

Critical swim speed and fast-start response in the African cichlid *Pseudocrenilabrus multicolor victoriae*: convergent performance in divergent oxygen regimes

K.M. Gotanda, E.E. Reardon, S.M.C. Murphy, and L.J. Chapman

Abstract: Dissolved oxygen (DO) can be a strong predictor of intraspecific variation in morphology and physiology in fishes. In the African cichlid *Pseudocrenilabrus multicolor victoriae* Seegers, 1990, fish reared under low DO develop larger gills, deeper bodies, and larger, wider heads than full siblings reared under high DO, which could influence swim performance. In this study, we compared critical swim speed (U_{crit}) and fast-start swimming in F₁-generation fish from two field populations (one high and one low DO) of *P. m. victoriae* reared under high or low DO. There was no difference in U_{crit} between populations or rearing treatments. However, females exhibited a lower U_{crit} than males. In fast-start trials, low-DO-reared fish reacted faster (lower response latency) and used double bends more often than high-DO-reared fish, but there was no difference in maximum velocity or acceleration. Low-DO-reared fish might compensate for morphological differences by using double bends to achieve similar performance as high-DO siblings. These results suggest that divergent morphotypes of *P. m. victoriae* are capable of achieving the same level of performance under their home DO condition and highlights the importance of developmental plasticity in facilitating adaptive response to alternative environments.

Key words: burst swimming, fitness cost, hypoxia, *Pseudocrenilabrus multicolor victoriae*, startle response.

Résumé : L'oxygène dissous (DO) peut constituer un important facteur prédictif de la variation interspécifique de la morphologie et de la physiologie chez les poissons. Chez le cichlidé africain *Pseudocrenilabrus multicolor victoriae* Seegers, 1990, les poissons élevés en conditions basses de DO développent des branchies plus élaborées, un corps plus grand et plus haut et une tête plus large que les membres de même fratrie élevés en forte teneur de DO, ce qui peut affecter leur performance de nage. Notre étude compare la vitesse de nage critique (U_{crit}) et la nage à départ précipité chez des poissons de génération F₁ de deux populations de terrain (de conditions élevée et basse de DO) de *P. m. victoriae* élevées dans des teneurs fortes ou faibles de DO. Il n'y a pas de différence de U_{crit} en fonction des populations, ni des conditions d'élevage. Cependant, les femelles possèdent une U_{crit} plus basse que les mâles. Dans les tests de départ précipité, les poissons élevés dans des conditions basses de DO réagissent plus rapidement (latence réduite de la réaction) et utilisent des courbures doubles du corps plus souvent que les poissons gardés en conditions élevées de DO, mais il n'y a pas de différence de vitesse maximale ou d'accélération. Les poissons élevés en conditions basses de DO peuvent compenser pour leurs différences morphologiques en utilisant des courbures doubles du corps pour atteindre une performance semblable à celle des membres de leur fratrie gardés en conditions élevées de DO. Ces résultats laissent croire que les morphotypes divergents de *P. m. victoriae* sont capables d'atteindre le même niveau de performance dans leurs conditions de DO d'origine en nature et soulignent l'importance de la plasticité au cours du développement pour faciliter une réaction adaptative à des environnements différents.

Mots-clés : nage précipitée, coût de la fitness, hypoxie, *Pseudocrenilabrus multicolor victoriae*, réaction de sursaut.

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Introduction

For fishes, the availability of dissolved oxygen (DO) is an important abiotic factor that can affect growth, survivorship, reproduction, and behavior (Wu et al. 2003; Pollock et al.

2007; Chapman and McKenzie 2009). Variation among habitats in aquatic oxygen availability creates habitat heterogeneity that might lead to divergent selection for traits related to oxygen acquisition. Field and laboratory studies on East African fishes have shown that variation in aquatic oxygen avail-

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ability correlates with intraspecific (or interdemographic) variation in morphological, physiological, biochemical, and life-history traits (reviewed in Chapman 2007). For example, in the African cichlid *Pseudocrenilabrus multicolor victoriae* Seegers, 1990, fish reared under low DO develop larger gills, larger heads (wider and longer), smaller brains, and deeper bodies than full siblings reared under high DO (Chapman et al. 2000, 2002, 2008; Crispo and Chapman 2010, 2011). Although not identical, similar patterns are observed among field populations from low- and high-DO environments (Chapman et al. 2000, 2008). The maintenance of these divergent phenotypes (e.g., large-gilled vs. small-gilled fish) in field populations might reflect fitness trade-offs between alternative DO environments. For example, large gills might be necessary under hypoxia but costly owing to energy required for ion pumping in association with maintaining osmoregulation (Nilsson 2007). Another potential cost of maintaining large gills might be suboptimal swim performance associated with differences in head shape, body depth, and body width (Videler 1993; Rouleau et al. 2010). This might limit the success of large-gilled fish (low DO) should they move into a high-DO habitat with small-gilled conspecifics and contribute to the maintenance of divergent phenotypes in the field (Schaack and Chapman 2003).

