Hypoxia and life-history traits in a eurytopic African cichlid

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This study quantified variation in key life-history traits of the widespread African mouth-brooding cichlid Pseudocrenilabrus multicolor victoriae. Egg size, number, batch reproductive effort, size at maturity and brooding efficiency were compared among field populations across a wide range of dissolved oxygen (DO) concentrations from extreme hypoxia to normoxia. In the laboratory, a similar suite of characters was quantified in F1 of low- and high-DO origin reared under low or high DO. In general, females from low-DO habitats and females reared under low DO were characterized by a smaller size at maturity and no difference in batch reproductive effort when compared with females from high-DO habitats or females reared under normoxia. A trade-off between egg size and number was evident in the field and in the laboratory-rearing experiment, but the direction of the trade-off differed. Egg size was negatively correlated with egg number across field populations; females collected from low-DO sites generally had more, smaller eggs relative to females from high-DO sites. In the laboratory-rearing experiment, F1 females of high-DO origin produced larger, fewer eggs than F1 females of low-DO origin, lending support to the field results and suggesting a heritable component to these traits. There was also an element of developmental plasticity, F1 females raised under low DO produced larger, fewer eggs compared with F1 females raised under high DO (regardless of population) suggesting that DO may interact with other variables to determine egg size in the field.

Key words: Cichlidae; East Africa; fish reproduction; oxygen.

INTRODUCTION

A central goal of physiological ecology is to understand physiological diversity in relation to the environments in which organisms live. For fishes, the availability of dissolved oxygen is one abiotic factor that can exert a strong selective force and has led to a diversity of strategies to efficiently extract oxygen from water or use atmospheric air. Chronic or periodic hypoxia (low oxygen) occurs naturally in many aquatic systems characterized by low light and low mixing and can be particularly acute in tropical waters where high temperatures promote organic decomposition and reduce oxygen tensions. Unfortunately, environmental degradation is increasing...
the occurrence of hypoxia as influx of municipal wastes and fertilizer runoff accelerates eutrophication and pollution of water bodies (Jensen et al., 1993; Charette & Prepas, 2003). Hypoxia is now recognized as a large-scale threat to fresh and coastal waters worldwide (GESAMP, 1990), which can result in changes in fish species composition, population decline and production of extensive dead zones affecting commercially and recreationally important fisheries (Diaz & Rosenberg, 1995; Charette & Prepas, 2003). Thus, it has become increasingly important to understand consequences of hypoxic stress for fishes. One way to explore response to hypoxic stress is to quantify intraspecific or interdemic variation in traits across an oxygen gradient to minimize phylogenetic effects.

Field studies of African fishes have demonstrated that alternative dissolved oxygen (DO) environments can be an important driver of intraspecific variation in fishes, particularly in respiratory traits (e.g. gills) and associated characters including the size and shape of the head (Smits et al., 1996; Chapman et al., 2000, 2008). Fitness trade-offs maintaining these divergent phenotypes may be reflected in interdemic variation in life-history traits. Short-term acclimation studies on marine and estuarine fishes and invertebrates have begun to explore patterns of variation within and across species, suggesting that hypoxia exposure can trigger an overall reduction in energy available for both somatic growth and reproduction with evidence of reduced juvenile growth rates, smaller size at maturity, smaller adult body size, lower egg number per brood, delayed spawning and overall reduced reproductive capacity (Bejda et al., 1992; Wu, 2002; Richmond et al., 2006; Landry et al., 2007; Thomas et al., 2007).

Far less is understood about long-term effects of hypoxic exposure, but given the widespread occurrence of hypoxia, and increasing frequency of hypoxia associated with anthropogenic influence, phenotypic change in response to low oxygen may be a frequent phenomenon in nature. Over many generations, strong selection for long-term hypoxia tolerance could lead to variation in reproductive strategies among populations that experience divergent aquatic oxygen environments. This may lead to further diversification if the benefits accrued by particular reproductive traits in hypoxic habitats result in sub-optimal performance in normoxic (high oxygen) waters.

Life-history theory predicts a balance or trade-off between traits affecting survival and traits relating to reproduction. Since limited resources are available to an organism for growth, maintenance and reproduction, under extreme conditions fundamental life-history trade-offs may become more apparent (Reznick, 1991; Jones & Reynolds, 1999). For example, under hypoxia, mouth-brooding fishes face a dual challenge of increasing both oxygen uptake efficiency to the parent and increasing availability of oxygen to the eggs through behavioural mechanisms (aquatic surface respiration, increased gill ventilation and habitat selection). Thus, reproductive compensation may be evident in decreased allocation to somatic growth (Wootton, 1979) and a reduced fecundity associated with a smaller body size (Landry et al., 2007).

Once resources have been allocated for reproduction, a female must parcel the package into either many small eggs or a few large eggs. The basic premise of this trade-off is that for a given reproductive event, females will optimize benefits accrued from investment towards individual offspring against the costs to the total number of offspring produced, resulting in a negative correlation between offspring size and number (Lack, 1947; Smith & Fretwell, 1974). In fishes, the trade-off between egg size and clutch size (batch fecundity) has received strong empirical support from comparative interspecific studies (Duarte & Alcaraz, 1989; Elgar, 1990).
Life-history variation across an oxygen gradient

and interdemic studies (Reznick & Endler, 1982; Fleming & Gross, 1990; Johnson & Belk, 2001) exploring divergent selective environments across alternative predator, food and latitudinal environments. Studies of variation in egg size and number in response to divergent aquatic oxygen environments are lacking. Life-history and maternal effects literature on fishes, however, predict that fish eggs should be smaller under hypoxic conditions (Heath & Blouw, 1998; Hendry et al., 2001). This prediction is based on the physiology of the surface area to volume ratio, where surface area represents ability to uptake oxygen and volume represents metabolic demand. If true, a large egg would have more limited oxygen uptake ability because volume increases faster than the surface area (Krogh, 1959). There is some debate, however, as to whether the entire egg is metabolically active (Einum et al., 2002, Rombough, 2007). Clearly there is need to test the generality of these laboratory studies across a broader range of taxa and under field conditions where other selective agents may interact with oxygen to influence egg size.

