Reproductive seasonality in a swamp-locked African cichlid

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Abstract – This study quantified the seasonal pattern of reproduction in a swamp-dwelling population of the African cichlid Pseudocrenilabrus multicolor victoriae. In the hypoxic waters of the Lwamunda Swamp, Uganda, P. multicolor was reproductively active throughout the year, even during the peak of the dry seasons. However, the degree of activity was seasonal, with rainfall providing a predictor of the percentage of ripe, mature females. There was no correlation between aquatic oxygen availability dissolved oxygen (DO) and either adjusted mean gonad mass or percentage of mature females, suggesting that DO is not limiting reproductive activity in this system. Reproductively mature females were larger during drier periods and may maximise their lifetime reproductive success by producing young throughout the year; but with a lower brooding efficiency. A comparison with Welcomme’s (1969) study of a river-swamp system feeding Lake Victoria suggests that reproductive patterning is variable among populations of P. multicolor and may reflect adaptive response to chronically hypoxic conditions in the Lwamunda Swamp.

Introduction

In many tropical fresh waters, fluctuations in rainfall represent the strongest seasonal change and one that affects both habitat quality and habitat availability for aquatic organisms. The dry seasons, in seasonally flooding areas, bring low water conditions that affect fish through habitat contraction, higher densities, lower condition, higher levels of parasitism, and higher mortality (Lowe-McConnell 1975, 1979; Chapman et al. 1991; Chapman & Chapman 1993a, b). In addition, dry season conditions in seasonally flooding habitats are also often correlated with reduced dissolved oxygen (DO) availability (Chapman & Kramer 1991; Chapman & Chapman 1993a; Chapman & Frankl 2000; Chapman et al. 2000a) and a decrease in food resources (Fryer & Iles 1972; Lowe-McConnell 1975; Witte 1981). In the rainy season, fish are released from many of these stressors when rivers begin to flow to capacity; more habitats are available, DO increases and food resources increase in abundance (Lowe-McConnell 1979; Welcomme 1979; Witte 1981). Seasonal patterns of food, habitat availability, water quality and other resources should be reflected in seasonal patterns of reproduction in fishes inhabiting these systems. Rainfall seems to be an important cue that triggers spawning in many tropical fish species, whether that spawning is at the beginning or end of the season (Fryer & Whitehead 1959; Welcomme 1969; McKaye 1977, Kramer 1978; Siddiqui 1979; Chapman & Frankl 2000; Chapman et al. 2000a; Duponchelle et al. 2000). Many fish from permanent waters (lakes, rivers) exploit seasonally available habitat as nursery areas for young; and the young return to the permanent waters after a period of fast growth in areas relatively low in predation risk (Fryer 1961; Welcomme 1969, 1979; Fryer & Iles 1972; Lowe-McConnell 1979). However, there is often variation in reproductive patterns among species from continuous breeders, to those exhibiting seasonal reproductive peaks, to species with extremely well-defined breeding periods (Lowe-McConnell 1979). One approach to understanding factors influencing reproductive patterning in tropical freshwaters is to...
explore variation among populations within species to minimise phylogenetic effects. The present study represents the first in series of studies to explore interdemic variation in the reproductive biology of the widespread African mouth brooder *Pseudocrenilabrus multicolor victoriae* (Seegers).

Lake Victoria was home to an estimated 500+ species of endemic, and often stenotopic, haplochroine cichlids prior to the introduction of the predatory species of endemic, and often stenotopic, haplochroine species. In this study, we describe the pattern of reproduction over a year in a swamp-dwelling population of *P. multicolor* that persists under extreme hypoxia throughout the year. Size at maturity (females only), adjusted mean gonad mass, and condition (both sexes) were quantified monthly, and observed patterns were related to seasonal changes in rainfall and DO concentration. We ask if there is a seasonal pattern of reproductive activity and whether there is seasonal variation in the size of reproducing females and condition of both sexes that may reflect temporal shifts in resource availability. We compare our results to the pattern observed in Welcomme’s earlier study of a riverine population to detect interdemic variation in reproductive patterning in *P. multicolor* and to explore costs and benefits of life in permanently hypoxic swamp.

