

Optimal offspring size influenced by the interaction between dissolved oxygen and predation pressure

Erin E. Reardon¹ and Xavier Thibert-Plante^{1,2}

¹*Biology Department and* ²*Redpath Museum, McGill University, Montreal, Quebec, Canada*

ABSTRACT

Question: How does optimal size at the beginning of the juvenile stage vary with dissolved oxygen and aquatic predator pressure?

Mathematical methods: An implicit model based on earlier offspring size and number optimality models, using empirical observations to motivate and interpret the results.

Key assumptions: A stable, density-independent system with high parental care that maximizes maternal fitness, with respect to offspring size and number.

Predictions: The model predicts a positive relationship between juvenile size and aquatic dissolved oxygen, with respect to maternal fitness and predation pressure. This prediction is based on observations in the literature that smaller fish are less sensitive to low dissolved oxygen and may use low dissolved oxygen habitats as predator refuges.

Keywords: body size, fish, hypoxia, implicit derivation model, predator–prey.

INTRODUCTION

A common observation in the fish literature is that smaller fish are less sensitive to hypoxia – that is, low dissolved oxygen (Doudoroff and Shumway, 1970; Lowe-Jinde and Niimi, 1983; Zanuy and Carrillo, 1985; Smale and Rabeni, 1995; Robb and Abrahams, 2003; Chapman and McKenzie, 2009). One mechanism that might explain this pattern is the observed negative allometric relationship for mass-specific gill-surface area. Smaller individuals may have more efficient gas exchange with their environment (Muir, 1969; Pauly, 1981; Hughes, 1984), and larger fish may be limited by the fixed size of the red blood cells for gas exchange (West *et al.*, 1997). Although this direct physiological explanation for smaller size serves to explain smaller fish size in oxygen-limited environments, there are theoretical reasons to suspect that oxygen may have additional indirect effects on the evolution of optimal size. Here, we consider one of those indirect effects – predation pressure.

Greater tolerance to hypoxia in smaller fish has the potential to alter interactions between predators and prey (Anjos *et al.*, 2008; Chapman and McKenzie, 2009). Hypoxic environments may act as refuges for small prey fishes, because the larger piscine predators may be unable to tolerate conditions available to the smaller piscine prey – that is, the larger predators are

Correspondence: Erin E. Reardon, Biology Department, McGill University, Montreal, Quebec H3A 1B1, Canada.
e-mail: erin.reardon@mail.mcgill.ca

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physiologically excluded (reviewed in Chapman and McKenzie, 2009). For example, in their study of physiological tolerance and hypoxia, Robb and Abrahams (2003) provided evidence for an ecological advantage of being small through greater tolerance to hypoxia (higher haematocrit and haemoglobin concentrations and lower ventilation frequency under low dissolved oxygen) in small fathead minnow (potential prey) compared with small and large yellow perch. Further evidence for the benefits of small size under hypoxia comes from studies of faunal loss and recovery in the Lake Victoria basin of East Africa, where the introduction of the large predatory Nile perch coincided with the disappearance of hundreds of native (mostly endemic) fishes (Kaufman *et al.*, 1997; Balirwa *et al.*, 2003). However, hypoxic wetlands have now been identified as important refuges for fishes that can tolerate such conditions, and also function as low-oxygen barriers to Nile perch (Chapman *et al.*, 1996a, 1996b, 2002a; Kaufman *et al.*, 1997; Balirwa, 1998; Schofield and Chapman, 1999; Balirwa *et al.*, 2003). Interestingly, many of the native fishes that persist in extremely hypoxic wetlands that are not air-breathing tend to be quite small in size (Chapman *et al.*, 1996a, 1996b), providing support for an advantage to small body size under hypoxia.