Swimming performance variables, such as critical swimming speed (U_{crit}) and fast-start swimming, are often used as indicators of fitness (Graham et al. 1990; Stobutzki and Bellwood 1994; Plaut 2001) and can be used to explore the maintenance of divergent morphologies in fishes (Taylor and McPhail 1985, 1986). U_{crit} is the speed at which a fish can maintain swimming for a prolonged period of time and is often used a relative indicator of aerobic capacity (Brett 1964; Kolok 1999; Reidy et al. 2000), though it is recognized that there are anaerobic contributions to U_{crit} (Wilson and Egginton 1994; Lee et al. 2003). Several studies report how body morphology can influence U_{crit} (Reidy et al. 2000; Rouleau et al. 2010), as well as reduce U_{crit} in response to short-term exposure to hypoxia across fish taxa (Dahlberg et al. 1968; Kaufmann and Wieser 1992; Carter and Wilson 2006; Dutil et al. 2007; Vagner et al. 2008). Environmental influences on development can affect adult performance (Álvarez and Metcalfe 2007), though effects of long-term (e.g., developmental) hypoxic exposure on swim performance are less well understood. However, Widmer et al. (2006) reported a lower U_{crit} in zebra danio (*Danio rerio* (Hamilton, 1822)) reared under low DO when compared with full siblings raised under normoxia.

Fast-start swimming is characterized by a rapid acceleration and fuelled anaerobically (Bennett 1991; Harper and Blake 1991; Wakeling and Johnston 1998; Webb 1998). It is used by fishes as a predatory striking mechanism and (or) a component of antipredator behavior used to evade an attack by a potential predator (Weihs 1973; Webb and Skadsen 1980; Eaton and Emberley 1991; Videler 1993; Domenici and Blake 1997; Domenici et al. 2007). As with U_{crit} , body shape has been shown to influence fast-start swimming (Andraso 1997; Ghalambor et al. 2004; Langerhans 2009). For example, predator-induced morphological changes in the form of deeper bodies in crucian carp (*Carassius carassius* (L., 1758)) were found to improve fast-start swimming (Domenici et al. 2008). Studies exploring the role of hypoxia on

fast-start swimming suggest that hypoxia might affect variables such as directionality of reaction and responsiveness (Lefrançois et al. 2005; Lefrançois and Domenici 2006; Canas et al. 2007) but might not affect other components such as response latency and maximal velocity (Lefrançois and Domenici 2006).

Some studies show an intraspecific trade-off between fast-start response and U_{crit} that might reflect the relative costs and benefits of both in the environment. For example, more streamlined, interior coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)) display a higher U_{crit} compared with their coastal counterparts, a reflection of evolutionary adaptation to more rigorous migration patterns (Taylor and McPhail 1985). In fast-start kinematic measures, freshwater three-spined sticklebacks (*Gasterosteus aculeatus* L., 1758) obtain a higher maximal velocity and distance travelled compared with an anadromous population (Taylor and McPhail 1986). In both cases, the body morphology differed between the populations and the less robust, sleeker populations had a higher U_{crit} but lower fast-start swimming performance relative to the more robust populations, indicating body shape can be indicative of differing achievements in swimming performance.

With the exception of Widmer et al. (2006), studies exploring the role of hypoxia on swim performance are short-term acclimation experiments (generally ranging from zero acclimation to approximately 2 weeks exposure). However, the frequency, duration, and severity of hypoxic episodes are increasing on a global scale associated with eutrophication and pollution of water bodies (Justić et al. 2005; Diaz and Breitburg 2009). Thus, studies comparing swim performance and morphology in response to life-long hypoxia are becoming increasingly relevant (Pollock et al. 2007).

In this study, we quantified swim performance variables in first generation (F_1) offspring of the cichlid *P. m. victoriae* from a hypoxic swamp population (Kantembwe) and a normoxic river site (Bunoga) from the Mpanga River drainage of western Uganda raised under low and high DO in the laboratory. These fish were reared as part of a larger study on six populations from the same drainage that quantified population and rearing (low vs. high DO) effects on morphological traits (Crispo and Chapman 2010, 2011). Regardless of population of origin, fish reared by E. Crispo and L.J. Chapman under low DO had larger gills (34% larger in total gill filament length and 50% larger in total hemibranch area) (Crispo and Chapman 2010) and deeper bodies and larger heads (lateral view) (Crispo and Chapman 2011) compared with fish reared under high DO. Using path analyses, Crispo and Chapman (2011) found that a large part of the variation in body shape was due to the plastic variation in gill size. We predicted that body shape variation induced by development under hypoxia in these F_1 offspring would lead to differences in swim performance between low-DO-reared and high-DO-reared fish. Although steady swimming is generally enhanced by a deeper anterior body, tapering to a narrow caudal peduncle (reviewed in Langerhans and Reznick 2010), *P. m. victoriae* reared under hypoxia develop a larger, wider head and a shorter body (Chapman et al. 2008; Crispo and Chapman 2010, 2011) that could negatively affect streamline and critical swimming speed, despite increased body depth. Similarly a larger, wider head and shorter body could negatively affect

fast-start swimming, because a greater posterior body allocation often characterizes species or populations with greater burst speed (Langerhans and Reznick 2010).