The goal of this study was to quantify variation in life-history traits across alternative oxygen environments in the eurytopic mouth-brooding African cichlid *Pseudocrenilabrus multicolor victoriae* Seegers and the degree to which DO may contribute to the observed variation. *Pseudocrenilabrus multicolor victoriae* is an excellent species for a study of this nature, because it is found across a wide range of dissolved oxygen availability in the field. Several life-history traits in eight field populations of *P. m. victoriae* that represent a range of DO concentrations from extreme hypoxia to normoxia were measured and compared. In the laboratory, a similar suite of characters in F1 of low-DO (swamp) and high-DO (lake) origin grown under low and high DO was quantified. Based on the premise that finite resources are available for growth, maintenance and reproduction, the following predictions were tested: (1) females from low-DO habitats or females reared under low DO will mature at a smaller size and earlier age to maximize possible lifetime broods produced, trading off growth (maternal body size) for reproduction and (2) females from low-DO field habitats and females grown under low DO (regardless of origin) will produce more, smaller eggs compared with females from high DO habitats and females grown under high DO. In this study, results of a field survey to test the above predictions using a correlative approach and a laboratory-rearing experiment to test for DO effects while removing confounding variables are reported. Comparisons of the field and laboratory patterns can provide valuable information on the importance of DO as a driver of divergence. If the patterns are the same, then DO may be the direct cause. If not, DO may be an indirect driver of the field patterns and interact with other drivers. Given the intensive effort required to raise, maintain and collect data for the laboratory-rearing experiment, F1 offspring were reared from only one high-DO and one low-DO population.

**Materials and Methods**

**Species Description**

*Pseudocrenilabrus multicolor victoriae* is a small (maximum total length $L_T$, c. 8 cm) cichlid found in the Nile River system and the Lake Victoria basin (Greenwood, 1965). This species occupies a wide range of habitats including fast-flowing rivers, intermittent streams, lakes, wetland ecotones and dense wetlands (Chapman et al., 1996a, b). Where it
occurs in dense papyrus (Cyperus papyrus) and Miscanthidium violaceum swamps, it is often the dominant species with respect to numbers of individuals and biomass (Chapman et al., 2002). Like all haplochromine cichlids, *P. m. victoriae* is a maternal mouth brooder; the eggs and developing fry are protected in the mouth of the female. Costs of mouth brooding are potentially high for *P. m. victoriae*, as the brooding females are unable to feed while carrying young (Oppenheimer, 1970). *Pseudocrenilabrus multicolor victoriae* feeds on a large variety of plants and animals including algae, insects and other fishes (Greenwood, 1965). Mechanisms facilitating the widespread distribution of this species remain largely unknown. Strong patterns of morphological variation (i.e. gill size and body depth) across populations, however, suggest locally adapted phenotypes (Chapman et al., 2000, 2002) that may vary in reproductive strategy.

**INTERDEMIC VARIATION IN LIFE-HISTORY TRAITS: FIELD SURVEY**

To quantify interdemic variation in reproductive traits of *P. m. victoriae*, fish were collected from eight sites in Uganda during four field expeditions carried out between 2004 and 2007. Although *P. m. victoriae* breed throughout the year, there are peaks in reproductive activity associated with peaks in rainfall (Welcomme, 1969; Reardon & Chapman, 2008). Expeditions were carried out in the period of late May to early June to standardize for potential seasonal effects on reproductive traits. Sites representative of the range of DO conditions experienced by this species were chosen; these included four sites in the Mpanga River drainage of western Uganda, and four sites in the Nabugabo region of the Lake Victoria basin (Fig. 1). The Mpanga River (mid-region) is located >150 km west of the Nabugabo system and joins the westward-flowing section of the Katonga River feeding into Lake George (0°03′ N; 30°15′ E). The entire Katonga River at one time flowed to the west, but its direction has been reversed by uplifting; and it now drains primarily to the east into Lake Victoria (0°07′ S; 31°58′ E). In the Katonga River valley, water flows in both directions from a swampy watershed and may maintain a contemporary link between the Victoria and the Edward and George systems; there is evidence that *P. m. victoriae* from both regions originated from one source population (Crispo & Chapman, 2008). Both low- and high-DO sites were sampled in both regions.

The study sites ranged from well-oxygenated river and lake habitats, to a river site characterized by high seasonal fluctuations in oxygen partial pressure (*P*O$_2$), to the chronically hypoxic waters of dense *C. papyrus* and *M. violaceum*-dominated swamps (Welcomme, 1969; Chapman et al., 1998). Seasonal patterns of *P*O$_2$ from five sites that reflect the range of habitats sampled in the survey are illustrated in Fig. 2. Sites in the dense interior of either *C. papyrus* (Kantembwe Swamp) or *M. violaceum*-dominated swamps (Lwamunda Swamp) are chronically hypoxic, although seasonal variation does occur (Fig. 2; Chapman et al., 1999). A one-year monitoring programme on Lake Kayanja (open water) and a flowing section of the Mpanga River (Sebatoli site) indicated normoxic conditions throughout the year in both systems (Fig. 2). The Mpanga Kahunge River site, although an open flowing river site, is characterized by highly fluctuating *P*O$_2$, driven by flushing of an extensive swamp system that feeds into the river upstream of the Kahunge site (Chapman et al., 2002). With the exception of the Mpanga Sebatoli River site, all sites were also sampled in the field survey.

