weirs, barrages and road-crossings) as a direct consequence of human demands on freshwater systems (Paul and Meyer 2001; Nilsson *et al.* 2005). Infrastructure within waterways can create barriers to fish movement via physical, hydraulic (e.g. high water velocities and turbulence), physicochemical (e.g. water temperature, low dissolved oxygen) and behavioural barriers (e.g. low light levels).

The survival and reproductive success of fish is dependent on their ability to move freely and efficiently within their environment (Fausch *et al.* 2002). Small-scale movements are necessary for accessing food (Clapp *et al.* 1990), defending territory and avoiding predators (Harvey 1991), whereas large-scale movements are important for reaching spawning grounds (particularly for obligate migratory species), habitat selection (Gowan and Fausch 2002) and population connectivity (Yamamoto *et al.* 2004). In-stream barriers may disrupt these

processes, and have been linked to local fish extinctions in Japan (Morita *et al.* 2009), Europe (Lundqvist *et al.* 2008), North America (Winston *et al.* 1991; Quinn and Kwak 2003) and Australia (Gehrke *et al.* 2002).

To restore waterway connectivity, the development of fish passes has been studied for decades (Clay 1995; Mallen-Cooper and Brand 2007); however, this research has predominantly focused on enabling fish movement around large-scale obstacles such as dams and barrages (Starrs *et al.* 2011; Bunt *et al.* 2012). Fewer studies have investigated the design of fish passes at less obvious, but pervasive barriers such as culverts (Feurich and Boubée 2006; MacDonald and Davies 2007; Norman *et al.* 2009; Feurich *et al.* 2011). Culverts allow for continued water connectivity below road-crossings, but generally at greater velocities than the natural waterway because of a reduced waterway cross-sectional area (Warren and Pardew 1998). The greater the water velocity, the greater the likelihood that fish will be unable to traverse the crossing (Warren and Pardew 1998). Culverts account for a large proportion of hydraulic barriers in developed waterways worldwide (Behlke 1987; Warren and Pardew 1998; Bouska and Paukert 2010), particularly in coastal Australia (Williams and Watford 1997).

Culverts were originally designed to maximise hydraulic capacity at a minimal expense; however, design recommendations have become increasingly focused on providing fish passage (O'Hanley and Tomberlin 2005). Design recommendations in Australia (New South Wales) limit water velocities through culverts to a maximum of 0.3 m s^{-1} and/or three fish body lengths (BL) s^{-1} . The validity of these recommendations remains untested for a wide range of native species, because these values are based on two primary datasets, pertaining to a size class of fish $>10 \text{ cm}$ total length (TL) (Mallen-Cooper 1999, 2001); despite the majority of upstream movements of native fishes being undertaken by small-bodied ($<10 \text{ cm}$ TL) adults and juveniles (Pusey *et al.* 2004). The 'weakest' swimmers in a system are small-bodied fishes, as maximum attainable swimming speed (m s^{-1}) increases with teleost BL (Fry and Cox 1970; Hammer 1995; Domenici 2001). Therefore, culvert-design recommendations based on the swimming ability of fish $>10 \text{ cm}$ TL would be likely to result in structures restricting small and juvenile fish migration.

An additional consideration in the design of culvert passes is the influence of water temperature on fish swimming performance. Ambient temperature exerts influence on swimming performance by affecting muscle contractility and fibre recruitment (Johnston *et al.* 1990; Rome 1990; Rome *et al.* 1992), the availability and storage of energy products (e.g. ATP, glycogen and phosphocreatine; Kieffer *et al.* 1994) and the capacity of the cardiovascular and respiratory systems to support aerobic metabolism (Farrell *et al.* 1996). Seasonal changes in water temperature have the potential to influence swimming performance; however, many fish have the ability to compensate for gradual thermal changes by modifying (acclimatising) their physiology to express seasonal phenotypes (Guderley and Blier 1988; Wilson and Franklin 2002). Alternately, fish movement can be compromised by anthropogenic thermal pollution (Ryan *et al.* 2002; Lyon *et al.* 2008). Hypolimnial water releases from dams during summer and spring can rapidly reduce natural water temperatures by $10\text{--}15^\circ\text{C}$, with thermal alterations persisting downstream for several hundred kilometres (Preece 2004). The potential impairment of fish swimming performance as a consequence of thermal pollution requires consideration when modelling traversable water velocities for culvert design.

The present study aimed to test the validity of current water-velocity recommendations for two small-bodied fish species. Fishway research has predominately focused on designing passes for commercial species with anadromous life histories (Blackett 1987; Peake *et al.* 1997a, 1997b; Roscoe and Hinch 2010), where large adults migrate upstream to spawn in freshwater. Australian fishes also undertake inter-biome migrations, but with upstream movements often occurring in small post-larvae and juvenile fishes, with catadromous and amphidromous life histories (Pusey *et al.* 2004; Humphries and Walker 2013). Catadromous fishes spawn at sea and small juveniles must migrate upstream to freshwater habitats to feed and mature. Similarly, newly hatched larvae of amphidromous fishes migrate to sea to feed, and small juveniles (typically $1.5\text{--}5 \text{ cm}$ TL) return upstream to freshwater habitats (McDowall 2007). Australian fishes can also be potamodromous, where adult and/or juveniles migrate within freshwater. So as to reflect the life-history strategies and typical size classes of migrating