**Materials and methods**

*Pseudocrenilabrus multicolor victoriae* is a small mouth brooding cichlid found throughout the Lake Victoria basin across a range of oxygen regimes and habitats. The species is widespread in shallow habitats dominated by marginal vegetation, weed beds, and seasonal habitats (Lowe-McConnell 1991). The maximum total length of *P. multicolor* is approximately 9 cm for males; females tend to be smaller (Reardon and Chapman, unpublished data). *Pseudocrenilabrus multicolor* has a varied diet, including algae, diatoms, insects, chironomids, mites, copepods and protozoa (Greenwood 1965; Welcomme 1969).

We quantified relationships between reproduction and seasonal variation in aquatic oxygen and rainfall in the Lwamunda Swamp surrounding Lake Nabugabo, Uganda. In this equatorial region of East Africa, there are two wet and two dry seasons per year. The Lwamunda Swamp is ~4 km wide and contains several permanent lagoons and small intermittent streams (Greenwood 1965; Chapman et al. 1996b). It surrounds much of Lake Nabugabo and acts as a filter for water outflowing from Lake Nabugabo headed to Lake Victoria; also separating Lake Nabugabo from Lake Victoria (see Chapman et al. 1996a, b, 2000b, 2002a for complete description). In the Lwamunda Swamp, Chapman et al. (2002a) found *P. multicolor* to be the most abundant species captured in minnow traps in the dense swamp interior; and this species persists in the hypoxic wetland interior throughout the year (Chapman and Reardon, unpublished data).
Chapman et al. (2002a) reported an average aquatic oxygen (DO) concentration in the Lwamunda Swamp (based on monthly samples over a 1-year period) of 1.5 mg m\(^{-1}\) (20% saturation) in the morning and 1.8 mg m\(^{-1}\) (24% saturation) in the early afternoon. They also detected seasonal variation in oxygen, but found that average DO levels remained far below saturation throughout the year.

For this study, size at maturity, index of maturity and condition were quantified over a period of 11 months to map seasonal variation in reproductive activity. Each month from June 2004 through April 2005, 50 female fish and 50 male fish were collected, euthanised with MS222 and preserved in 4% paraformaldehyde buffered with phosphate buffered saline (PBS). DO and water temperature were recorded at the same time in the upper 20 cm of the water column using a YSI Model 57 meter (Yellow Springs Instruments). These characters were measured at 10 micro-sites within each of two swamp lagoons and the surrounding wetland matrix; this represents the sites from which fish were collected. Water depth averaged 30 cm at these sites over the year of sampling. Water temperature and DO were measured early in the morning and mid-day and values were averaged across micro-sites to produce a monthly average. Daily rainfall data during the sampling period were available through the National Center for Environmental Prediction branch of NOAA. Ten years (1994–2003) of average monthly rainfall data were available from the National Meteorological Center of Uganda. For both sexes, standard length and body mass were measured to evaluate body condition. For females, the gonads were macroscopically staged and weighed for size at maturity and index of maturity estimates. Standard length measurements were used instead of total length to control for damaged and missing tail fin commonly associated with aggression and mating in this species. Traditionally in the literature, size at first maturity can be estimated by calculating the length at which 50% of the individuals are mature, also known as the \(L_{50}\) (Balirwa 1998). In the context of this study, we used the \(L_{50}\) and the \(L_{80}\) (the size at which 80% of individuals are mature) to characterise fluctuations in the size of reproducing females throughout the year. A female was considered to be mature if she had gonads with any ripe oocytes (stage III and higher for this species; following Welcomme 1969; Balirwa 1998), if she was brooding when caught, or if there was evidence of recent brooding (i.e., a dropped jaw). For each month, the \(L_{50}\) and \(L_{80}\) estimates were calculated using binary logistic regression models. The function, \[ \text{maturity} = \frac{1}{1 + \beta e^{r \times \text{size}}} \] produced an S-shaped curve for each population where: size is the standard length of a given female, \(r\) is a model parameter that affects the inflection points or the horizontal shape of the curve, and \(\beta\) is a model parameter that effects 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. Index of maturity (measured as the percentage of mature female fish with ripe gonads, ready for spawning) was calculated for each month over the year, providing an index of reproductive activity. In addition, the adjusted mean gonad mass of sexually mature females was calculated each month using analysis of covariance (ANCOVA) with log gonad mass as the dependent variable, log somatic mass (minus the gonad mass) as the covariate, and month as a fixed factor. In order to take into account the large variation in size of mature females over the year, we quantified adjusted mean gonad mass for mature females at or above the mean size of maturity (\(L_{50} = 3.45\) cm) for the year. December was removed from the gonad mass ANCOVA because of low sample size. To quantify condition of the fish, the adjusted mean mass of females and males was calculated each month using ANCOVA with log somatic mass as the dependent variable, log standard length as the covariate, and month as a fixed factor. For both ANCOVA analyses, all values were log_{10} transformed. Males and females were analysed separately for body condition, because of significant differences in the slopes of the relationship between genders.