Pseudocrenilabrus multicolor victoriae (Seegers) is a small, mouth-brooding cichlid found throughout the Lake Victoria basin of western Uganda and exhibits strong interdemarc variation in morphology, physiology, and life-history traits across an oxygen gradient (e.g. Chapman *et al.*, 2000, 2002a, 2002b, 2008; Martinez *et al.*, 2009; Reardon and Chapman, 2009, in press a). Reardon and Chapman (2009, in press a, in press b) provided evidence for a positive relationship between body size and dissolved oxygen for eggs, juveniles, and adults. The evidence from this suite of studies also supports a trade-off between egg size and number, with no difference in reproductive effort across an oxygen gradient and supports increased tolerance to hypoxia in fish from waters with low dissolved oxygen. This example provided the motivation for our present analysis and thus the model is developed to be consistent with the *P. multicolor* system. Additional motivation for this study stems from the growing body of evidence suggesting that hypoxia is one of the most pressing environmental stressors on aquatic systems due to anthropogenically driven eutrophication and pollution of water bodies (reviewed in Diaz, 2001; Diaz and Breitburg, 2009).

Despite the empirical evidence for an interaction among prey fish body size, predation pressure, and aquatic dissolved oxygen, the reproductive trade-offs that may drive this pattern are not clear. Optimality models of offspring size and number might thus provide a useful framework for exploring these interactions. Based on observations from the above literature, we predict a positive relationship between optimal body size and aquatic dissolved oxygen. Here we attempt to formalize this prediction mathematically through an implicit modelling approach. We developed an optimality model to predict the trend of offspring size in response to changes in aquatic dissolved oxygen and predator pressure. The model is based on a series of assumptions and predictions derived from earlier optimality models of offspring size and number, and from relationships previously demonstrated among the target variables. This approach is particularly useful because it allows us to identify potential gaps in our logic and key parameters in our predictions.

THEORETICAL FRAMEWORK

This model is based on models proposed by Smith and Fretwell (1974) and extended by Hendry *et al.* (2001) and Hendry and Day (2003). A key component of these models is that any given organism has a finite amount of energy available for growth, maintenance, and

reproduction. Thus, at any point in time, we assume that a finite amount of energy is available for reproduction (Smith and Fretwell, 1974; Roff, 1992; Stearns, 1992). We also assume that: (1) maternal fitness is determined by the product of juvenile fitness and the total number of offspring; (2) juvenile fitness is a function of juvenile size and predator pressure; (3) the total number of juveniles is a function of juvenile size and total mass of all offspring ('total offspring mass'); and (4) total offspring mass is a function of juvenile size and aquatic dissolved oxygen.

In a given aquatic habitat, low dissolved oxygen can influence both maternal fitness and offspring fitness, because dissolved oxygen is suggested to relieve predation pressure from water-breathing, piscivorous fishes (reviewed in Chapman and McKenzie, 2009) and to cause shifts in optimal size to maximize oxygen uptake (Hendry *et al.*, 2001; Einum *et al.*, 2002; Hendry and Day, 2003; Reardon and Chapman, 2009). Independent of oxygen, juvenile size is also predicted to influence predation risk: the larger the juvenile, the lower the risk of predation because of gape size limitations of possible predators (Rodd and Reznick, 1997; Nilsson and Bronmark, 2000; Magnhagen and Heibo, 2001; Truemper and Lauer, 2005). Thus, for this modelling exercise, we made the following assumptions. Predator pressure is assumed to represent aquatic predators and is influenced by both juvenile size and aquatic dissolved oxygen in density-independent, stable systems where maternal fitness is at an optimum. In addition, our model is parameterized for fish that exhibit some level of post-spawning parental care under the assumption that parental care mitigates any direct impact of dissolved oxygen on juvenile survival (Wourms and Lombardi, 1992; Breitburg *et al.*, 1994; Jones and Reynolds, 1999; Goodwin *et al.*, 2002; Chapman and McKenzie, 2009; Reardon, 2009).