**Size at maturity**

To estimate size at maturity, an average of 48 females was captured live per population per year sampled (range: 22–74) using metal minnow traps. The fish were euthanized in tricaine methanesulphate (MS-222, 1 g l$^{-1}$ buffered with 4 g of sodium bicarbonate to neutral pH). Standard length (*L*$_S$) and mass (*M*) were recorded for each fish. For females, gonads were removed, weighed (*M*$_G$) and macroscopically classified into standard maturity stages following staging described in the literature (Welcomme, 1969; Balirwa, 1998). Staging data were used to derive estimates of size at maturity and brooding efficiency. The fish and removed gonads were preserved in 4% paraformaldehyde buffered with phosphate-buffered...
FIG. 1. Map of the River Katonga system in Uganda, a river that flows both east and west due to the historical rift uplifting. (a) Inset illustrates the location of four sampling sites (*) on the Mpanga River that flows into the westward-flowing Katonga River and eventually into Lake George; the fifth site (Sebatoli) was sampled over 1 year for environmental dissolved oxygen profiling but \textit{Pseudocrenilabrus multicolor victoriae} are not found at this site. (b) Inset illustrates the four sampling sites in the Lake Nabugabo system where the Katonga River meets lowlands and flows into Lake Victoria.

Saline (PBS). Size at maturity was estimated in field populations as the $L_S$ at which 50\% of the individuals were mature ($L_{S50}$). A female was considered to be mature if she had gonads with ripe oocytes (stage III and higher; Welcomme, 1969), if she was brooding when caught, or if there was evidence of recent brooding (\textit{i.e.} a dropped jaw). Sites were sampled for size at maturity as follows: Mpanga Bunoga, Lwamunda Swamp and Lake Kayanja 2004–2007; Kaz Lagoon 2004–2006; Mpanga Kahunge 2004–2005; Mpanga Kamwenge 2004 and 2007; Kantembwe Swamp 2007; Manywa Swamp Pool 2005. For each year sampled, binary logistic regression models were used to estimate $L_{S50} = [1 + \beta(e^{-rL_S})]^{-1}$ for each population. The function $L_{S50} = [1 + \beta(e^{-rL_S})]^{-1}$ produced an S-shaped curve for each population each year, where $r$ is a model parameter that affects the inflection points or the horizontal shape of the curve and $\beta$ is a model parameter that affects the height of the curve. Both $r$ and $\beta$ were determined using an Excel function that produced the lowest sum of squares for all of the females in a population. Within each population, interannual differences in $L_{S50}$ were not
Fig. 2. Seasonal variation in oxygen partial pressure (\(P_{O_2}\)) for three sites in the Mpanga River [high dissolved oxygen, DO, Sebatoli (■); low DO, Kantembwe Swamp (●); fluctuating DO, Kahunge (▲)] and two sites from the Nabugabo region [high DO, Lake Kayanja (○); low DO, Lwamunda Swamp (□)]. Data were adapted from seasonal data collected on these systems by the Kibale Fish Project over the past decade: Sebatoli, July 1996 to May 1998, Kantembwe Swamp, July 2006 to September 2007, Kahunge July 2006 to September 2007, Lwamunda Swamp, June 2004 to April 2005 and Lake Kayanja, October 1999 to September 2000.

statistically significant (\(P > 0.05\)), so estimates were calculated on the combined-year data sets.

For each site, a suite of environmental data was recorded in the afternoon on days when fish were sampled, including DO, water temperature, conductivity, pH and transparency. Aquatic DO concentration was converted from mg l\(^{-1}\) to \(P_{O_2}\) (mm Hg), correcting for temperature and altitudinal differences across sites. Linear regression was used to test for a relationship between \(L_{SS0}\), and both \(P_{O_2}\) (mm Hg) and water temperature (° C).

Brood traits

Females mouth-brooding young in all stages of development (unhatched eggs to fully developed fry) were captured. Only broods of unhatched, fertilized eggs were used to estimate brood traits with the exception of brooding efficiency. Females are very secretive while brooding, making them difficult to catch in the field. Brood data were combined across years to increase power. It was not possible to test for an effect of year on brood traits; but as stated above, season sampled was controlled for. When a brooding female was live-captured, the brood was removed; each brood was counted for egg number and preserved in 4% paraformaldehyde buffered with phosphate-buffered saline. Each egg was weighed (wet mass, \(M_{EW}\)) and placed in a drying oven for 24 h at 60° C to achieve dry mass (\(M_{ED}\)). The \(M_{EW}\) and \(M_{ED}\) of each individual egg were measured to 0.001 mg using a Sartorius Microbalance (http://www.balances.com/sartorius/microbalance.html). Percentage of water was calculated as: \((M_{EW} - M_{ED}) / M_{EW}\). Individual egg volume (\(V_E\)) was calculated using the equation for a
spheroid \( V_E = 1.33 \pi (0.5D_1 + 0.5D_2) \) (Niciu, 1995). \( D_1 \) and \( D_2 \) (two perpendicular diameters of each egg) were measured using digital photography and the imaging software, Motic Images 2000 1.3 (www.motic.com).

ANCOVA was used to test for differences in the slopes and intercepts of the bilogarithmic relationship between egg size traits and female \( L_S \), and egg number and female \( L_S \) among populations. Within populations, none of the egg size traits \( (V_E, M_{EW}, \% \text{ water}) \) was related to female \( L_S \); therefore, ANOVA was used to produce means to explore the egg size and number relationship across populations. For egg number, there was a positive relationship between egg number and female \( L_S \) across populations (ANCOVA, \( F_{6,53}, P < 0.05 \)), but also a significant interaction term between female size and egg number \( (P < 0.05) \). Sequential removal of the populations with the most divergent slopes revealed that heterogeneity was the result of just one population (Lake Kayanja). Common slope coefficients were similar when calculated with or without Lake Kayanja (with, \( \beta = 2.270 \); without, \( \beta = 2.508 \)), and the size-standardized egg number values were similar regardless of which coefficient was used. Thus, the size-standardized egg number using the common slope of the body size–egg number relationship in ANCOVA using seven populations was applied. Size standardization followed Reist (1986) and Hendry et al. (2002). Batch reproductive effort (total brood dry mass) was calculated for each population by multiplying the mean \( M_{ED} \) by the standardized number of eggs for each brood. ANOVA was used to test for a population effect for size-standardized egg number and batch reproductive effort.