Materials and methods

Species description and rearing conditions

Pseudocrenilabrus multicolor victoriae is a widespread, eurytopic mouth-brooding cichlid found throughout the Lake Victoria basin in East Africa (Greenwood 1974; for full description see Chapman et al. 1995; Crispo and Chapman 2008; Reardon and Chapman 2009). Parental stock were collected from a high-DO site in the Mpanga River drainage of western Uganda referred to as the Bunoga site (mean DO: $7.9 \text{ mg O}_2\cdot\text{L}^{-1}$) and a low-DO swamp site in the same drainage referred to as Kantembwe (mean DO: $0.3 \text{ mg O}_2\cdot\text{L}^{-1}$; see Figs. 2 and 3 in Crispo and Chapman 2008) and were live-transferred to aquarium facilities at McGill University. These populations are well-suited for this study, as they occur in the same river basin (Mpanga River), thus minimizing potential phylo-geographic influences. As part of a larger rearing study described in Crispo and Chapman (2010, 2011), the F_1 generation was split into two groups and reared in three separate tanks under either high DO ($7.8 \pm 0.3 \text{ mg O}_2\cdot\text{L}^{-1}$, mean \pm SE) or low DO ($1.1 \pm 0.1 \text{ mg O}_2\cdot\text{L}^{-1}$), levels reflective of DO concentrations in the field (Crispo and Chapman 2008, 2010). The low-DO treatment was maintained using a Point Four oxygen-controlling system, which gently bubbled nitrogen through a diffuser when DO levels rose above $1.3 \text{ mg O}_2\cdot\text{L}^{-1}$. Aquaria were maintained at a mean water temperature of $24.5 \pm 0.5 \text{ }^\circ\text{C}$ on a 12 h light : 12 h dark photoperiod. Fish were fed TETRA flakes ad libitum daily. To ensure maturity was reached, the F_1 fish were reared for at least 10 months before beginning assessment of swim performance variables. Gill size and body shape traits for fish from these same families were summarized in the introduction and reported in Crispo and Chapman (2010, 2011). All fish were maintained and handled in accordance with McGill University Animal Care Committee (protocol No. 5029).

For all trials, each fish was not fed for 24 h prior to testing to achieve a postabsorptive state. For individual fish, gender, total and standard lengths, and body mass were recorded at the end of each trial. Only males and nonbrooding females were used to remove potential confounding effects of mouth-brooding on swimming performance (e.g., James and Johnston 1998). For both U_{crit} and fast-start response variables, all fish were tested under a DO level close to their rearing environment ($8.0 \pm 0.4 \text{ mg O}_2\cdot\text{L}^{-1}$ for fish reared under normoxia and $1.9 \pm 0.2 \text{ mg O}_2\cdot\text{L}^{-1}$ for fish reared under hypoxia). All hypoxia trials were run at $0.8 \text{ mg O}_2\cdot\text{L}^{-1}$ above rearing DO to ensure that all U_{crit} trials were conducted above the critical oxygen tension (P_{crit} mean $1.2 \text{ mg O}_2\cdot\text{L}^{-1}$; Reardon and Chapman 2010a), as swimming for prolonged periods (primarily aerobically fuelled) below the P_{crit} could result in mortality. In both experimental set-ups, low-DO levels were maintained using a LoliOxy DO controller that gently bubbled nitrogen into the testing tank through a diffuser when DO rose above $1.9 \text{ mg O}_2\cdot\text{L}^{-1}$.

U_{crit} experimental protocol

We used an incremental velocity test in a swim perform-

ance tunnel to quantify the U_{crit} of *P. m. victoriae* (reviewed in Plaut 2001). The swim tunnel was constructed of a clear Plexiglas flume (dimensions: 70 cm long, 8 cm diameter), and black mesh encircling 17 cm of the flume length allowed the fish to be shielded from other stimuli while still being observed (modified from Vogel and LaBarbera 1978). The flume had a baffle made of tightly fitted straws in the swim chamber to achieve a uniformly microturbulent flow of water through the flume (Bell and Terhune 1970). Water flow was controlled by a rheostat connected to a standard water pump, and flow speed was calibrated using a Höntzsch vane wheel flow meter. Temperature was maintained at $25 \pm 0.1 \text{ }^\circ\text{C}$.