Pearson correlation was used to detect relationships between reproductive traits, body condition, and environmental characters. Monthly rainfall was expressed either as the rainfall total for the 30-day period prior to the collection date or the 10-year average for the sampling month. A paired t-test was used to test for differences in adjusted monthly mean condition between male and female \(P.\) multicolor.

**Results**

Total monthly rainfall during our sampling period (June 2004–April 2005) was highly correlated with the 10-year average (1994–2003) for the region \((r = 0.779, P = 0.003)\); however, rainfall in 2004–2005 was generally higher than average (Table 1, Fig. 1). The months of January and February are historically dry season months associated with the shorter of the two dry seasons, but this dry period was wetter than usual in 2005 (Fig. 1). Mean monthly water temperatures at the Lwamunda Swamp varied little over the year, averaging 23.5 °C, and ranging from 22.4 to 25.1 °C. DO concentration was low throughout the year, averaging 1.06 mg m^{-1}, or 14% saturation, in the morning (range = 0.37–1.61 over the year of monthly samples) and 2.63 mg m^{-1}, or 36% saturation, in the afternoon (range = 1.69–3.99, Table 1, Fig. 1). There was no relationship between
DO and total monthly rainfall (Pearson correlation, am values: $r = -0.254, P = 0.452$; pm values: $r = -0.215, P = 0.526$; pm values: $r = -0.123, P = 0.734$). Similarly, we found no relationship between water temperature and monthly rainfall (am values: $r = 0.326, P = 0.327$; pm values: $r = -0.320, P = 0.367$), or between water temperature and the 10-year average for monthly rainfall (am values: $r = 0.326, P = 0.327$; pm values: $r = 0.171, P = 0.638$).

Monthly changes in the percentage of mature fish (with ripe, mature gonads) and adjusted mean gonad mass were used to evaluate seasonal patterns of reproduction. Females with late-stage mature gonads as well as brooding females were found throughout the year (Fig. 2). There was no correlation between percentage of ripe, mature fish and the total monthly rainfall or the 10-year average rainfall (Pearson correlation, total monthly rainfall: $r = 0.284, P = 0.398$; 10-year average rainfall: $r = 0.300, P = 0.369$, Fig. 2a). However, there was a significant positive correlation between percentage of mature fish and the total rainfall of the month preceding the fish collection (Pearson correlation, percentage of mature fish: $r = 0.695, P = 0.018$, Fig. 2a), suggesting that rainfall may be the cue to inducing maturity of gonads, or the cue could be a variable highly correlated with rainfall. In addition, there was a significant negative correlation between gonad mass and the 10-year average rainfall (Pearson correlation, $r = 0.633, P = 0.049$), and a marginal correlation between gonad mass and total monthly rainfall (Pearson correlation, $r = 0.611, P = 0.061$; Fig. 2b), suggesting a drop in gonad mass as the rainy season proceeds. There was no correlation between gonad mass and the month preceding the fish collection ($r = -0.193, P = 0.594$).

Binary logistic regressions of seasonal size at maturity indicated a high degree of variation across the year in the length of mature females (Fig. 3). The $L_{50}$ ranged from 2.85 to 3.94 cm and the $L_{80}$ ranged from 3.05 to 4.35 cm. In general, wet season months

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**Table 1.** The observed environmental parameters, size of 50% and 80% maturity, log$_{10}$ adjusted mean gonad mass and percentage of female *Pseudocrenilabrus multicolor* with ripe, mature gonads from June 2004 to April 2005 for the Lwamunda Swamp. Rainfall differential is the absolute difference in rainfall between the year of study and a 10-year average.