Australian fishes, we examined swimming performance of the adult life stage of a potamodromous species, empire gudgeon (*Hypseleotris compressa* Krefft, 1864), and the juvenile life stage of a catadromous fish, Australian bass (*Percales novemaculeata* Steindachner, 1866). Adult *H. compressa* is typically 7 cm TL, and completes its entire life cycle within freshwater (Pusey *et al.* 2004), with migratory movements anecdotally occurring between autumn and winter months. *P. novemaculeata* is an obligate migratory species, with adults migrating downstream to spawn in estuaries and juveniles (typically $2\text{--}10 \text{ cm}$ TL) migrating upstream to freshwater habitats between late winter and early summer (Harris 1988).

Hypseleotris compressa and *P. novemaculeata* were used as model species to test the validity of current water-velocity recommendations (0.3 m s^{-1} and three BL s^{-1}) for small-bodied fishes, and experimentally assess the thermal sensitivity of swimming performance. To achieve this, the following hypotheses were tested:

- (1) *P. novemaculeata* and *H. compressa* will be unable to attain swimming speeds $\geq 0.3 \text{ m s}^{-1}$ or three BL s^{-1} without fatigue, thereby invalidating the current water-velocity recommendations, and
- (2) acute reductions in water temperature will coincide with significant reductions in critical swimming speeds of both *P. novemaculeata* and *H. compressa*, whereas long-term exposure to cold water temperatures will elicit acclimatory responses, having no effect on swimming performance.

Swimming ability was assessed by measuring swimming endurance (i.e. time to fatigue) across a range of fixed velocities (Hammer 1995). Endurance data were analysed using a novel and robust approach (Tobit analysis, Tobin 1958), where the top performers were included in analysis. Swimming-endurance models were related to length and flow characteristics of culverts, estimating maximum water velocity allowing upstream fish passage. The influence of water temperature was determined by assessing critical swimming speeds (Hammer 1995) in response to acute and long-term thermal treatments, mimicking temperature fluctuations associated with thermal pollution and seasonality, respectively.

Materials and methods

Fish collection and maintenance

Juvenile *P. novemaculeata* individuals were obtained from Hanwood fish hatchery (Murgon, Queensland, Australia) ($n = 113$; TL: mean \pm s.d. $5.7 \pm 0.13 \text{ cm}$; range $3.2\text{--}7.7 \text{ cm}$). Adult *H. compressa* individuals were collected from the Brunswick River catchment (Mullumbimby, New South Wales, Australia) using bait traps ($n = 121$; TL: mean \pm s.d. $4.9 \pm 0.07 \text{ cm}$; range $3.5\text{--}7.8 \text{ cm}$). Fish were transported to The University of Queensland and maintained in 45-L glass aquaria ($L \times W \times H$, $60 \times 30 \times 30 \text{ cm}$). Water temperature was initially set at 21°C for *P. novemaculeata* (to match hatchery water temperature) and at 15°C for *H. compressa* (to match water temperature of collection stream). Aquaria contained Brisbane city tap water conditioned using water primer (Prime, Seachem, Georgia, USA), with water chemistry (pH, nitrogen and ammonia) being monitored weekly. Fish were fed commercially

supplied bloodworms (*Chironomidae*) to satiation daily. Photoperiod was set to a constant 12-h light : 12-h dark cycle.

Experimental design

Thermal acclimation treatments were selected to reflect seasonal water temperatures naturally encountered by the species, based on data from the [New South Wales Office of Water \(2012\)](#). *P. novemaculeata* individuals were randomly assigned to one of the following four thermal-acclimation treatments: 18°C ($n = 26$), 21°C ($n = 28$), 25°C ($n = 30$) or 28°C ($n = 29$) \pm 1°C. Three aquaria, each containing 8–12 fish, were assigned to each temperature treatment. *H. compressa* individuals were randomly assigned to one of the following three thermal-acclimation treatments: 15°C ($n = 41$), 20°C ($n = 40$) or 25°C ($n = 40$) \pm 1°C. Two aquaria, each containing 20–25 fish, were assigned to each temperature treatment. Water temperature was either increased or decreased at a rate of 2°C day⁻¹, until desired water temperature was reached. Submersible water heaters (200 W, Aqua One, Ingleburn, Australia) were used to maintain aquaria water at a constant temperature, for a minimum of 5 weeks before swimming trials.