The focal fish was introduced into the swim flume, and following a 2 h acclimation period at a speed of $5 \text{ cm}\cdot\text{s}^{-1}$, water velocity was increased incrementally by $5 \text{ cm}\cdot\text{s}^{-1}$ every 20 min (Hammer 1995; Kolok 1999). The 2 h acclimation period allowed for *P. m. victoriae* to return to standard metabolic rate, which is achieved within 90 min from transfer (Reardon and Chapman 2010b). When the fish tried to rest against the material at the end of the swim chamber, the observer gently tapped the fish through the mesh to induce it to remain swimming. Once the fish no longer maintained a position under the black mesh and did not respond to gentle tapping, the fish was pronounced fatigued. Once fatigued, the water velocity was slowly returned to zero, and the fish was then returned to its holding tank. Following Brett (1964), U_{crit} was calculated as $U_i + U_{ii}\cdot(T_i/T_{ii})$, where U_i is the velocity last swum by the fish for the entire 20 min trial period, U_{ii} is the velocity increment, T_i is the total time elapsed when the fatigue velocity is achieved, and T_{ii} is the time interval of each velocity increment.

Fast-start experimental design and video analysis

A circular enclosure (diameter = 30 cm) made of opaque tank dividers was placed within a $61 \text{ cm} \times 30 \text{ cm} \times 30 \text{ cm}$ aquarium tank, and water depth was maintained at 5 cm to prevent vertical movement. Bubble wrap was placed on top of the water to help maintain oxygen levels and to prevent aquatic surface respiration (ASR), which might affect startle response behavior (Lefrançois et al. 2005), although no fish attempted ASR during trials. Water temperature was maintained at $25 \pm 1 \text{ }^\circ\text{C}$. Below the experimental tank, a mirror was angled 45° directly underneath the enclosed area and a Lolitech Troubleshooter video camera was placed approximately 23 cm from the edge of the mirror, also below the tank, so the resulting video was as though the camera was filming from directly underneath the enclosed area. The camera filmed at 500 Hz and was tethered to a computer using Midas version 4.0 software (Xcitex Inc., Cambridge, Massachusetts, USA) to record the trials. The sides of the aquarium and area around the video camera were covered with black cloth to minimize external stimuli. An individual fish was transferred to the experimental aquarium and acclimated for 30 min prior to the first trial, and there was a 15 min acclimation period between subsequent trials. For each trial, a golf ball was dropped onto the bubble wrap from a height of approximately 22 cm above the water surface. The golf ball was used as an artificial stimulus to induce the startle response. It is possible the stimulus could induce a visual reaction, but we feel the bubble wrap precluded any visual stimulus by obscuring the shape, and that the reaction is

based on when the ball physically came into contact with the bubble wrap. This procedure was repeated five times per fish to ensure at least one response per fish.

Video analyses were conducted using Image J software (<http://rsbweb.nih.gov/ij/>). If there were multiple trials where a fish responded to the stimulus, the trial with the shortest response latency was analyzed (Ghalambor et al. 2004). A 1 cm × 1 cm grid taped to the bottom of the tank was used to standardize distance measurements for analysis of distance time variables. Five response variables were evaluated: response latency, response duration, response type, maximum velocity, and maximum acceleration (e.g., Webb 1978; Domenici and Blake 1997). Response latency was calculated as the time, in milliseconds, between when the stimulus touched the bubble wrap (first noticeable movement in the bubble wrap based on the frame-by-frame analysis) and the first detectable movement of the fish. Response duration was defined as the time from when the fish began to move and ended when the fish had maximally bent laterally and formed a characteristic C-shape (Webb 1978; Domenici and Blake 1997). For response type, a single bend was noted when the fish did not achieve a full flip in the opposite direction of the initial reaction, whereas a double bend was noted if there was a full return flip (Domenici and Blake 1991; Kasapi et al. 1993; Spierts and Van Leeuwen 1999; Lefrançois et al. 2005).

To calculate maximum velocity and acceleration, the distance between the center of mass (CM) in subsequent frames was measured with velocity as the change in distance per unit time and acceleration being the change in velocity per unit time. A 5-point smoothing regression (Lanczos 1956) was used to estimate instantaneous velocity and acceleration. Velocity and acceleration were measured from when the fish reacted to the stimulus to a few frames past its achieving a C-shape for single-bend responses and a few frames past the end of the return flip for double-bend responses. The maximal velocity and acceleration calculated during that duration were recorded. CM was estimated using 10 preserved field specimens each from a high- and low-DO field population. For each specimen, a pin was inserted 90° laterally along the midline of the fish and then the fish was balanced. The distance from the snout to the pin was measured when the fish was balanced so its midline was parallel to the floor. There was no statistical difference between populations (two-tailed Student's *t* test, $p = 0.286$), so 44.99% of the standard length (SL) was used as the CM for all video analysis.