The above relationships can be summarized using the fitness function in equation (1):

$$W[s(o), P(o, s(o)), E(o, s(o))] = F[s(o), P(o, s(o))] \times N[s(o), E(o, s(o))] \quad (1)$$

This equation states that maternal fitness (W) is a function of juvenile size (s), predator pressure (P), and total offspring mass (E), with P and E as functions of aquatic dissolved oxygen content (o) and juvenile size (s), which is also a function of aquatic dissolved oxygen. Maternal fitness (W) is equal to individual juvenile fitness (F) multiplied by the total number of juveniles (N). Juvenile fitness (F) is a function of juvenile size (s) and predator pressure (P). Total number of juveniles (N) is a function of juvenile size (s) and total juvenile mass (E). The definitions of s , E , and P are described above. This model maximizes maternal fitness with respect to juvenile size (cf. Smith and Fretwell, 1974; Hendry *et al.*, 2001; Hendry and Day, 2003). So, optimal juvenile size should occur when the first derivative of equation (1) with respect to juvenile size equals zero (at optimum: $\partial W/\partial s = 0$) and the second derivative with respect to juvenile size is negative (for maximization: $\partial^2 W/\partial s^2 < 0$).

Equation (1) was differentiated with respect to dissolved oxygen, and the resulting equation differentiated with respect to juvenile size. The outcome of this differentiation is rearranged to leave ds/do on the left-hand side of the equation and is given in equation (2) below:

$$\frac{ds}{do} = \frac{-\left[\frac{\partial E}{\partial s \partial o} \frac{\partial W}{\partial E}\right] - \left[\frac{\partial^2 P}{\partial s \partial o} \frac{\partial W}{\partial P}\right] - \left[\frac{\partial E}{\partial o} \frac{\partial^2 W}{\partial s \partial E}\right] - \left[\frac{\partial E}{\partial o} \frac{\partial E}{\partial s} \frac{\partial^2 W}{\partial E^2} \frac{\partial^2 W}{\partial s \partial E}\right]}{\left[\frac{\partial^2 E}{\partial s^2} \frac{dW}{dE}\right] + \left[\frac{\partial^2 P}{\partial s^2} \frac{dW}{dP}\right] + \left[\frac{dE}{ds} \frac{\partial^2 W}{\partial s \partial E}\right] + \left[\frac{\partial^2 E}{\partial s^2} \frac{\partial^2 W}{\partial E} \frac{\partial^2 W}{\partial s \partial E}\right] + \left[\frac{\partial P}{\partial s} \frac{\partial E}{\partial s} \left(\frac{\partial^2 W}{\partial s \partial E}\right)^2\right] + \left[\frac{\partial E}{\partial s} \frac{\partial^2 W}{\partial s \partial E}\right] + \left[\frac{\partial P}{\partial s} \frac{\partial^2 W}{\partial P^2}\right] + \frac{\partial^2 W}{\partial s \partial P} + \frac{\partial^2 W}{\partial s^2}} \quad (2)$$

ds/do represents how the optimal size at the beginning of the juvenile stage changes in relation to aquatic dissolved oxygen. The direction of this relationship is determined by overall sign of the terms interacting on the right-hand side of the equation. If this relationship is positive, juvenile size should increase as the mother is exposed to increasing dissolved oxygen; if it is negative, the opposite is true – juvenile size should decrease as the mother is exposed to increasing dissolved oxygen. Note that we are here examining juvenile size, when selection might apply at multiple stages, including adults. We do so to simplify the analyses and because juvenile and adult size are generally correlated in fishes (summarized in Heath and Blouw, 1998; Reznick, 1991). And this association holds in the system that piqued our interest in examining this problem: African cichlid *Pseudocrenilabrus multicolor* across an oxygen gradient (Reardon, 2009; Reardon and Chapman, 2009).

We will now explore each term on the right-hand side of equation (2). $\partial E/\partial s$ represents how the total juvenile mass changes with respect to a change in individual juvenile size. This relationship is equal to zero ($\partial E/\partial s = 0$), given that we assume total juvenile mass (E , also reproductive effort) is the product of the total number of young in a brood and the average size of each individual. That is, given finite resources for reproduction, as juvenile size changes, total offspring mass should remain the same because changes in the total number of young will offset changes in juvenile size (e.g. Smith and Fretwell, 1974; Roff, 1992; Stearns, 1992; Hendry *et al.*, 2001). Although there is strong empirical support for this relationship across fish taxa (e.g. Duarte and Alcaraz, 1989; Elgar, 1990), we acknowledge that several models do predict a positive relationship between juvenile size and total offspring mass. However, the design and many of the assumptions in these models are tailored to organisms with life histories that are not relevant in the context of our model [e.g. insects that become gravid at a feeding site and travel for ovipositioning of eggs or organisms where juvenile survival is density dependent (Parker and Begon, 1986; McGinley, 1989)].