Swimming endurance

Swimming trials were conducted in a 10-L, flow-controlled hydraulic flume (Loligo, Tjele, Denmark; swimming-chamber dimensions = L \times W \times H, 40 \times 10 \times 10 cm). A flow meter (Hontzsch, Bondby, Denmark) was used to calibrate water-velocities generated by the flume. The swimming flume was constantly aerated and water temperature was maintained by using a submersible heater (300 W, Aqua One, Sydney, Australia). Fish were tested individually, in a post-absorptive state (fasted for 24 h), with a minimum of 24-h rest between trials. Test speed was randomly assigned to fish, and individuals were tested a maximum of two times throughout the entire experiment to avoid training effects ([Davison 1997](#)). Swimming-endurance measurements were based on protocol previously described by [Brett \(1967\)](#), involving evaluation of endurance over a range of fixed swimming speeds of 0.25, 0.35, 0.40, 0.55 and 0.7 m s⁻¹ for *P. novemaculeata* and 0.05, 0.13, 0.17 and 0.25 m s⁻¹ for *H. compressa*. Fish were allowed to adjust to conditions in the flume for a minimum of 30 min, after which water velocity was rapidly increased to the desired test velocity, at a rate of 0.05 m s⁻¹ every minute for *P. novemaculeata* or 0.04 m s⁻¹ every minute for *H. compressa*. Time until fatigue (i.e. endurance) was recorded, with fatigue defined as the fish resting against the back wall of the flume for ≥ 3 s. Fish were tested at water temperatures matching respective thermal-acclimation treatments. Trials lasted for a maximum of 60 min and swimming speeds maintained for >60 min were treated as censored (unobservable) data points and analysed accordingly by using a censored regression model ([Tobin 1958](#); [McDonald and Moffitt 1980](#)).

Thermal sensitivity and plasticity of swimming performance

Thermal sensitivity and plasticity of swimming performance was assessed in 15°C- and 25°C-acclimated *H. compressa*, and in 18°C- and 28°C-acclimated *P. novemaculeata* individuals. Fish were swum once at two test temperatures (15°C and 25°C, $n = 15$,

for each acclimation group at each treatment for *H. compressa*; 18°C and 28°C, $n = 10$, for each acclimation group at each temperature for *P. novemaculeata*) and the order of temperature exposure was randomised. Fish were left to adjust to water temperature within the swimming flume for 1 h before testing. Swimming-performance tests began at a water velocity of 0.04 m s⁻¹ and water speed was increased at a rate of 0.02 m s⁻¹ every 5 min until fish fatigued. Total swimming time until fatigue and water velocity at fatigue were recorded to calculate critical swimming speed (U_{crit}), using [Brett's \(1964\)](#) equation, as follows:

$$U_{crit} = U_f + \left[U_i + \left(\frac{T_f}{T_i} \right) \right], \quad (1)$$

where U_f is the highest water velocity maintained for an entire 5-min interval (m s⁻¹), U_i is the water velocity increment (0.02 m s⁻¹), T_f is the amount of time swum in the final increment (s) and T_i is the time interval (300 s). Critical swimming-speed measurements were standardised for fish size, in terms of standard BL per second (BL s⁻¹), and denoted as relative critical swimming speed (U_R).

Morphological measurements

Total BL and body mass were included in all analyses as co-variables. Following the completion of swimming trials, fish were blot-dried, weighed (to the nearest 0.01 g), and photographed. Photographs were used to measure total BL, body depth and cross-sectional area by using SigmaScan software (Systat Software Incorporation, Chicago, IL, USA). Cross-sectional body area of all fish was less than 10% of the cross-sectional area of the swimming flume chamber; therefore, corrections for the solid-blocking effect ([Bell and Terhune 1970](#)) were not necessary.

Statistical analyses

Analyses were performed using the programming package R (version 2.10.1.) using the following two packages: vector-generalised linear and additive models (VGAM) ([Yee and Wild 1996](#)) and non-linear mixed-effects models (nlme) ([Pinheiro *et al.* 2012](#)). Censored regression analysis ([Tobin 1958](#)) was used to model swimming endurance as a function of total BL, thermal-acclimation treatment and water velocity. Indicator variables were incorporated for each level of acclimation temperature and water velocity. Minimal adequate models were determined for each fish species by using log-likelihood ratio chi-square tests. Assumptions of homoscedasticity and normality of errors were graphically checked and response variables were log₁₀-transformed where necessary. A Wald *post hoc* test was used to discern statistical differences among thermal-acclimation treatments, where necessary. Censored regression models are in the following form:

$$E = \hat{a} + \hat{a}_1 l + \hat{a}_2 t_1 + \hat{a}_3 t_2 + \hat{a}_4 t_3 + \hat{a}_5 v_1 + \hat{a}_6 v_2 + \hat{a}_7 v_3 + \hat{a}_8 v_4, \quad (2)$$

where E is endurance, \hat{a} the intercept, \hat{a} values are the coefficient of each variable, l is total BL, t 's are thermal-acclimation treatment indicator variables and v are water-velocity treatment indicator variables. The effects of acute and long-term (chronic) thermal treatments on relative critical swimming speed were

analysed using a non-linear mixed-effects model. Acclimation and test temperatures were treated as fixed binary-factor variables, and fish identification number was included as a random-effect factor. The minimal adequate model was determined using maximum likelihood simplification. Statistical significance was set at the level of $P \leq 0.05$.