A total of 37 fish (U_{crit}) and 32 fish (fast-start) were tested under the aquatic oxygen level in which they were reared. We used SL as a covariate for U_{crit} . For fast-start performance, we first tested for a potential wall effect (Plaut 2001) using a linear regression with maximal velocity on the *y* axis and the distance the CM was from the wall at the start of the response. There was no relationship between how close a fish was to a wall and the maximum velocity achieved ($R^2 = 0.003$, $p = 0.770$).

For both U_{crit} and fast-start variables, ANOVA was used to detect family effects within each population of origin with treatment and gender as fixed factors within the model. Family effects were not detected on either U_{crit} or fast-start variables ($p > 0.05$), and removed from further analyses. ANOVA or ANCOVA was used to test for effects of rearing treatment

population or origin, and their interaction on U_{crit} , response latency (ms), response duration (ms), maximum velocity ($m \cdot s^{-1}$), and maximum acceleration ($m \cdot s^{-2}$). SL was included as a covariate for U_{crit} , maximum velocity, and maximum acceleration. Interactions between the covariate (SL) and the fixed factors were not significant (two-way interactions tested only) and were therefore removed from the models. A Fisher's exact test was performed to assess the effects of rearing environment, population of origin, or gender on response type (single or double bend).

Results

For U_{crit} , we found no effect of treatment, population, or their interaction on U_{crit} (Table 1). However, U_{crit} was significantly lower in female *P. m. victoriae* than in male *P. m. victoriae*, regardless of population or treatment (Table 1, Fig. 1). SL was not a significant covariate (Table 1) and removal of SL from the model did not significantly alter the results. Similarly, the three-way interaction among the fixed factors was not significant ($p = 0.819$) and was removed from the final model presented in Table 1.

For fast-start swimming performance, fish reared under low DO reacted sooner than fish reared under high DO regardless of population of origin (Table 1, Fig. 2). Fish reared under low DO also responded more often with a double bend than fish reared under high DO (Fig. 3, $p = 0.049$, Fisher's exact test or FET). However, there was no difference in the proportion of double bends between the population of origin (Fig. 3; $p = 1.0$, FET) or gender ($p = 1.0$, FET). Although not statistically significant, fish that responded with a double bend tended to have a higher maximum velocity than those that reacted with a single bend (ANOVA: $F_{[1,28]} = 3.143$, $p = 0.087$). There was no effect of population, gender, treatment, or their interactions on the mean response duration, maximum velocity, or maximum acceleration (Table 1, Fig. 2).

Discussion

Regardless of rearing DO and population of origin (low-DO swamp vs. high-DO river), *P. m. victoriae* were capable of achieving the same level swim performance (U_{crit} , maximum velocity, maximum acceleration). The lack of a population effect might reflect the high degree of developmental plasticity in these populations. Much of the variation in gill size, head width, and overall body shape between high-DO-reared and low-DO-reared fish species has been attributed to developmental plasticity (Chapman et al. 2008; Crispo and Chapman 2010, 2011). In addition, there is evidence for high gene flow between these two populations in the wild (Chapman et al. 2008). The lack of a treatment effect on U_{crit} was more surprising, given the larger heads and deeper bodies that characterize hypoxia-reared fish driven by their enlarged gills (Crispo and Chapman 2010, 2011). However, the large gills of low-DO-reared fish in association with developmental plasticity in other physiological traits related to oxygen uptake (e.g., Martínez et al. 2009; Reardon and Chapman 2010a) might mitigate performance costs under hypoxia, thus allowing the maintenance of aerobic capacity at a level comparable with small-gilled, normoxia-reared siblings. Our results are contrary to previous work by Widmer et al.

Table 1. ANOVA and ANCOVA results for the effect of population of origin, rearing DO environment, gender, and their interactions on response variables for critical swimming speed (U_{crit}) and fast-start swimming variables of the African cichlid *Pseudocrenilabrus multicolor victoriae*.

Response variable	Factor	df	F	p
U_{crit} (cm·s ⁻¹)	Rearing DO	1, 27	0.221	0.642
	Population	1, 27	0.242	0.627
	Gender	1, 27	11.435	0.002
	Rearing DO × population	1, 27	2.368	0.135
	Population × gender	1, 27	0.519	0.477
	Rearing DO × gender	1, 27	1.399	0.247
	SL	1, 27	0.582	0.452
Response latency (ms)	Rearing DO	1, 25	4.475	0.045
	Population	1, 25	0.240	0.628
	Gender	1, 25	0.101	0.753
	Rearing DO × population	1, 25	0.064	0.802
	Population × gender	1, 25	0.072	0.790
	Rearing DO × gender	1, 25	0.384	0.541
	SL	1, 25	0.002	0.969
Response duration (ms)	Rearing DO	1, 25	0.002	0.969
	Population	1, 25	1.701	0.204
	Gender	1, 25	0.025	0.875
	Rearing DO × population	1, 25	1.482	0.235
	Population × gender	1, 25	0.862	0.362
	Rearing DO × gender	1, 25	0.000	0.997
	SL	1, 25	0.000	0.997
Maximum velocity (m·s ⁻¹)	Rearing DO	1, 24	0.112	0.741
	Population	1, 24	0.137	0.715
	Gender	1, 24	0.013	0.910
	Rearing DO × population	1, 24	0.117	0.735
	Population × gender	1, 24	0.497	0.488
	Rearing DO × gender	1, 24	2.324	0.140
	log ₁₀ -transformed SL	1, 24	2.308	0.142
Maximum acceleration (m·s ⁻²)	Rearing DO	1, 24	0.327	0.573
	Population	1, 24	0.759	0.392
	Gender	1, 24	0.290	0.595
	Rearing DO × population	1, 24	0.310	0.583
	Population × gender	1, 24	0.152	0.700
	Rearing DO × gender	1, 24	0.144	0.708
	log ₁₀ -transformed SL	1, 24	4.958	0.036