$\partial E/\partial O$ represents how the total offspring mass changes in response to changes in aquatic dissolved oxygen. We assume no relationship here ($\partial E/\partial O = 0$) because no difference in total juvenile mass (reproductive effort) is seen across an aquatic dissolved oxygen gradient in *Pseudocrenilabrus multicolor* (Reardon and Chapman, 2009). The relationship between $\partial^2 W/\partial s \partial P$ is also zero because $\partial W/\partial s = 0$ (as above). With these three terms at zero, many of the terms in equation (2) cancel out, leaving a simplified version of the model (equation 3):

$$\frac{ds}{do} = \frac{-\left[\frac{\partial^2 P}{\partial s \partial o} \frac{\partial W}{\partial P}\right]}{\left[\frac{\partial^2 P}{\partial s^2} \frac{\partial W}{\partial P}\right] + \left[\frac{\partial P}{\partial s} \frac{\partial^2 W}{\partial P^2}\right] + \left[\frac{\partial^2 W}{\partial s^2}\right]} \quad (3)$$

where s , o , P , and W are defined as above.

RESULTS AND DISCUSSION

Using the framework outlined above, we can ask how optimal juvenile size changes with aquatic dissolved oxygen and predation pressure. To address this question, we evaluate the sign of each of the terms in equation (3) to determine if ds/do is positive (> 0) or negative (< 0). If ds/do is positive, optimal juvenile size increases as the aquatic dissolved oxygen

increases. If ds/do is negative, optimal juvenile size decreases as aquatic dissolved oxygen increases.

As explained earlier, $\partial^2 W/\partial s^2$ is negative (< 0), because we are dealing with a fitness maximum. Next, $\partial W/\partial P$ represents how maternal fitness changes in relation to changes in predation pressure. Our basic understanding of predator–prey systems suggests that prey fish have a lower fitness under high predation pressure due to the higher chance of mortality (e.g. Lima and Dill, 1990). Following this logic, maternal fitness decreases under increasing predation pressure ($\partial W/\partial P < 0$; Fig. 1). The sign of $\partial^2 W/\partial P^2$, the second derivative of maternal fitness differentiated with respect to predation pressure, must also be determined. Here we must know the curvature (if any) of the $\partial W/\partial P$ relationship. Empirical evidence for the curvature of this relationship is unavailable in the literature, but three potential relationships are illustrated in Fig. 1. $\partial^2 W/\partial P^2$ may be negative ($\partial^2 W/\partial P^2 < 0$, line (c), Fig. 1) if, for example, a fish can employ predator escape responses at low predation pressure, with negligible impacts on maternal fitness. But once predation pressure passes a threshold, predator escape responses break down and maternal fitness decreases with increased predation pressure. However, $\partial^2 W/\partial P^2 > 0$ is also possible if a given increase in predation pressure has a weaker effect on maternal fitness if predator pressure is high than if it is low (line (a), Fig. 1). This scenario is supported by the idea of predator saturation