Modelling traversable water velocities through culverts

Water velocities allowing successful upstream passage of juvenile *P. novemaculeata* and *H. compressa* were modelled for culverts of varied length (2–60 m) by using the equation described by Peake *et al.* (1997a), as follows:

$$V_f = V_s - (d \times E_{V_s}^{-1}) \quad (3)$$

where V_f is traversable water velocity within the culvert (m s^{-1}), V_s is the swimming speed of the smallest-sized fish (m s^{-1}), d is the length of the culvert (m) and $E_{V_s}^{-1}$ is the endurance of the fish swimming at V_s (s). The censored regression equation relating to the relevant fish species was used to calculate E_{V_s} values. Equation 3 corrects for an inherent limitation of swimming-flume trials, where fish swimming speed is required to equal but not exceed water velocity; thus, positive ground is not achieved. This limitation is corrected for in Eqn 3, by recognising that fish must swim faster than oncoming water velocity to move forward in a culvert.

Separate traversable water-velocity models were generated for *H. compressa* and juvenile *P. novemaculeata*, based on the smallest fish in each respective dataset and the thermal-acclimation treatment best reflecting field water temperature during peak migration time (i.e. 3.2 cm (TL) *P. novemaculeata*, and 3.5 cm (TL) *H. compressa* swimming at 20°C). Additional traversable water-velocity models were generated for *H. compressa* swimming at three water temperatures, namely, at 15°C, 20°C and 25°C, to gauge the impact of water temperature on culvert-design criteria.

Results

Swimming-endurance models

The relationship among swimming endurance (E_{\min}) and total BL (L_{cm}), water velocity ($V_{\text{ms}^{-1}}$) and thermal-acclimation treatment (T_{c}) is described by the following regressions:

$$\begin{aligned} \log(E) = & 2.77 + (2.26 \times 10^{-1} L) - (5 \times 10^{-1} V_{0.35}) \\ & - (1.43 V_{0.40}) - (3.45 V_{0.55}) - (3.82 V_{0.70}) \\ & \text{(for } \textit{Percalates novemaculeata} \text{) (log-likelihood} \\ & = -54.49, \text{ adjusted } R^2 = 0.71, \text{ d.f.} = 195), \end{aligned} \quad (4)$$

and

$$\begin{aligned} \log(E) = & (6.24 \times 10^{-1}) + (1.66 \times 10^{-1} L) + (1.04 T_{20}) \\ & + (8.05 \times 10^{-1} T_{25}) - (1.22 V_{0.13}) - (2.11 V_{0.17}) \\ & - (2.99 V_{0.25}) \text{ (for } \textit{Hypseleotris compressa} \text{)} \\ & \text{(log-likelihood} = -90.29, \text{ adjusted } R^2 = 0.19, \\ & \text{d.f.} = 234). \end{aligned} \quad (5)$$

Body mass was excluded from all analyses because of high correlation with total BL. Covariate interactions among total BL, water-velocity and thermal-acclimation treatment were not significant in either analysis, and, therefore, were ignored in the final models. Swimming endurance was inversely related to water velocity (i.e. swimming speed) in both *P. novemaculeata* and *H. compressa* ($P < 0.001$; Figs 1, 2a–c). Thermal-acclimation treatments had no significant ($P > 0.05$) effect on endurance in *P. novemaculeata* and these variables were excluded from the final endurance model. In contrast, variation was observed in swimming endurance among thermal-acclimation treatments of *H. compressa* (Fig. 2a–c). Wald *post hoc* analyses showed that swimming endurance was significantly reduced in 15°C-acclimated *H. compressa* compared with that in 20°C- and 25°C-acclimated fish ($P = 0.028$); however, no significant difference was observed in endurance between 20°C- and 25°C-acclimated fish ($P = 0.83$; Fig. 2a–c). A significant ($P < 0.001$) positive relationship between total BL and swimming endurance was found in *P. novemaculeata*, with larger fish being able to swim for longer durations before fatigue. In contrast, total BL of *H. compressa* had no significant ($P = 0.43$) effect on swimming endurance.

Thermal sensitivity and plasticity of swimming performance

Relative critical swimming speed (U_R) was independent of thermal-acclimation treatment for both species, with no difference observed in swimming performance between 15°C- and 25°C-acclimated *H. compressa* ($P = 0.34$, d.f. = 29; nlme) and between 18°C- and 28°C-acclimated *P. novemaculeata* at both test temperatures ($P = 0.69$, d.f. = 19; nlme; Fig. 3). Test temperature had a significant overall effect on U_R , with reduced swimming performance observed for *H. compressa* ($P < 0.001$, d.f. = 29; nlme) and *P. novemaculeata* ($P = 0.005$, d.f. = 19; nlme) at the lower test temperature (Fig. 3). Mean BLs of the fish in 15°C- and 25°C-acclimated treatment groups of *H. compressa* ($P = 0.86$, d.f. = 29, Student's *t*-test) and in 18°C- and 28°C-acclimated

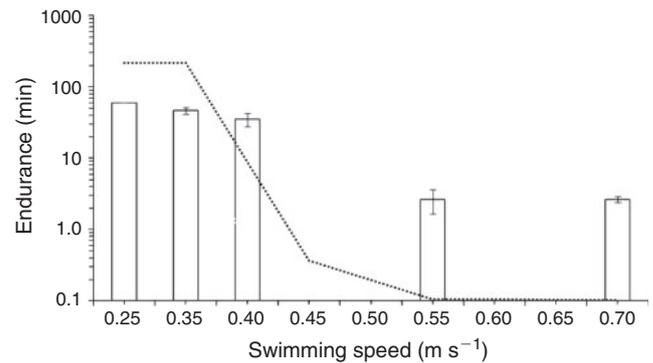


Fig. 1. Fatigue curve (dotted line) describing the relationship between swimming speed (m s^{-1}) and endurance (time to fatigue, min) for an average-sized (5.7 cm total length) juvenile Australian bass, *Percalates novemaculeata* (censored regression, adjusted $R^2 = 0.71$; $n = 113$). Covariate interactions among total body length, water velocity and thermal-acclimation treatment were not significant in either censored regression analyses, and therefore were ignored in the final model. Bars represent observed data and values are expressed as a mean \pm s.e.