<table>
<thead>
<tr>
<th>Month</th>
<th>Season</th>
<th>Rainfall 2004–2005 (mm)</th>
<th>10-year rainfall mean (mm)</th>
<th>Rainfall differential (mm)</th>
<th>Depth (m)</th>
<th>Mean DO (mg/l$^{-1}$)</th>
<th>Mean temp. ($^\circ$C)</th>
<th>$L_{50}$ (cm)</th>
<th>$L_{80}$ (cm)</th>
<th>Log$_{10}$ adj. mean gonad mass</th>
<th>Females with mat gonads (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>Dry</td>
<td>45.2</td>
<td>32.5</td>
<td>12.7</td>
<td>37.2</td>
<td>1.49</td>
<td>22.4</td>
<td>3.44</td>
<td>3.75</td>
<td>1.587</td>
<td>14.0</td>
</tr>
<tr>
<td>July</td>
<td>Dry</td>
<td>23.8</td>
<td>12.0</td>
<td>11.8</td>
<td>30.2</td>
<td>1.26</td>
<td>23.9</td>
<td>3.94</td>
<td>4.35</td>
<td>1.599</td>
<td>7.0</td>
</tr>
<tr>
<td>August</td>
<td>Dry</td>
<td>68.7</td>
<td>43.5</td>
<td>25.2</td>
<td>32.0</td>
<td>2.55</td>
<td>23.0</td>
<td>3.89</td>
<td>3.89</td>
<td>1.312</td>
<td>6.4</td>
</tr>
<tr>
<td>September</td>
<td>Dry</td>
<td>59.2</td>
<td>53.6</td>
<td>5.6</td>
<td>26.2</td>
<td>2.14</td>
<td>23.7</td>
<td>3.53</td>
<td>3.83</td>
<td>1.101</td>
<td>18.4</td>
</tr>
<tr>
<td>October</td>
<td>Wet</td>
<td>105.7</td>
<td>87.2</td>
<td>18.5</td>
<td>28.0</td>
<td>2.56</td>
<td>23.7</td>
<td>3.48</td>
<td>3.90</td>
<td>1.031</td>
<td>14</td>
</tr>
<tr>
<td>November</td>
<td>Wet</td>
<td>130.6</td>
<td>110.6</td>
<td>20.0</td>
<td>36.7</td>
<td>2.02</td>
<td>22.8</td>
<td>2.85</td>
<td>3.05</td>
<td>1.148</td>
<td>16.3</td>
</tr>
<tr>
<td>December</td>
<td>Wet</td>
<td>143.6</td>
<td>108.9</td>
<td>34.7</td>
<td>35.6</td>
<td>1.31</td>
<td>22.7</td>
<td>3.85</td>
<td>8.3</td>
<td>1.27</td>
<td>20.6</td>
</tr>
<tr>
<td>January</td>
<td>Wet</td>
<td>142.0</td>
<td>54.0</td>
<td>88.0</td>
<td>29.8</td>
<td>1.48</td>
<td>22.9</td>
<td>3.36</td>
<td>3.62</td>
<td>1.412</td>
<td>31.8</td>
</tr>
<tr>
<td>February</td>
<td>Dry</td>
<td>84.4</td>
<td>48.0</td>
<td>36.4</td>
<td>28.5</td>
<td>2.03</td>
<td>22.9</td>
<td>3.35</td>
<td>3.60</td>
<td>1.412</td>
<td>31.8</td>
</tr>
<tr>
<td>March</td>
<td>Wet</td>
<td>137.1</td>
<td>122.6</td>
<td>14.5</td>
<td>24.7</td>
<td>1.09</td>
<td>23.1</td>
<td>3.22</td>
<td>3.53</td>
<td>1.28</td>
<td>17.4</td>
</tr>
<tr>
<td>April</td>
<td>Wet</td>
<td>125.6</td>
<td>151.7</td>
<td>-26.1</td>
<td>22.8</td>
<td>1.81</td>
<td>25.1</td>
<td>3.07</td>
<td>3.30</td>
<td>1.176</td>
<td>27.5</td>
</tr>
</tbody>
</table>