Note: Values in boldface type indicate significant *p* values. Response duration, response latency, maximum velocity, and maximum acceleration were log₁₀-transformed. Standard length (SL) was the covariate for U_{crit} , whereas log₁₀-transformed SL was the covariate for maximum velocity and maximum acceleration. Three-way interactions among the main factors were not significant and were removed from the models.

(2006) who found lower U_{crit} in low-DO-reared *D. rerio* regardless of testing conditions compared with their high-DO-reared conspecifics. It is possible that *D. rerio* might not exhibit sufficient developmental plasticity in other morphophysiological traits when reared under hypoxia to compensate for the challenge of sustained swimming.

Although our results indicated that U_{crit} tested in the rearing environment does not differ between respiratory phenotypes of *P. m. victoriae*, other factors might impose a cost to movement into an alternative DO environment in nature. For example, Schaack and Chapman (2003) reported reduced size of key trophic muscles and reduced feeding performance in large-gill phenotypes of the African cyprinid *Barbus neu-mayeri* Fischer, 1884 from a hypoxic swamp compared with conspecifics from a nearby well-oxygenated stream. They argued that reduced respiratory performance in small-gilled fish when exposed to hypoxia (Olowo and Chapman 1996) and indirect costs of large gills (e.g., reduced feeding performance) might contribute to the maintenance of local pheno-

Fig. 1. Mean critical swimming speed (U_{crit}) for male and female F₁ *Pseudocrenilabrus multicolor victoriae* reared under high dissolved oxygen (DO) or low DO. Probability values for population of origin, rearing DO, and gender are presented in Table 1.

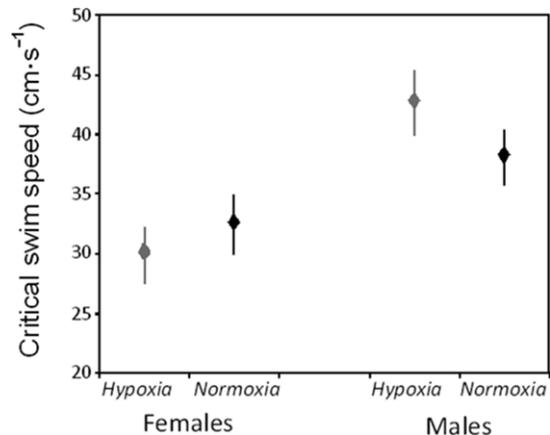


Fig. 2. (a) Adjusted mean maximum acceleration ($\text{m}\cdot\text{s}^{-2}$) and (b) mean latency for F₁ *Pseudocrenilabrus multicolor victoriae* of high DO (Bunoga) and low DO (Kantembwe) origin reared under high DO or low DO. Data were log₁₀-transformed and standard length (SL) was used as the covariate for maximum acceleration. Probability values for population of origin, rearing DO, and gender are presented in Table 1.