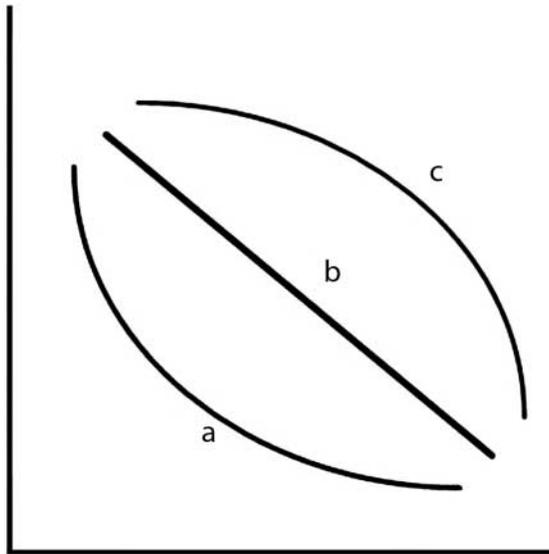


Fig. 1. This figure illustrates the potential shapes of the negative relationship between terms with second derivatives, $\partial^2 W/\partial P^2$ and $\partial^2 P/\partial s^2$ (a–c). In the case of $\partial^2 W/\partial P^2$, line (a) represents a scenario where a given increase in predator pressure would have a weaker effect on maternal fitness if predation pressure is high than if it is low. Line (b) represents a linear relationship between maternal fitness and predator pressure. Line (c) represents a scenario where a given increase in predator pressure would have a stronger effect on maternal fitness if predation pressure is high rather than if it is low. For $\partial^2 P/\partial s^2$, line (a) represents a scenario where minute increases in juveniles of small size will have a relatively large reduction in the risk of predation. Line (b) represents a linear relationship between juvenile size and predator pressure. Line (c) represents a scenario where minute increases in juveniles of large size will have a relatively large reduction in the risk of predation.

(e.g. Holling, 1959; Neal, 2004). That is, a predator saturation curve, or predator swamping curve, has the same shape as line (a) in Fig. 1. We have chosen $\partial^2 W/\partial P^2 > 0$ (line (a)) as our function because it has the most support in the literature, although both function forms are biologically possible.

$\partial P/\partial s$ represents the risk of predation on juveniles of different sizes – independent of aquatic dissolved oxygen. This relationship is negative ($\partial P/\partial s < 0$), because risk of predation decreases as juvenile size increases – because of gape size limitations of many predators (Schael *et al.*, 1991; Rodd and Reznick, 1997; Nilsson and Bronmark, 2000; Magnhagen and Heibo, 2001; Truemper and Lauer, 2005). We now need to define the curvature of the $\partial P/\partial s$ relationship to determine the sign of the second derivative, $\partial^2 P/\partial s^2$ (Fig. 1). One hypothesis is that $\partial^2 P/\partial s^2 < 0$ (line (c), Fig. 1), especially if predation risk is primarily a matter of the gape limitation of predators. However, another way to illustrate this relationship is to think about one very large juvenile and one very small juvenile. If each juvenile experienced the same, very small increase in body size, the size increase would benefit the small juvenile more because the size gain relative to its original body size is greater than for a larger juvenile. Following this logic, a small increase in the body size of a small juvenile will reduce the predation risk, via increased escape performance and/or gape limitations associated with larger size, more than for a large juvenile experiencing the same size increase. Although this needs to be tested empirically, we predict this relationship to be positive ($\partial^2 P/\partial s^2 > 0$; line (a), Fig. 1) because it takes into account more than just predator gape limitations. We will revisit this prediction in a later section in association with $\partial^2 W/\partial P^2$.

$\partial^2 P/\partial s \partial o$ represents the change in predator pressure in relation to changes in juvenile size and changes in aquatic dissolved oxygen. The relationship between $\partial P/\partial s$ is negative based on evidence described above. We predict the relationship between predator pressure and dissolved oxygen to be positive (reduced predator pressure with reduced dissolved oxygen; $\partial P/\partial o > 0$) based on evidence outlined in the Introduction. When juveniles are large, predation risk should be low regardless of dissolved oxygen, because the juveniles will be outside of the gape range of the predators. However, when juveniles are small, predation risk will be lower under low dissolved oxygen conditions because there are fewer predators. And so, $\partial^2 P/\partial s \partial o < 0$ (Fig. 2).