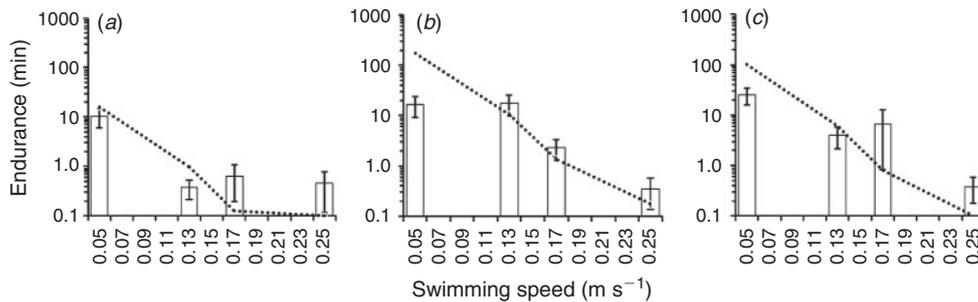


Fig. 2. Fatigue curves (dotted line) describing the relationship between swimming speed (m s^{-1}) and endurance (time to fatigue, min) for an average-sized (4.9 cm total length) empire gudgeon, *Hypseleotris compressa*, at the following three water temperatures: (a) 15°C, (b) 20°C and (c) 25°C (censored regression, adjusted $R^2 = 0.19$, $n = 121$). Bars represent observed data and values are expressed as a mean \pm s.e.

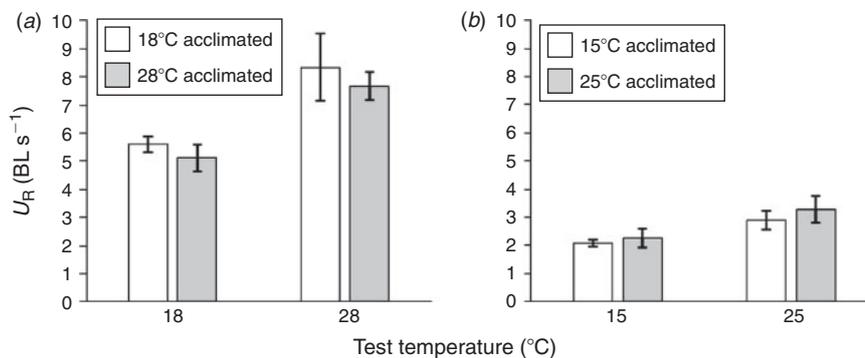


Fig. 3. Effect of test temperature on critical swimming speed (U_R , body lengths s^{-1}) of (a) juvenile Australian bass, *Percalates novemaculeata*, acclimated to 18°C or 28°C, and (b) empire gudgeon, *Hypseleotris compressa*, acclimated to 15°C or 25°C. Swimming performance was reduced at colder test temperatures compared with warmer test temperatures in both species ($P < 0.005$; non-linear mixed-effects model), regardless of the thermal-acclimation treatment. Values are expressed as mean critical swimming speed (U_R , body lengths s^{-1}) \pm s.e.

treatment groups of *P. novemaculeata* ($P = 0.43$ d.f. = 19, Student's *t*-test) were not significantly different.

Traversable water-velocity models

Water velocities allowing successful upstream passage of *H. compressa* decreased with increasing culvert length (Fig. 4). A similar pattern was observed for *P. novemaculeata*; however, this trend was only applicable across the culvert length range of 2–15 m, because maximum water velocity plateaued at $\sim 0.38 \text{ m s}^{-1}$ (Fig. 4). To allow for transit of juvenile *P. novemaculeata* through small (2–3 m), intermediate (<15 m) and long (15 to ≤ 60 m) culverts, water velocity would need to be ≤ 0.51 , 0.39 and 0.38 m s^{-1} , respectively (Fig. 4). In contrast, water velocity would need to be ≤ 0.13 , 0.10 and 0.03 m s^{-1} to allow for transit of *H. compressa* through small, intermediate and long culverts (Fig. 4). Maximum water velocity allowing transit of *H. compressa* varied depending on water temperature, with allowable velocities markedly lower at 15°C than at 20°C and 25°C (Fig. 5).