At the population level, brooding efficiency was estimated by dividing the mean number of young brooded in the mouth by the mean number of eggs produced in the gonad (Welcomme, 1969). Only broods in the later stages of development (fully developed fry and hatched young with a reduced yolk sac) were used to calculate the mean number of young brooded in the mouth, since this better reflects the number of live young produced. The number of oocytes in late-stage, mature gonads (stages 4 and 5, Welcomme, 1969) were used to calculate mean number of eggs produced per female for each population. The mean number of oocytes, fertilized eggs and young were calculated after per-brood number data were size-standardized as described for egg number above. Two sites (Manywa Swamp Pool and Mpanga Kamwenge) were not included in the brooding efficiency analysis due to low sample size of brooding females and females with ripe gonads. Among populations, Pearson correlation was used to detect significant relationships between mean egg size and mean egg number (both \( V_E \) and \( M_{ED} \)), and to test for a relationship between egg number per brood, brooding efficiency, and both \( P_{O_2} \) (mm Hg) and water temperature (°C).

**Developmental plasticity study**

Parental stocks from two populations were collected and transported live from Uganda to the aquatic facility. One low-DO site (Lwamunda Swamp) and one high-DO site (Lake Kayanja) were chosen. These two sites were chosen because they lie in the same drainage basin but exhibit contrasting DO regimes (Fig. 1). The Lwamunda Swamp is a dense hypoxic wetland that surrounds Lake Nabugabo and separates it from Lake Victoria. This site is chronically hypoxic, but does show seasonal variation in DO that is typical of wetlands in the region (Fig. 2). Females reproduce year round at this site but show peaks in spawning correlated with rainfall peaks (Reardon & Chapman, 2008). Lake Kayanja is a satellite lake of Lake Nabugabo characterized by relatively high and stable DO in the open water (Figs 1 and 2). Fish were caught around the grassy margin of the lake where DO averaged 6-10 mg l\(^{-1}\) over the year.

The F1 generation fish originating from the two populations (low- and high-DO origin) were raised under extreme hypoxia (mean ± s.e. DO 1.48 ± 0.02 mg l\(^{-1}\); \( n = 6804 \)) and normoxia (mean ± s.e. DO 7.49 ± 0.06 mg l\(^{-1}\); \( n = 3689 \)). Broods from four families per population were used to provide family-level replication; the number of families was limited due to the complexity of measuring key target traits (size at maturity, age at maturity, brood quality: number of eggs, \( V_E \), \( M_{EW} \), \( M_{ED} \) and egg \% water content). Brooding pairs of parental stock were held in separate, normoxic aquaria until the young were completely released from the female’s mouth. When a brood was released by a female, it was divided into two groups and randomly allocated to one of 16–76 l aquaria; half maintained at high-DO and half under...
low-DO. Broods were cropped randomly to approximately eight young per aquarium after 3 months. Based on earlier studies in the laboratory, this density allowed fish to grow to a size reflective of some field populations.

DO in experimental tanks was controlled by pulsing nitrogen through a diffuser to reduce DO levels. Underwater filtration was achieved by a Mag-drive pump (with sponge biofiltration) modified by 19 mm tubing to ensure adequate circulation. Aquaria were held at mean temperature of 24-7 °C and exposed to a 12L:12D photoperiod. Fish were fed once per day on HBH fry bites (www.hbhpet.com) (until 3 months old) and then Tetramin food flakes (www.tetra-fish.com). The first female started brooding at 6-4 months (192 days), and the last female brooded at 11-0 months (340 days); all data were collected during this period. Fish were monitored daily and were carefully observed three times a week for evidence of first maturity (i.e. development of orange egg spot on male anal fin, courtship behaviour and brooding females). Each time a female was observed to have eggs in her mouth, the eggs were gently removed, and the \( M \) and \( L_S \) of the female were measured. The body size measurement from when each female produced her first brood was used to estimate age and size at maturity. For each brood, eggs were preserved for measurements of \( V_E \), \( M_{EW} \) and \( M_{ED} \), % of water and number of eggs using the same methods as described for the field survey. After completion of the experiment, females were euthanized, and their gonads removed and staged to calculate brooding efficiency following methods described for the field survey.

Nested-ANOVA was used to detect effects of treatment (low v. high-DO rearing environment), population of origin (low-v. high-DO origin and their interaction on size, age at maturity, mean \( V_E \), mean \( M_{EW} \), \( M_{ED} \) and mean egg % water content. For the egg size characters (the last four), female was included in the model as a random factor, but no effect of female body size on the last four characters was detected (bilogarithmic regressions, \( P > 0.05 \)), so it was not included as a covariate. There was a weak positive but non-significant relationship between female \( L_S \) and egg number (ANCOVA, \( F_{1,33}, \ P > 0.05 \)), and no significant interaction terms between either population of origin (\( P > 0.05 \)) or treatment (\( P > 0.05 \)) and female \( L_S \). Egg number was size-standardized using a common slope (\( \beta = 2.017 \)) in ANCOVA across populations and treatments. Batch reproductive effort (total brood dry mass) was calculated using the size-standardized egg number. Nested-ANOVA was used to detect effects of population, treatment and their interaction on size-standardized egg number and total brood mass with female as a random factor in the model. All data except egg % water content were \( \log_{10} \) transformed. The \( P \) values were not corrected using Bonferroni correction (Garcia, 2004).

Females from at least three families per population per treatment were sampled in an effort to integrate genetic variation, with the exception of the fish of high-DO origin grown under low-DO where only one family out of four produced broods. This may be due, in part, to a sex bias in some tanks, where no males were produced to fertilize eggs. Thus, because of the imbalance in the dataset, it was not possible to test for family level effects in the full model. To address this issue, ANOVA within populations were performed to test for effects of family and DO on each of the egg size characters and egg number. Within each population, no effect of family [low-DO origin: \( P > 0.05 \); high-DO origin (high-DO treatment only): \( P > 0.05 \)] on the characters measured was detected.