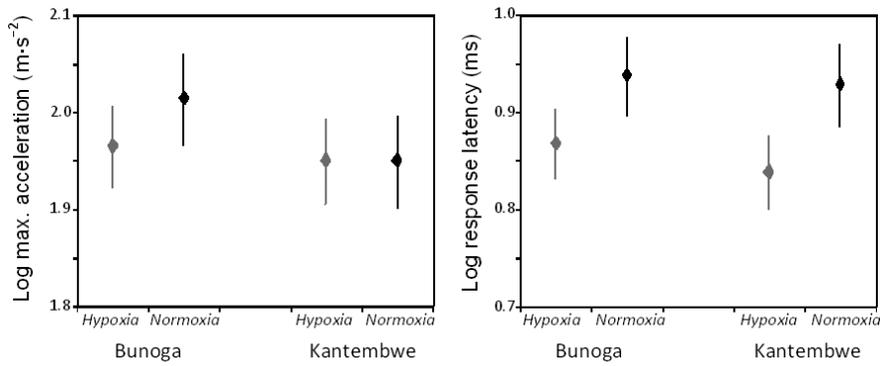
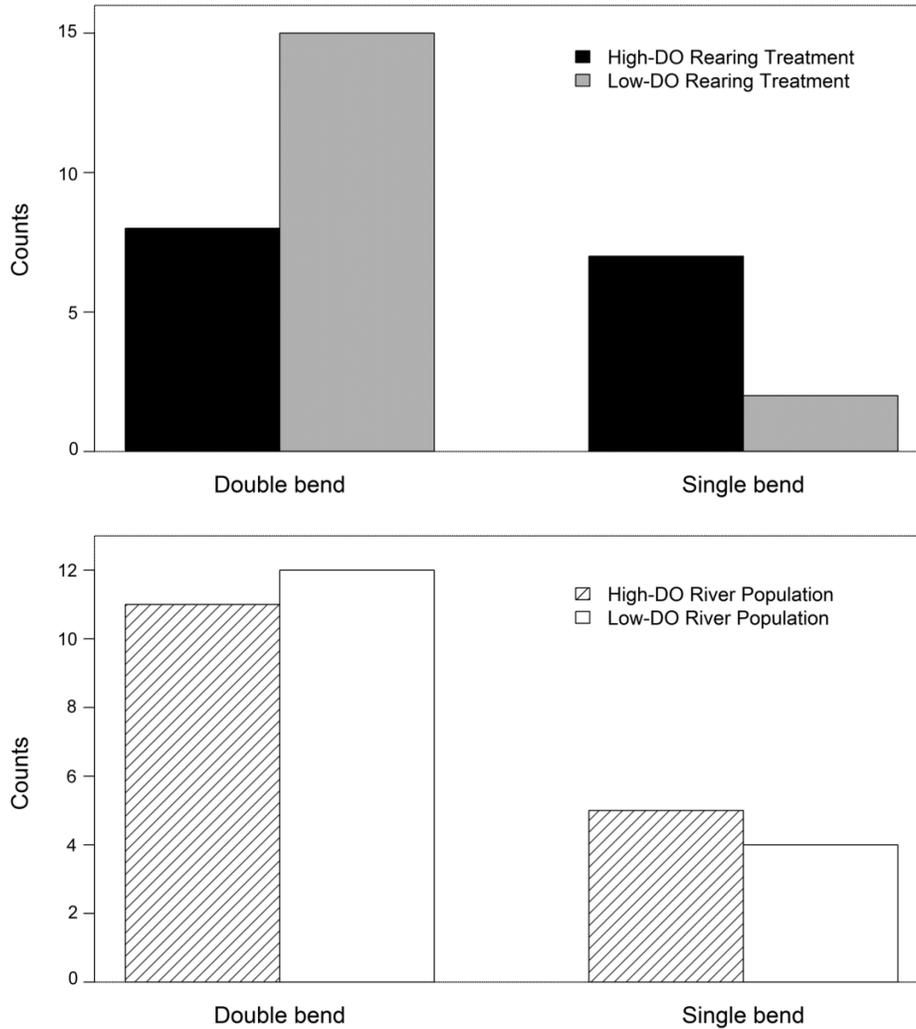


Fig. 3. Frequency of response type (single or double bend) for F₁ *Pseudocrenilabrus multicolor victoriae* separated by (a) rearing DO environment (high or low) and (b) population of origin.



types of *B. neumayeri* in contrasting oxygen environments. For *P. m. victoriae*, a logical extension of this study is to determine if fish perform suboptimally in the alternative environment, which would be the case if phenotypes dispersed into an alternative oxygen environment in the field. For example, we might expect fish reared under high DO to per-

form suboptimally when U_{crit} is tested under low DO because they might not have the morphological or physiological adaptations necessary to meet their active metabolic demand under low DO. If true, this might contribute to explaining the maintenance of divergent phenotypes that we observe in the field.