Discussion

Culvert-design recommendations currently limit water velocity to a maximum of 0.3 m s^{-1} or three BL s^{-1} , on the basis of findings from Mallen-Cooper (1999) and Mallen-Cooper

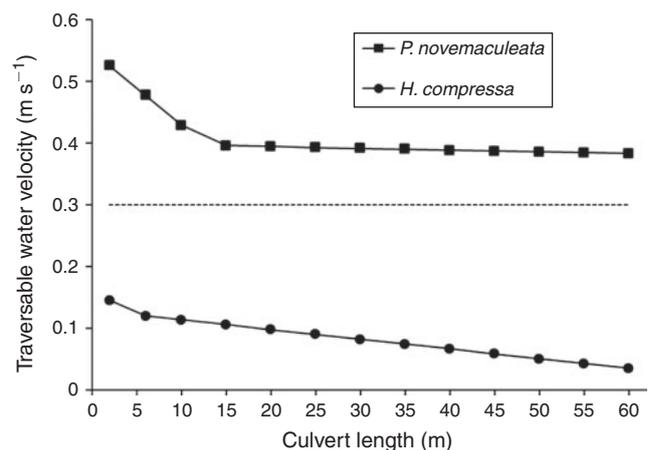


Fig. 4. Modelled traversable water velocities (m s^{-1}) allowing upstream passage of juvenile Australian bass, *Percalates novemaculeata*, and empire gudgeon, *Hypseleotris compressa*, through culverts 2–60 m in length. Estimates are modelled for the smallest-sized fish in each dataset, at the acclimation temperature best reflecting field water temperature during peak migration season (i.e. 3.2 cm (total body length, TL) Australian bass, and 3.5 cm (TL) empire gudgeon, swimming at 20°C). Horizontal dotted line marks recommended water-velocity limits (0.3 m s^{-1}) in Australia (New South Wales).

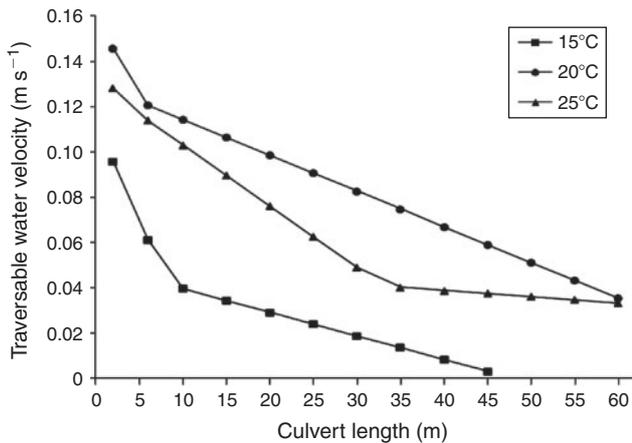


Fig. 5. Modelled traversable water velocities (m s^{-1}) allowing upstream passage of empire gudgeon, *Hypseleotris compressa*, through culverts 2–60 m in length. Estimates are modelled for a 3.5-cm (total body length) fish at three water temperatures of 15°C, 20°C and 25°C.

(2001), respectively. At this velocity maximum, culvert transit is likely to be unrestricted for *P. novemaculeata* but compromised for *H. compressa*. Furthermore, reductions in water temperature, similar to those caused by cold-water releases from dams, were found to significantly impair swimming performance in both study species, regardless of thermal-acclimation treatment. These findings question the validity of the current recommendations and highlight the need to account for the thermal dependence of fish swimming performance.

Swimming endurance: effects of body size, water velocity and comparisons to other fishes

Fatigue-time curves derived for both species displayed an inverse relationship between endurance and swimming speed. The general relationship of decreasing swimming endurance with increasing swimming speed has been well documented (Winger *et al.* 1999; Breen *et al.* 2004; Zeng *et al.* 2009). As swimming speed and intensity increase, muscle power output and demands on cardiovascular and respiratory systems increase exponentially, exceeding sustainable thresholds (Webb 1978). A positive relationship between BL and swimming performance has been observed in numerous fish species (White and Seymour 2011) and is thought to be due to body size being associated with greater muscle mass (Videler 1993) and enhanced metabolic efficiency during swimming (Beamish 1978). In line with previous findings (Hammer 1995), swimming endurance of *P. novemaculeata* was positively correlated with BL; however, *H. compressa* appears to be an exception to the general trend, with swimming endurance being independent of BL (within the size range tested). This finding may be a reflection of poor prolonged swimming ability irrespective of body size, or low variance among the size range tested.

Percalates novemaculeata markedly outperformed *H. compressa* in swimming-endurance trials, despite the similar size range of each species (*P. novemaculeata* 3.2–7.7 cm TL; *H. compressa* 3.5–7.7 cm TL). The strong swimming capacity of *P. novemaculeata* may be due to the obligatory nature of its inter-biome, catadromous life-history strategy (Harris 1988); in

contrast, *H. compressa* is potamodromous, with movements being confined to freshwater (Pusey *et al.* 2004). Swimming ability of *H. compressa* may have been underestimated, particularly in individuals prone to station-holding behaviour. *Hypseleotris compressa* was observed to resist displacement during swimming trials, by grasping the substratum with pectoral fins (i.e. station-holding); this is a strategy that requires less energy than free-swimming, allowing fish to exploit turbulence by coinciding free-swimming efforts with low-velocity pockets (Webb 1989). However, station-holding is largely ineffective within an artificial flume, because the smooth surface promotes slippage and turbulence is limited. *Hypseleotris compressa* may also be reliant on burst swimming speeds, unmeasured in the present study, complemented with station-holding recovery periods, for culvert transit. *In situ* evaluation of swimming behaviour and performance, where station-holding is effective, may provide valuable insight.