### RESULTS

#### ENVIRONMENTAL VARIABLES

The \( P_{O2} \) (measured on fish sampling days) ranged across sites from 4-0 to 125-9 mmHg and was generally much lower in the swamp sites (Table I). The exception was the Manywa Swamp Pool, where periphyton mats associated with high levels of organic input elevated DO during the day. Water temperature also varied among sampling sites, ranging from 19-5 to 24-8 °C; however, there was no relationship between temperature and \( P_{O2} \) across sites (Pearson correlation, \( n = 8, r = -0.092; \)

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Table I. Summary of brooding efficiency and oxygen data for six field populations and for
F1 in the laboratory from different populations of origin (low-dissolved oxygen, DO, and
high DO) reared under low and high-DO treatments (low DO c. 1.49 mg l\(^{-1}\), high DO c.
7.49 mg l\(^{-1}\)). *Pseudocrenilabrus multicolor victoriae* brooding efficiency is estimated as the
per brood ratio of the mean number of young brooded in mouth to the mean number of oocytes
produced in the gonad. For the field populations, the number of late-stage hatched embryos
per brood was used to calculate the population mean for young brooded in the mouth. In
the laboratory, broods were collected from the mother before hatching. Thus, unhatched eggs
were used to calculate the mean for young brooded in the mouth. Note that mean values were
used to calculate brooding efficiency for each population producing a sample size of one for
each population.

<table>
<thead>
<tr>
<th>Field population</th>
<th>Mean DO (mm Hg)</th>
<th>Mean oocytes produced</th>
<th>Mean fry brooded</th>
<th>Brooding efficiency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mpanga Bunoga</td>
<td>125.87</td>
<td>36</td>
<td>25</td>
<td>69</td>
</tr>
<tr>
<td>Mpanga Kahunge</td>
<td>72.81</td>
<td>41</td>
<td>28</td>
<td>68</td>
</tr>
<tr>
<td>Kantembwe Swamp</td>
<td>4.00</td>
<td>57</td>
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<td>46</td>
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<td>Lake Kayanja</td>
<td>117.37</td>
<td>43</td>
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<tr>
<td>Kaz Lagoon</td>
<td>29.32</td>
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<td>37</td>
<td>62</td>
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<tr>
<td>Lwamunda Swamp</td>
<td>17.52</td>
<td>59</td>
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<td>49</td>
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</tbody>
</table>

<table>
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<tr>
<th>Laboratory population of origin</th>
<th>Treatment</th>
<th>Mean oocytes produced</th>
<th>Mean eggs brooded</th>
<th>Brooding efficiency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Kayanja</td>
<td>Low DO</td>
<td>34</td>
<td>9</td>
<td>26</td>
</tr>
<tr>
<td>Lake Kayanja</td>
<td>High DO</td>
<td>19</td>
<td>13</td>
<td>69</td>
</tr>
<tr>
<td>Lwamunda Swamp</td>
<td>Low DO</td>
<td>17</td>
<td>11</td>
<td>65</td>
</tr>
<tr>
<td>Lwamunda Swamp</td>
<td>High DO</td>
<td>23</td>
<td>13</td>
<td>58</td>
</tr>
</tbody>
</table>

\( P > 0.05 \). Among sampling sites, pH ranged from 5.63 to 7.82, and conductivity
(adjusted to 25° C) ranged from 142.5 to 318.5 ms cm\(^{-1}\). In general, the swamp
sites were characterized by low pH and low conductivity relative to the lake and
river sites.

**INTERDEMIC VARIATION IN LIFE-HISTORY TRAITS**

**Size at maturity**

Among eight populations of *P. m. victoriae*, female \( L_{50} \) ranged from 3.15 to
4.65 cm (Fig. 3), and the \( L_{50} \) increased with \( P_O \) (Pearson correlation, \( r = 0.761, P < 0.05; \) Fig. 4). There was no relationship, however, between \( L_{50} \) and water
temperature (\( r = 0.232, P > 0.05 \)).

**Brood traits**

There was a significant population effect on egg size (ANOVA, mean \( V_E F_{6,52}, \)
\( P < 0.001 \); mean \( M_{EW} F_{6,52}, \) \( P < 0.001 \); mean \( M_{ED} F_{6,52}, \) \( P < 0.001 \)), mean egg
% water content (\( F_{6,52}, P < 0.01 \)) and mean \( L_S \) standardized egg number (\( F_{6,52}, P < 0.05 \)). Interdemic variation in egg size was substantial ranging from 3.04 \( \mu g \)
in the Manywa Swamp Pool population to 6.85 \( \mu g \) in the Mpanga Bunoga popu-
lation. Similarly, size-standardized egg number was highly divergent in range from
68 eggs in the Manywa Swamp Pool population to 26 eggs in the Mpanga Bunoga

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Fig. 3. Binary logistic regressions estimating the standard length ($L_s$) at which 50% of female *Pseudocrenilabrus multicolor victoriae* were mature ($L_{SS0}$) for each of eight field populations: Mpanga Kamwenge (●), Mpanga Bunoga (●), Lake Kayanja (▲), Mpanga Kahunge (■), Kaz Lagoon (◇), Manywa Swamp Pool (△), Lwamunda Swamp (□) and Kantembwe Swamp (○). $L_{SS0}$ was estimated by the size at which 50% of the females had mature gonads (●). Open symbols indicate low-dissolved oxygen (DO) swamp sites; filled symbols indicate high-DO river and lake sites; grey symbols indicate the fluctuating-DO river site.

Fig. 4. Relationship between standard length at maturity ($L_{SS0}$) for female *Pseudocrenilabrus multicolor victoriae* and aquatic oxygen partial pressure ($P_{O2}$) for eight sites in Uganda. Environmental data were collected from multiple micro-sites within each location on the same days that the female fish were collected.
population. There was no difference among populations for batch reproductive effort (ANOVA, standardized total brood mass $F_{6,52}$, $P > 0.05$). Across populations, both $V_E$ and $M_{ED}$ were negatively correlated with standardized egg number, supporting an egg size-number trade-off (Pearson correlation, $M_{ED} n = 7$, $r = -0.810$, $P < 0.05$; $V_E n = 7$, $r = -0.868$, $P < 0.05$; Fig. 5). There was no correlation between egg size and % water content across populations (Pearson correlation, $M_{ED} n = 7$, $r = -0.481$, $P > 0.05$; $V_E n = 7$, $r = -0.400$, $P > 0.05$).