**Fig. 1.** Total rainfall, average morning and average afternoon dissolved oxygen (DO) concentration for the Lwamunda Swamp, Uganda collected monthly from June 2004 to April 2005.
were characterised by smaller mature females compared with the dry season months (Fig. 3; Table 1). The observed minimum standard length of mature females was 2.7 cm, and the maximum was 4.65 cm. $L_{80}$ was negatively correlated with total monthly rainfall indicating that sexually mature females were larger during drier conditions ($L_{80}$, $r = -0.748$, $P = 0.020$). $L_{50}$ showed a similar, although nonsignificant trend (correlation, $L_{50}$: $r = -0.511$, $P = 0.108$). $L_{80}$ estimates are missing for December and August because large, mature females were not caught during these months. The month of December (illustrated in Fig. 3. Binary logistic regressions estimating the size at which 50% and 80% of female *Pseudocrenilabrus multicolor* were mature over 11 months (June 2004–April 2005) in the Lwamunda Swamp, Uganda. Black represents wet season months, white represents dry season months, and the grey month is December, a month that is usually drier than in 2004. $L_{80}$ estimates are missing for December and August because large, mature females were not caught during these months.)
grey in Fig. 3) shows a larger size of reproducing females relative to the other wet season months, and interestingly this month was much wetter than the 10-year average.

Fish condition for both males and females varied significantly across months (slopes were homogeneous, ANCOVA test for intercepts: males $P < 0.001$; females $P < 0.001$, Fig. 4). The most notable trend was a drop in condition in female $P.\ multicolor$ coincident with the November–December spawning period. Across months, condition of females was consistently lower than condition of males (paired $t$-test, $t = 57.38$, $P < 0.001$), but changes in condition over the seasonal cycle were correlated between males and females ($r = 0.891$, $P < 0.001$, $N = 11$, Fig. 4). There was no correlation between the condition of females and adjusted mean gonad mass or between the condition of females and the percentage of ripe, mature fish (Pearson correlation, percentage of mature fish: $r = 0.221$, $P = 0.513$; adjusted mean gonad mass: $r = -0.321$, $P = 0.365$) or between these traits and a month lag in female condition (Pearson correlation, percentage of mature fish: $r = -0.379$, $P = 0.280$; adjusted mean gonad mass: $r = -0.220$, $P = 0.541$).

Discussion

In the hypoxic waters of the Lwamunda Swamp, $P.\ multicolor$ was reproductively active throughout the year, even during the peak of the dry seasons, which is consistent with our earlier dry season fish surveys of this swamp between 1995 and 1999 (Chapman, unpublished data). However, there was evidence for seasonal variation in reproductive activity, with rainfall providing a predictor of reproductive patterning. The percentage of ripe, mature females was positively correlated with rainfall 1 month prior to sampling, suggesting that rainfall (or factors correlated with rainfall) may induce maturity of gonads. The adjusted mean gonad mass (representing the gonad mass of females above the average size at maturity) showed a negative trend with rainfall, which may reflect spawning and loss of gonad mass as the rainy season progresses. Seasonal changes in resource availability stimulated by rainfall may account for these seasonal trends. Rainfall in these shallow wetlands can increase habitat available, as well as promoting nutrient increase from land run off that stimulates rapid growth of plants, invertebrates, and micro-organisms and, thus, provides an increase in food abundance and cover for fish (Lowe-McConnell 1964, 1975, 1979; Welcomme 1969, 1979; Roberts 1973; Goulding 1980; Katunzi 1983; Chapman & Frankl 2000). Increases in food resources associated with rains have also been used to explain seasonal peaks in breeding activity in several other cichlid groups (Fryer & Iles 1972; Lowe-McConnell 1975; McKaye 1977, 1983; Witte 1981; Marsh et al. 1986; Goldschmidt & Witte 1990; Gordon & Bills 1999; Jepsen et al. 1999; Duponchelle et al. 2000). More generally, the number of spawning events and total egg production has been directly, positively correlated with food supply in several species (Wootton 1973, 1979; Wootton and Evans 1976).

In mouth brooding cichlids, the energetic cost to the brooding parent is thought to be high; and, thus a seasonal flux of food resources may be particularly important to successful reproduction in this group. $P.\ multicolor$ females hold their developing young in the mouth for up to a month after fertilisation. This intensive parental care process requires energy reserves for the female to survive, because feeding is inhibited while the female is brooding (Wilhelm 1980; Smith & Wootton 1994, 1995). In $P.\ multicolor$ from the Lwamunda Swamp,
we found fish condition was lower in females than in the males. Although there was no significant correlation between female condition and estimated spawning peaks across months, the generally lower conditions of the females may reflect, at least to some degree, the costs of mouth brooding.