From equation (3), terms $\partial^2 P/\partial s \partial o$, $\partial P/\partial s$, $\partial W/\partial P$, and $\partial^2 W/\partial s^2$ are negative and $\partial W^2/\partial^2 P$ and $\partial^2 P/\partial s^2$ are positive. As summarized in equation (4), both the numerator and the denominator become negative, thus the outcome of the model is positive.

$$\frac{ds}{do} = \frac{- [- -]}{[+ -] + [- +] + [-]} = \frac{-}{[-] + [-] + [-]} = + \quad (4)$$

In short, our model provides a formal hypothesis for earlier conjectures relating body size and dissolved oxygen (ds/do), which was based on observations of smaller prey body size under hypoxia (e.g. Pauly, 1981; Robb and Abrahams, 2003; Chapman and McKenzie, 2009). Although the physiological mechanisms that should drive the smaller body size are well described (e.g. Pauly, 1981; Robb and Abrahams, 2003), there is still some debate as to whether the relationship can be generalized (Nilsson and Östlund-Nilsson, 2008) and, if so, the direction of the relationship. For example, in Amazonian oscars (*Astronotus ocellatus*), one study supports the positive outcome of this model by providing evidence to suggest that small fish are more tolerant of hypoxia, with lower aquatic surface respiration thresholds [index of hypoxia tolerance (reviewed in Chapman and McKenzie, 2009)] and increased preference for hypoxic habitats, compared

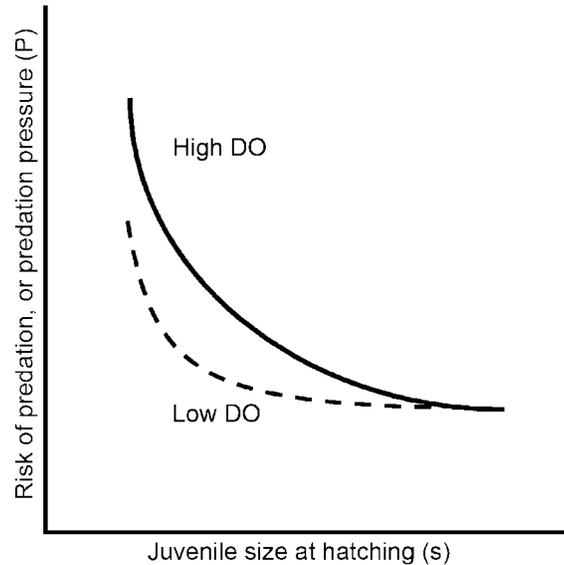


Fig. 2. This figure illustrates the interaction of predator pressure (P), aquatic dissolved oxygen (o), and juvenile size (s) under high and low dissolved oxygen (DO) scenarios. The relationship between predator pressure and juvenile size is negative as described in Fig. 1. Yet, the relationship between predator pressure and oxygen is positive. When juveniles are small, predation risk will be lower under low dissolved oxygen conditions relative to high dissolved oxygen because there are fewer predators. When juveniles are large, predation risk should be low regardless of dissolved oxygen because the juveniles will be outside of the gape range of the predators.

with large fish (Sloman *et al.*, 2006). Yet, another study suggests that tolerance of hypoxia actually increases with body size because of higher anaerobic capacities in larger individuals (Almeida-Val *et al.*, 2000). If there is indeed a negative relationship between hypoxia and body size in oscars, most likely we would see the sign of either $\partial^2 W/\partial P^2$ or $\partial^2 P/\partial s^2$ shift from positive to negative, based on predictions described earlier.

Although we have empirical support for the functions of most terms in our model, the functions of $\partial^2 W/\partial P^2$ and $\partial^2 P/\partial s^2$ are less well described in the literature. Regardless of whether they are positive or negative, if the signs of these two terms are the same, then the outcome of our model remains unchanged ($ds/do > 0$). Yet, if the signs of $\partial^2 W/\partial P^2$ and $\partial^2 P/\partial s^2$ oppose each other, the outcome of the model becomes negative. Biologically, both the positive and negative functional forms are possible. We chose to use the positive functional forms in our model based on the logic outlined earlier. This model suggests that empirically assessing the shapes of the relationships between maternal fitness and predation pressure ($\partial^2 W/\partial P^2$) and between predation pressure and juvenile body size ($\partial^2 P/\partial s^2$) is critical to understanding the relationship between body size and oxygen with respect to predation.