Late-stage mouth broods from 81 females and oocytes from 94 females with ripe gonads were used to calculate brooding efficiency for six populations: two high DO (Mpanga Bunoga, Lake Kayanja), three low DO (Kaz Lagoon, Lwamunda Swamp, Kantembwe Swamp) and one fluctuating (Mpanga Kahunge). Brooding efficiency ranged from 45·6% (Kantembwe Swamp) to 69·4% (Mpanga Bunoga, Table I) and was correlated with $L_{SS0}$ (Pearson correlation, $n = 6$, $r = 0.902$, $P < 0.05$) and a weak, but non-significant trend with $P_{O2}$ ($n = 6$, $r = 0.720$, $P > 0.05$).

**DEVELOPMENTAL PLASTICITY STUDY**

*Size and age at maturity*

A total of 26 females reached maturity and produced broods during the experiment. The population of high-DO origin (Lake Kayanja) had 13 females representing three families, and the population of low-DO origin (Lwamunda Swamp) had 13 females representing four families. Mean $L_{SS0}$ ranged from 2.9 to 3.9 cm across treatments and populations. No significant effect of population or treatment on $L_{SS0}$
was detected, but there was a highly significant interaction [Fig. 6(a) and Table II]. F1 females originating from the low-DO population matured at smaller \( L_S \) when reared under low DO relative to high DO [Fig. 6(a) and Table II], and females originating from the low-DO population exhibited a smaller size at maturity than females originating from the high-DO population when reared under low DO (ANOVA, \( F_{1,9} \), \( P < 0.05 \)). There was no difference, however, between populations in the high-DO treatment (ANOVA, \( F_{1,14} \), \( P > 0.05 \)). Regardless of treatment, females originating from the low-DO population matured at an earlier age than females originating from the high-DO population [Fig. 6(b) and Table II].

**Brood traits**

ANOVA was used to test for an effect of treatment on egg size with female included as random factor in the model. Mean egg size (\( V_E \) and \( M_{EW} \)) was larger in
females raised under low DO regardless of origin; mean $M_{ED}$ did not differ [Fig. 7(a) and Table II]. For $V_E$, a population effect was also detected; females originating from the high-DO population had larger eggs ($V_E$) than females originating from the low-DO population; dry mass showed a similar, but weak and non-significant ($P > 0.05$) trend [Fig. 7(a), (b) and Table II]. Mean % water per egg did not differ between populations; however, eggs grown under low DO showed a weak, but non-significant, trend of higher percentage of water [$P > 0.05$; Fig. 7(d) and Table II]. The differences in environmentally induced egg size in the laboratory were far smaller than observed across populations in the field (4.74–7.80% difference in volume between laboratory treatments $v.$ 56% in the field).

### Table II. Summary of statistical tests for standard length at maturity ($L_{50}$), age at maturity (ANOVA), egg volume ($V_E$), egg wet mass ($M_{EW}$), egg dry mass ($M_{ED}$), egg % of water content, $L_S$ standardized egg number and $L_S$ standardized total brood dry mass (nested-ANOVA with female as a random factor) to detect the effect of population (high DO or low DO) of origin, treatment (low DO c. 1.48 mg l$^{-1}$ v. high DO c. 7.49 mg l$^{-1}$), and their interaction on life-history traits of *Pseudocrenilabrus multicolor victoriae*. All variables except egg % water content were log$_{10}$ transformed.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Effect</th>
<th>$F$</th>
<th>d.f.</th>
<th>$P$</th>
</tr>
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<tr>
<td>$L_{50}$</td>
<td>Population</td>
<td>0.904</td>
<td>1,25</td>
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<td></td>
<td>Treatment</td>
<td>0.021</td>
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<td>&gt;0.05</td>
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<td></td>
<td>Population × treatment</td>
<td>10.806</td>
<td>1,25</td>
<td>&lt;0.01</td>
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<tr>
<td>Age at maturity</td>
<td>Population</td>
<td>6.520</td>
<td>1,25</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>0.416</td>
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<td>&gt;0.05</td>
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<tr>
<td></td>
<td>Population × treatment</td>
<td>0.876</td>
<td>1,25</td>
<td>&gt;0.05</td>
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<tr>
<td>$V_E$</td>
<td>Population</td>
<td>5.417</td>
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<td>&lt;0.05</td>
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<tr>
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<td>Treatment</td>
<td>5.657</td>
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<td>&lt;0.05</td>
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<td></td>
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<td>&gt;0.05</td>
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<td>Treatment</td>
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<td>&lt;0.05</td>
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<td>&gt;0.05</td>
</tr>
<tr>
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<td>Population × treatment</td>
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<td>&gt;0.05</td>
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<tr>
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<tr>
<td>Egg % water</td>
<td>Population</td>
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<td>&gt;0.05</td>
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<tr>
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<td>Treatment</td>
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<td>&gt;0.05</td>
</tr>
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<td>Population × treatment</td>
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<td>&gt;0.05</td>
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<td>Standardized egg number</td>
<td>Population</td>
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<td>&gt;0.05</td>
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<td></td>
<td>Treatment</td>
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<td>1,33</td>
<td>&lt;0.05</td>
</tr>
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<td>Population × treatment</td>
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<td>&gt;0.05</td>
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<td>&gt;0.05</td>
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<tr>
<td>Standardized total brood dry mass</td>
<td>Population</td>
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<td>1,32</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
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<td>1,32</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td></td>
<td>Population × treatment</td>
<td>0.003</td>
<td>1,32</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>0.704</td>
<td>20,13</td>
<td>&gt;0.05</td>
</tr>
</tbody>
</table>
Fig. 7. Reaction norms derived from univariate ANOVA for mean ± s.e. (a) egg volume ($V_E$), (b) egg dry mass ($M_{ED}$) and (d) egg % water, and from ANCOVA for (c) egg number for F1 *Pseudocrenilabrus multicolor victoriae* from low-dissolved oxygen (DO) (O) and high-DO (●) origin raised under either low or high DO. Data for all traits except per cent water per egg were log_{10} transformed. Each line joins the mean value for low- and high-DO treatments for one population. Probability values for treatment effect (DO) and population effect are presented in Table II. DO × population interactions were not significant.