Similar to U_{crit} , low-DO-reared and high-DO-reared *P. m. victoriae* achieved the same mean maximal velocity and acceleration when startled with an artificial stimulus. Because fast-start swimming is anaerobically fuelled, this suite of responses might be less susceptible to changes in DO levels (e.g., Bennett 1991; Wakeling and Johnston 1998; Webb 1998; Schaack and Chapman 2003). At the same time, this result was surprising given the known morphological differences fish have between rearing treatments. Domenici and Blake (1997) reviewed how morphology differed between fish species depending on their swimming specialization (e.g., cruising, acceleration, or maneuvering), and noted factors such as body depth and fin shape affect fast-start responses. Webb (1978) also noted muscle mass and body depth were factors affecting fast-start performance. Thus, we had expected the low-DO-reared fish with fatter heads and deeper bodies to differ in their swimming performance compared with their high-DO reared siblings. However, regardless of DO treatment, we did see a trend ($p = 0.087$) for fish to demonstrate a higher maximum velocity when they engaged in a double-bend response, a finding that is supportive of earlier studies (Domenici and Blake 1991; Lefrançois et al. 2005). Interestingly, fish reared under low DO reacted sooner and used a double bend more frequently than fish reared under high DO. The faster response, coupled with the double bend in hypoxia-reared fish is interesting, because a common response to hypoxia exposure is to reduce behaviors that are energetically costly (Kramer 1987; Abrahams et al. 2005; Marks et al. 2005; Gotanda et al. 2011) and there was no evidence of hyperactivity (K.M. Gotanda and S.M.C. Murphy, personal observations) in the hypoxia-reared fish to account for their faster response. Our results suggest that the extra bend might be energetically costly, but necessary in the context of predator avoidance (Webb and Skadsen 1980; Eaton and Emberley 1991; Walker et al. 2005), and might allow fish reared under low DO to achieve the same performance as siblings reared under high DO.

Trade-offs between burst and endurance swimming have been detected in a range of vertebrates including some fishes, amphibians, and mammals (e.g., Dohm et al. 1996; Ojanguren and Braña 2003). Thus, for fish reared in the same environmental conditions, we might expect a trade-off between maintenance of aerobic (U_{crit}) and anaerobic capacity (fast-start swimming) as has been observed in *O. kisutch* (Taylor and McPhail 1985) and *G. aculeatus* (Taylor and McPhail 1986). However, similar to swim performance trials on larvae of the African Clawed Frog (*Xenopus laevis* (Daudin, 1802)) (Wilson et al. 2002) and juvenile sea bass (*Dicentrarchus labrax* (L., 1758)) (Nelson and Claireaux 2005), we found no evidence for a relationship between burst and endurance swimming suggesting that an intraindividual trade-off might not be occurring. In their study on swim performance of Atlantic cod (*Gadus morhua* L., 1758), Reidy et al. (2000) suggest that the relationship between aerobic and anaerobic performance could reflect the “good athlete–bad athlete” hypothesis, as opposed to trade-offs in performance types. We suggest that low-DO-reared fish might utilize compensatory mechanisms to achieve the same “good athlete” performance as their high-DO-reared siblings. Evidence to support this idea comes from a recent study on the developmental plasticity of hypoxia on *P. m. victoriae* reared under high and low

DO where fish reared under low DO had a higher marginal metabolic scope compared with siblings reared under high DO (Reardon and Chapman 2010a), and from recent work in our laboratory that suggests better swim performance in hypoxia-reared *P. m. victoriae* than normoxia-reared *P. m. victoriae* when tested under normoxia (S.M.C. Murphy, unpublished data). The larger gill size of fish reared under low DO might contribute to their higher marginal metabolic scope relative to high-DO-reared fish by providing them with a larger “engine” to meet their metabolic demand (e.g., Pauly 1981; Neill and Bryan 1991). Another consideration is that testing DO levels might have been too high to induce differences in swim performance between DO treatments. The hypoxia U_{crit} trials were run at DO levels above the P_{crit} of the fish to ensure that we quantified aerobic swimming capacity. If DO levels had been conducted at or below the P_{crit} , we might expect to see a reduction in swimming capacity associated with the transition from oxygen-independent to oxygen-dependant metabolism.

Females exhibited a lower U_{crit} than males, but we did not detect any gender related differences in fast-start response variables. The lower U_{crit} observed in females is consistent with recent findings that demonstrated a lower metabolic scope in female *P. m. victoriae* regardless of whether they were reared under low-DO or high-DO treatments (Reardon and Chapman 2010a). In *P. m. victoriae*, males are aggressive and territorial, while females are maternal mouth brooders and therefore bear the energetic cost of caring for the embryos. Female *P. m. victoriae* produce broods several times throughout the year (Reardon and Chapman 2008), and while mouthbrooding (approximately 2–3 weeks), females are cryptic, inactive, and do not eat (Mrowka and Schierwater 1988; Reardon and Chapman 2010b). Thus, it is possible that females invest more energy into producing large, competitive offspring and in the maintenance of anaerobic capacity (for predator avoidance) at the expense of aerobic capacity.

Conclusions

Aquatic systems worldwide are experiencing increases in the frequency and occurrence of hypoxic stress as a result of eutrophication and pollution (Justić et al. 2005; Chapman and McKenzie 2009; Diaz and Breitburg 2009). Thus, it has become increasingly important to understand how aquatic organisms might respond to both acute and long-term hypoxic events. Results of this study demonstrate that regardless of rearing DO environment and resulting divergent morphotypes, *P. m. victoriae* are capable of achieving the same end performance ability. There might be an underlying energetic cost to this performance in fish reared under low DO; however, the results of this study highlight the importance of developmental plasticity in facilitating comparable performance of local phenotypes in divergent aquatic oxygen environments.

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