In addition, the predictions of our model hinge on our assumptions. And, it must be recognized that an additional constraint lies in factors not taken into account that may nevertheless be important, such as density dependence, age, and growth, or other forms of predation (e.g. aerial). One additional caveat is that we did not allow dissolved oxygen to directly impact juvenile survival, even though this was the direct topic of investigation in

Hendry and Day's (2003) salmonid-based model. The reason we did not do so is that the true relationship between dissolved oxygen and juvenile survival remains unclear. While some researchers have reported no relationship between dissolved oxygen and juvenile survival (e.g. Oppen-Berntsen *et al.*, 1990; Ciuhandu *et al.*, 2005; Reardon, 2009), others found that survival decreases with decreasing dissolved oxygen (e.g. Czerkies *et al.*, 2001; Einum *et al.*, 2002; Hassell *et al.*, 2008; Wu, 2009). Interestingly, all studies reporting a negative impact of dissolved oxygen on survival were for species with no post-spawning parental care. A study on the maternal mouth brooder *P. multicolor*, the main species that motivated and grounded our model, found no evidence for a difference in survival of juveniles brooded under either high or low dissolved oxygen (Reardon, 2009). In addition, Chapman and McKenzie (2009) noted that in hypoxic habitats, a relatively high proportion of species exhibit post-spawning parental care relative to other more normoxic waters. This suggests that parental care may offset negative impacts of hypoxia on juvenile survival. A deeper understanding of how dissolved oxygen impacts offspring survival across taxa that represent a broad range of reproductive strategies from no post-spawning parental care to viviparity may be necessary to evaluate the generality of this model.

Implicit modelling as utilized here is useful in determining gaps in the empirical data and identifying the important variables driving relationships identified in the model. Validating the outcome of our model and the underlying question of how offspring size is affected by predation and oxygen availability requires more empirical work. The mosaic of wetlands, lakes, and rivers in the Lake Victoria basin of East Africa may be an excellent system to explore the relationships put forward in this model because this basin is characterized by dramatic variation in aquatic dissolved oxygen availability and there are empirical data on fish distributions that highlight the importance of hypoxic habitats as refuges for small fishes (e.g. Chapman *et al.*, 1996a, 1996b; Balirwa *et al.*, 2003). For example, in one low dissolved oxygen swamp population of the cichlid *P. multicolor*, predation pressure from large piscine predators is very low (Chapman *et al.*, 1996a, 1996b, 2002a). Aerial predation from kingfishers is the dominant source of predation pressure on this population (Randle and Chapman, 2004). Since kingfishers do not target juveniles, a smaller body size should be better in terms of maximizing oxygen uptake. Yet populations of *P. multicolor* from high dissolved oxygen river and lake sites live in sympatry with other cichlids that consume juveniles (Binning and Chapman, 2008), and thus bigger should be better in habitats of high dissolved oxygen (Reznick, 1991).

Although Reardon and Chapman (2009, in press a, in press b) and Reardon (2009) provide evidence for a positive relationship between body size and dissolved oxygen across life stages, the next step in validating our optimality model is to quantify and compare life-history traits between populations across a range of sites that facilitate evaluation of the interaction of dissolved oxygen and predation. Although this paper is parameterized by a specific system, the interaction between dissolved oxygen and predation may be a frequent phenomenon in nature. As the global hypoxia crisis grows, a broader understanding of the combined impacts of predation and dissolved oxygen on fitness could be very important for predicting how fish communities may respond to changes in the oxygen profile of many aquatic systems around the world.