F1 females produced fewer eggs ($L_S$ standardized) when reared under low DO than females raised under high DO [Fig. 7(c) and Table II]; however, there was no significant population effect on egg number. Batch reproductive effort was evaluated using $M_{ED}$ (each multiplied by standardized egg number). ANOVA indicated no effects of treatment, population or their interaction on total brood dry mass (Table II). Females originating from the high-DO population reared under low DO exhibited a lower brooding efficiency (26%) than females from the same population reared under high DO (69%; Table I); whereas females originating from the low-DO population when reared under low DO had a brooding efficiency (65%) similar to those reared under high DO (58%).

**DISCUSSION**

**HIGH LEVELS OF INTERDEMIC VARIATION IN LIFE-HISTORY TRAITS**

Since limited resources are available to an organism for growth, maintenance and reproduction, fundamental life-history trade-offs may become more apparent
under extreme conditions (Reznick, 1991; Jones & Reynolds, 1999). The present field survey of the eurytopic cichlid *P. m. victoriae* demonstrated a high level of interdemic variation in life-history traits. In general, females from low-DO waters were characterized by a smaller size at maturity than those from high-DO waters. There was evidence for a trade-off between egg size and number across populations observed in the negative correlation between the two traits. In the field and the laboratory, females originating from low DO produced a larger number of small eggs per batch than those originating from high DO. There was no difference in batch reproductive effort (laboratory or field) indicating that populations are allocating a similar relative amount of resources to each brood but allocating them differently depending on habitat.

Other studies that explore the long-term consequences of alternative oxygen environments on reproduction are few. Thomas *et al.* (2007) provided some of the first field evidence of hypoxia-induced reproductive disorder (reduced fecundity due to endocrine disruption) in populations of Atlantic croaker *Micropogonias undulatus* (L.) across a gradient of DO concentrations in the Pensacola Bay estuary system in Florida. The negative effects of hypoxia in the present study system seem less severe than those reported in Thomas *et al.* (2007). It is possible that *P. m. victoriae* originating from low-DO habitats are better adapted to chronic hypoxia, because the oxygen remains low year round v. hypoxia that is episodic and relatively short-term (weeks). Other studies that have compared morpho-physiological response of fish populations across oxygen gradients from high to chronically low DO have found that DO is a strong predictor of intraspecific variation. For several fish species, low-DO populations have been characterized by traits that maximize aerobic or anaerobic capacities such as larger gills, lower gill ventilation rates, more efficient use of aquatic surface respiration, higher haematocrit and higher liver lactate dehydrogenase (LDH) relative to high-DO populations (Olowo & Chapman, 1996; Chapman & Hulen, 2001; Martinez *et al*., 2004; Timmerman & Chapman, 2004, Chapman *et al*., 2008).

**DEVELOPMENTAL V. INTERDEMIC RESPONSE**

Both the laboratory and field findings suggest that females are allocating their reproductive resources differently depending on the environment. In the laboratory, regardless of rearing treatment, females originating from the high-DO population produced fewer, larger eggs than females originating from the low-DO population [Fig. 7(a)–(c)]. This finding is consistent with field trends and suggests an element of fixed genetic variation in egg size across populations. This supports the prediction of smaller eggs under hypoxia, the larger surface area to volume ratio may facilitate higher oxygen uptake under hypoxia. Across field populations, smaller eggs produce smaller juveniles (unpubl. data), which again may be advantageous as this increases the area for oxygen exchange, because the whole body of the post-hatching offspring is metabolically active, and respiration occurs predominately through the skin in early life (Moyle & Cech, 1996). Interestingly, the environmentally induced effect in the laboratory study contradicts the egg size–oxygen relationship exhibited in the field survey (smaller eggs from low-DO field populations), but does support the study of Einum *et al.* (2002) on brown trout *Salmo trutta* L.

Einum *et al.* (2002) found evidence for greater survival of larger *S. trutta* eggs under hypoxia and hypothesized that a positive relationship between effective surface...
area to volume ratio and egg size could occur if the amount of metabolically active tissue does not differ between large and small eggs. Rombough’s (2007) study on the surface area and metabolic demand of large and small Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) eggs supported the hypothesis by Einum *et al.* (2002) that larger eggs may be bigger under hypoxia due solely to higher water content that would produce a greater surface area for oxygen diffusion. In laboratory-reared *P. m. victoriae*, there was a trend towards higher egg % water content in broods produced under low DO. Although there may be additional differences in the composition of the laboratory eggs, egg size differences between laboratory DO treatments may, in part, be explained by water. This trend does not hold in the field survey, as there was no relationship between egg size and water content across populations. It is notable that the range in egg size across populations in the field was very large relative to that induced by DO treatment in the laboratory-rearing experiment (4.74–7.80% in the laboratory, 56% in the field). The population effect was also small, but in the range of variation observed between these two populations in the field. Smaller egg size may be advantageous in a hypoxic environment in that small eggs produce small young; however, if the egg is not at all metabolically active, there may also be an advantage to increasing the surface area over which oxygen may diffuse if water content can be increased.