Swimming speeds of both study species fit well with previously reported estimates of swimming ability in small-bodied fishes (Kilsby and Walker 2010; Starrs *et al.* 2011), with *P. novemaculeata* ($U_{\text{crit}} = 0.5 \text{ m s}^{-1}$, 8.8 BL s^{-1}) at the upper end of the performance spectrum, and *H. compressa* ($U_{\text{crit}} = 0.24 \text{ m s}^{-1}$, 2.25 BL s^{-1}) at the lower end. Compared with other small-bodied Australian fishes, *P. novemaculeata* has similar swimming ability, whereas *H. compressa* is a weaker swimmer. For instance, critical swimming speed of juvenile Macquarie perch (*Macquaria australasica*, 7.9–26.1 cm TL) ranged between 0.3 and 0.6 m s^{-1} (Starrs *et al.* 2011). Similarly, Kilsby and Walker (2010) reported maximum prolonged swimming speeds of juvenile Australian smelt (*Retropinna semoni*, mean TL = 6.5 cm) and juvenile flat-headed gudgeon (*Philypnodon grandiceps*, mean TL = 6.7 cm) of 0.5 m s^{-1} and 0.27 m s^{-1} , respectively. From an international standpoint, juvenile *P. novemaculeata* appears to be a marginally stronger swimmer than are other small-bodied fishes, whereas *H. compressa* is, again, on the lower end of the performance spectrum (e.g. Mitchell 1989; Breen *et al.* 2004; Zeng *et al.* 2009). For example, critical swimming speeds of three small-bodied (<10 cm TL) fishes inhabiting central and temperature Eurasian streams (stone loach, *Barbatula barbatula*; gudgeon, *Gobio gobio*; spined loach, *Cobitis taenia*) ranged between 0.25 and 0.42 m s^{-1} (Wolter and Arlinghaus 2003; Knaepkens *et al.* 2007). Furthermore, juvenile fishes endemic to China have inferior relative critical swimming speeds compared with *P. novemaculeata*, and superior speeds compared with *H. compressa* (i.e. largemouth bronze gudgeon, *Coreius guichenoti*, $U_{\text{crit}} = 7.37 \text{ BL s}^{-1}$, 1.28 m s^{-1} ; southern catfish, *Silurus meridionalis*, $U_{\text{crit}} = 3.4 \text{ BL s}^{-1}$, 0.33 m s^{-1} ; Zeng *et al.* 2009; Tu *et al.* 2012).

Censored regression models used in the present study did not explain all observed variation in swimming endurance, particularly for *H. compressa*. Training effects associated with the repeated use of fish in the swimming trials may have contributed to this variation; however, such effects were expected to be minimal in the present study because repeated use was set to a maximum of two swims per fish. Additional variation may stem from unmeasured factors such as motivation to swim (Castro-Santos 2004). For example, cues such as photoperiod, water temperature and chemical stimuli can be integral to stimulate migratory events (Benoit *et al.* 2010; Forsythe *et al.* 2012,

Leonard *et al.* 2012); however, little is known about which migratory cues are important to our study species.

Thermal dependence of swimming: implications of seasonal and acute thermal challenges

Swimming performance was markedly reduced at the cold (10°C or 15°C) test temperature, irrespective of thermal-acclimation treatment in both species. Impaired swimming performance at low temperatures may be a reflection of reduced function in a suite of physiological processes, including muscular power output (Randall and Brauner 1991; Rome *et al.* 1992; Franklin and Johnston 1997), muscle fibre-contraction and -relaxation rates (Johnston *et al.* 1985; Fleming *et al.* 1990) and cardiac function (Claireaux *et al.* 2000; Joaquim *et al.* 2004). However, further experimental work is required before identifying the physiological basis of reduced performance shown here. Our findings are similar to those of Lyon *et al.* (2008), where fast-start performance of golden perch was found to be significantly reduced by rapid reductions in water temperature of 10°C. Here, we build on these findings, showing that not only fast-start swimming performance can be compromised by acute reduction in water temperature, but also prolonged swimming performance. Our data suggest that swimming ability, and thus culvert transit, may be hindered in winter, and in populations inhabiting thermally polluted river reaches in spring and summer. Consequently, if culverts are to allow for transit of fish in seasonally cold or thermally polluted waters, water-velocity maximums need to be revised down to reflect the thermal dependence of swimming performance. For example, the peak migrations of *P. novemaculeata* and *H. compressa* occur between autumn and winter and between late winter and early spring, respectively. Thus estimates of swimming ability at colder water temperatures (15–20°C) are most relevant to these species.