A comparison of seasonal patterning of reproduction between *P. multicolor* from the Lwamunda Swamp and the population studied by Welcomme (1969) from the Kafunta River-swamp system suggests that reproductive patterning is variable among populations. Both studies assessed spawning activity with similar methodology and observed seasonal spawning peaks associated with seasonal peaks of precipitation. However, the Kafunta River population did not breed continuously, with ripe fish and brooding females appearing only in the wet months, although adults were present throughout the dry season (Fig. 5). Welcomme reported that maturation of both males and females took place in the river, after which both sexes tended to remain in the river; and adults captured in the surrounding swamps were mostly brooding females. The small marginal swamps in this river system were used as nurseries until the young reached about 2.4 cm SL when they migrated to open waters. Welcomme reported the L50 (size at maturity) as 3.0 cm for females from the Kafunta River. This is close to the average L50 value (3.2 cm) that we observed during the wetter months for *P. multicolor* in the Lwamunda Swamp. However, we found that the size of reproducing females varied over a year and was negatively correlated with rainfall; generally reproducing females were larger in the dry season, a time of year when females in the Kafunta system were not sexually active. During the drier periods when available habitat and presumably food resources are more limited, smaller females with higher mass-specific energy requirements may not have sufficient energy reserves to allocate to both growth and reproduction.

In addition, in this species there is evidence for a decrease in brooding efficiency with body size (Welcomme 1969). Larger females brood proportionately fewer young than smaller females, suggesting a cost to mouth brooding in larger fish (Welcomme 1969). Although, in some fish species larger females invest in larger eggs (e.g., Salmonids; Quinn et al. 1995; Hendry et al. 2001), we have found that egg size is not influenced by female size in *P. multicolor* (Reardon, unpublished data). Larger females may maximise their lifetime reproductive success by producing young throughout the year; but with a lower brooding efficiency.

We suggest that the interdemic variation in reproductive patterning between the Kafunta system and the Lwamunda Swamp may reflect, at least in part, the seasonal availability of alternative habitats and adaptive response to chronically hypoxic conditions. In the Kafunta system, Welcomme (1969) reported lower rainfall, but more dramatic peaks than we observed in the Lwamunda Swamp. It is possible that we may have observed a different pattern of seasonal reproduction in a lower rainfall year, as 2004–2005 was above the 10-year average; however, brooding females have been captured during dry periods at our Lwamunda Swamp sites since 1997. In both the Kafunta and the Lwamunda systems, the swamp serves as the important nursery site; however, in the Kafunta system fish greater than 2.4 cm SL return to the river for a period of growth and maturation (Welcomme 1969). The marginal swamps are used as nurseries during the time of year when they are more readily available, deeper and DO is higher. Welcomme (1969) reported DO levels between 0.3 and 1.9 mg l⁻¹ in the marginal nursery swamp of the Kafunta in the dry season and 2.5–3.2 mg l⁻¹ during the wet season. The use of marginal wetlands as nursery areas is widespread in fishes in both temperate (Jude & Pappas 1992; Wilco & Meeker

![Fig. 5. Percentage of female *Pseudocrenilabrus multicolor* with late-stage mature gonads over a 1-year period relative to total monthly rainfall (mm) for the Kafunta River System at Bugungu, Uganda (1963–1964; from Welcomme 1969) with the same data from the Lwamunda System superimposed in grey for comparison. Data were collected throughout the year in the Kafunta system, months missing bars are months in which no mature females were captured.](image-url)
and decomposition of organic materials from adjacent grasslands and grazing lands.

Differences in reproductive patterning are not the only sources of variation among populations of *P. multicolor*. For example, we have found that *P. multicolor* from hypoxic swamps are characterised by a larger gill size, a wider head, a greater body depth, and lower critical oxygen tension than *P. multicolor* from well-oxygenated lake or river sites (Chapman et al. 2000b, 2002b). Developmental plasticity contributes to patterns of morphological and physiological variation in this species, although there is also evidence of heritable variation (Rosenberger & Chapman 2000; Chapman et al. 2002a, b). Given the observed changes in rainfall patterns over the past 30 years within this region (Chapman et al. 2005), the ability to alter reproductive patterning in response to rainfall and other environmental factors may be important to long-term persistence of this species (and others). Studies of interannual variation within and among systems relative to environmental change will be informative in evaluating the degree of flexibility in reproductive patterning in this species.

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**References**