Egg size variation in the field may also reflect the interaction of DO and other agents of selection such as predation pressure or food quality. A suite of studies on the Malawian rock cichlids and the Trinidadian guppies *Poecilia reticulata* Peters (both with high levels of parental care) showed that changes in predation pressure can influence egg size and number within a population or species and the direction of this change (more, smaller or fewer, larger) depends on the nature and the severity of the predation (Fryer & Iles, 1972; Reznick & Endler, 1982). Several studies indicate that when predation and other environmental factors are both influencing a population, predation is the more significant driver (Roberts, 1973, Reznick *et al.*, 2001). In addition, hypoxia may modulate predator–prey interactions by reducing predation pressure on prey fishes living in hypoxic waters (Robb & Abrahams, 2003). Several studies in the Lake Victoria basin have identified hypoxic wetlands as important low-oxygen refuges for fishes that can tolerate wetland conditions, and function as barriers to dispersal of Nile perch *Lates niloticus* (L.) (Chapman *et al.*, 1996b, 2002; Schofield & Chapman, 1999). The production of large eggs in the high-DO lake and river sites may serve to decrease vulnerability of offspring to predators when they leave the sanctuary of the mouth, though clearly other differences among sites may contribute to the patterns observed. The low-DO sites in the field study may have fewer aquatic predators, thus potentially relaxing selection for large egg size.

It is important to take potential maternal effects into consideration when exploring brood characteristics. Although a positive relationship between egg size and female body size has been reported in some studies of fishes, it is not as widespread as the positive relationship between fecundity and body size (Reznick, 1991; Heath & Blouw, 1998). For *P. m. victoriae*, fecundity increased with female body size in both the field and laboratory-rearing study. Although there was a weak positive relationship between egg size and female size across the field populations, there was no relationship within field populations or experimental groups. Given a larger range in body sizes, it is possible that an egg size–maternal size relationship could become more apparent as is the case with several other cichlid species of larger size (Fryer
& Iles, 1972); however, the present sampling did cover the range of female body size that is characteristic of the field populations. Results from both the field survey and laboratory-rearing experiment support other studies that have reported smaller size at maturity under hypoxia (Landry et al., 2007). It was not possible to measure age of maturity in the field populations. In the laboratory-rearing experiment, however, F1 females originating from the low-DO population matured at an earlier age than F1 females originating from the high-DO population. The lack of a treatment effect suggests that age of maturity trait is not phenotypically plastic but may vary among populations due to heritable variation. Thus, in the wild, low-DO populations of *P. m. victoriae* may be maturing at a younger age in addition to a smaller size. Further studies are needed to confirm this hypothesis given the small number of families that were raised, but it is consistent with predictions from the life-history literature for changes in size at maturity in a stressed environment (Roff, 1992; Steams, 1992, Heino & Dieckmann, 2008). If females from low-DO field populations do have shorter life span and a longer interbrood interval (E. E. Reardon, unpubl. data), lifetime reproductive effort could be lower in hypoxic sites even though there is no difference in batch reproductive effort between across field populations.

Similar to egg size, observed disparities in size at maturity between the laboratory-grown fish and the field-collected specimens suggest that selection factors other than DO availability differ across sites. This could lead to interdemic variation that has an environmental and genetic basis. Such differences in selective agents are likely to be found in environmental characters such as turbidity and conductivity of the water, diet and food quality, and predator pressure. For example, $L_{50}$ was consistently lower in fish from low-DO field sites and in laboratory fish originating from low DO in raised under low DO, but not in fish originating from high DO. The low-DO swamp has a more fluctuating oxygen environment (between 0.5 and 4.0 mg l$^{-1}$), while the high-DO lake is much more stable throughout the year (between 6.5 and 7.4 mg l$^{-1}$). Thus, it is possible that the lake population has become canalized and lost flexibility in this character. Several studies across a range of taxa support the idea that phenotypic plasticity is more common in fluctuating environments relative to stable environments (Schaefer & Ryan, 2006; Svanback & Eklov, 2006).

It is also important to consider that life-history variation observed in the field may not necessarily reflect contemporary patterns of selection, but rather historical contingencies. Crispo & Chapman (2008) reported low genetic variation at neutral markers across populations of *P. m. victoriae* in this system that could reflect high gene flow or recent colonization. Life-history trait variation observed in the present study may reflect contemporary ecological pressures, given the strong correlations between trait variation and environmental factors (DO) and the similarity in characteristics of low-DO populations from both basins. Future studies that include additional comparisons of high and low-DO sites across several basins will be valuable in determining the relative role of ecology in shaping life-history variation in this system.

Apart from female size and egg production, the ability of the mother to carry the full brood term may be compromised in low-DO waters; as was the trend with the brood efficiency data in the laboratory and field. It may be possible that brooding efficiency is lower in populations where the females are smaller (low DO), these females simply may not have the energy reserves to brood all of the eggs they produce to full-term. Interestingly, a long-term acclimation study on a low-DO population of

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P. m. victoriae revealed that the length of the brooding period (from egg-laying to release of fry) was c. 27% shorter in females acclimated to low DO compared with females acclimated to high DO, with fry emerging fully developed in both treatments (unpubl. data). Although this study did not record brooding efficiency, these findings suggest that reduction in brooding period maybe an adaptive strategy to deal with the expense of providing parental care under hypoxia.

BROADER IMPLICATIONS

These results provide evidence for divergence in life-history traits between alternative DO environments. There was a strong element of plasticity in brood characters, but also evidence for a genetic component to phenotypic variation between populations. These findings are relevant in the Lake Victoria region where hypoxia is extensive and increasing. Flexibility in life-history traits in response to divergent oxygen environments may contribute to the widespread distribution of P. m. victoriae and foster its persistence in light of dramatic environmental change in the Lake Victoria basin.

The direction of the relationships between life-history traits and oxygen exhibited by P. m. victoriae in the present study may provide useful insights as to how other fishes with advanced parental care may respond to the increasing threat of hypoxia worldwide. The effects of DO on some of these traits may be direct (i.e. smaller size at maturity, smaller eggs that produce smaller young), while others may be indirect effects acting through predation (i.e. lower predation pressure in hypoxic habitats selects for smaller egg size).

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