In addition to reduced swimming performance at cold water temperatures, we found that long-term (chronic) exposure to constant thermal environments did not elicit compensatory responses in swimming performance, in either species. This finding contradicts our original hypothesis (Hypothesis 2) and was unexpected, because many other fish species possess the capacity to alter physiological function and locomotor performance in response to water temperature (Taylor *et al.* 1996; Wieser and Kaufmann 1998; Johnston and Temple 2002). This inability or limited capacity to acclimate swimming performance may have been confounded by a constant photoperiod (12-h light : 12-h dark), rather than a seasonal photoperiod (e.g. winter 10-h light : 14-h dark ; summer 14-h light : 10-h dark), because the coupling of corresponding seasonal cues has been shown to enhance acclimatory responses in fish swimming performance (Kolok 1991; Smiley and Parsons 1997; Day and Butler 2005). Nonetheless, this finding increases the vulnerability of our study species to thermal pollution, because compensatory responses to prolonged reductions in water temperature may not be possible.

Culvert passageway applications: traversable water velocities and design recommendations

In agreement with our first hypothesis, current velocity recommendations (maximum of 0.3 m s⁻¹ or three BL s⁻¹) were shown to be inappropriate for providing passage of weak-swimming,

small-bodied fishes such as *H. compressa*. The traversable water-velocity models, generated from swimming-endurance data, suggest that to provide transit of *H. compressa* or fishes with a similar swimming ability, culverts need very low water velocities. For example, the cross-sectional area of a culvert with a velocity criterion of 0.3 m s⁻¹ would need to be doubled to meet a 0.15 m s⁻¹ criterion, simultaneously doubling the monetary cost of culverts. Alternatively, simple changes in culvert designs (e.g. the use of baffles or rest areas) could greatly improve the prospects of fish passage (Feurich *et al.* 2011). Culverts can be retrofitted with rest structures such as baffles, which have been found to simultaneously reduce water velocities and provide fish with low-velocity refuges (Feurich *et al.* 2011). An additional option is roughening (Bates and Powers 1998), where the artificial, smooth concrete of culverts is lined with natural substrates, such as rocks, to mimic natural stream beds. Roughening can increase turbulence within culverts to beneficial levels, as fish have been observed to actively exploit areas of low velocity, thereby lowering energetic costs of swimming (Taguchi and Liao 2011).

Outputs from our traversable water-velocity models were also similar to estimates derived for other small-bodied fishes (e.g. Mitchell 1989; Castro *et al.* 2010). Similar to models derived for *P. novemaculeata*, Mitchell (1989) assessed swimming capacity in juveniles of five diadromous species (3–8 cm TL), predicting passage to be unrestricted at water velocities of <0.3 m s⁻¹; however, one weak-swimming species was identified, flathead mullet (*Mugil cephalus*), requiring very low water velocities (0.05 m s⁻¹), in line with the needs of *H. compressa*. Even more striking, estimates of maximum traversable water velocity for small characin (*Bryconamericus stramineus*) (5.3–6.4 cm TL) and juvenile *P. novemaculeata* are the same, namely <12 BL s⁻¹ (Castro *et al.* 2010).

Comparisons between water velocities through existing culverts in the field and modelled traversable water velocities (Table S1, available as Supplementary Material for this paper) suggest that during base (low) conditions, the majority (74% for *H. compressa* and 48% for *P. novemaculeata*) of existing culverts would be considered hydraulic barriers. Furthermore, of the six structures considered to be hydraulically suitable to pass both fish species, four had been recently remediated to limit internal water velocity. These data highlight that many existing culverts (in New South Wales, Australia) require remediation before transit of weak-swimming, small fishes is possible.

Although traversable water-velocity models can be a powerful tool in culvert design, the limitations of these models require consideration. Estimates of swimming performance derived from fixed-velocity, non-volitional trials can underestimate the true ability, because fish often attain significantly greater swimming speeds in open-channel, volitional trials (Hinch and Bratty 2000; Peake 2004). The swimming-performance data provided here are likely to be a conservative estimate of the true swimming ability and field validation of our findings is necessary. Furthermore, our models are a simplification of culvert transit, being based on a single, prolonged swimming effort at a fixed velocity. Under field conditions, swimming behaviour and performance are likely to be influenced by fine-scale hydrodynamics, with turbulence and boundary-layer effects coming into play (Bates and Powers 1998). In complex hydraulic conditions,

fish may employ a suite of swimming behaviours (e.g. station-holding) and modes (i.e. sustained, prolonged and burst). Therefore, *in situ* confirmation of our findings should aim to build on our models by accounting for the effects of fluid dynamics on swimming behaviour and performance.

Nonetheless, our findings provide baseline swimming-performance data, strongly suggesting that culvert-design recommendations require urgent revision. To ensure passage of small-bodied, weak-swimming fishes, such as *H. compressa*, the following initiatives are recommended:

- (1) urgent *in situ* confirmation of swimming-performance data under volitional conditions,
- (2) if confirmed, velocity maxima need to be revised down to $\leq 0.1 \text{ m s}^{-1}$ or 2.86 BL s^{-1} , for culverts $\leq 15 \text{ m}$ in length,
- (3) the thermal dependence of swimming performance needs to be accounted for in revised recommendations (particularly for thermally polluted waters), and
- (4) existing culvert barriers require remediation and new culverts need to be designed and installed in line with revised recommendations.

As outlined, a holistic revision of culvert design is likely to have far-reaching benefits by reconnecting the aquatic environment, where upstream passage is provided for the entire fish community, large and small.

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