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REFERENCES

- Almeida-Val, V.M.F., Val, A.L., Duncan, W.P., Souza, F.C.A., Paula-Silva, M.N. and Land, S. 2000. Scaling effects on hypoxia tolerance in the Amazon fish *Astronotus ocellatus* (Perciformes: Cichlidae): contribution of tissue enzyme levels. *Comp. Biochem. Physiol. B*, **125**: 219–226.
- Anjos, M.B., De Oliveira, R.R. and Zuanon, J. 2008. Hypoxic environments as refuge against predatory fish in the Amazonian floodplains. *Braz. J. Biol.*, **68**: 45–50.
- Balirwa, J. 1998. Lake Victoria wetlands and the ecology of the Nile tilapia, *Oreochromis niloticus* (L.). Rotterdam: University of Wageningen.
- Balirwa, J.S., Chapman, C.A., Chapman, L.J., Cowx, I.G., Geheb, K., Kaufman, L. *et al.* 2003. Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? *Bioscience*, **53**: 703–715.
- Binning, S.A. and Chapman, L.J. 2008. Feeding ecology and diet overlap in riverine cichlids from western Uganda. *Verhandlungen Internationale Vereinigung Limnologie*, **30**: 283–286.
- Breitburg, D.L., Steinberg, N., Dubeau, S., Cooksey, C. and Houde, E.D. 1994. Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar. Ecol. Progr. Ser.*, **104**: 235–246.
- Chapman, L.J. and McKenzie, D. 2009. Behavioural responses and ecological consequences. In *Hypoxia in Fishes* (J.G. Richards, A.P. Farrell and C.J. Brauner, eds.), pp. 26–77. San Diego, CA: Elsevier.
- Chapman, L.J., Chapman, C.A. and Chandler, M. 1996a. Wetland ecotones as refugia for endangered fishes. *Biol. Conserv.*, **78**: 263–270.
- Chapman, L.J., Chapman, C.A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L. and Keiter, A.E. 1996b. Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Conserv. Biol.*, **10**: 554–561.
- Chapman, L.J., Chapman, C.A., Nordlie, F.G. and Rosenberger, A.E. 2002a. Physiological refugia: swamps, hypoxia tolerance, and maintenance of fish biodiversity in the Lake Victoria region. *Comp. Biochem. Physiol. A*, **133**: 421–437.
- Chapman, L.J., Nordlie, F.G. and Seifert, A. 2002b. Respiratory oxygen consumption among groups of *Pseudocrenilabrus multicolor victoriae* subjected to different oxygen concentrations during development. *J. Fish Biol.*, **61**: 242–251.
- Chapman, L.J., Albert, J. and Galis, F. 2008. Developmental plasticity, genetic differentiation, and hypoxia-induced trade-offs in an African cichlid fish. *Open Evol. J.*, **2**: 75–88.
- Ciuhandu, C.S., Stevens, E.D. and Wright, P.A. 2005. The effect of oxygen on the growth of *Oncorhynchus mykiss* embryos with and without a chorion. *J. Fish Biol.*, **67**: 1544–1551.
- Czerkies, P., Brzuzan, P., Kordalski, K. and Luczynski, M. 2001. Critical partial pressures of oxygen causing precocious hatching in *Coregonus lavaretus* and *C. albula* embryos. *Aquaculture*, **196**: 151–158.
- Diaz, R.J. 2001. Overview of hypoxia around the world. *J. Environ. Qual.*, **30**: 275–281.
- Diaz, R.J. and Breitburg, D.L. 2009. The hypoxic environment. In *Hypoxia in Fishes* (J.G. Richards, A.P. Farrell and C.J. Brauner, eds.), pp. 80–81. San Diego, CA: Elsevier.
- Doudoroff, P. and Shumway, D.L. 1970. *Dissolved Oxygen Requirements of Freshwater Fishes*. FAO Fisheries Technical Paper #86. Rome: Food and Agriculture Organization of the United Nations.
- Duarte, C.M. and Alcaraz, M. 1989. To produce many small or few large eggs: a size-independent reproductive tactic of fish. *Oecologia*, **80**: 401–404.
- Einum, S., Hendry, A.P. and Fleming, I.A. 2002. Egg size evolution in aquatic environments: does oxygen availability constrain size? *Proc. R. Soc. Lond. B*, **269**: 2325–2330.

- Elgar, M.A. 1990. Evolutionary compromise between a few large and many small eggs: comparative evidence in teleost fish. *Oikos*, **59**: 283–287.
- Goodwin, N.B., Dulvy, N.K. and Reynolds, J.D. 2002. Life-history correlates of the evolution of live bearing in fishes. *Phil. Trans. R. Soc. Lond. B*, **357**: 259–267.
- Hassell, K.L., Coutin, P.C. and Nugegoda, D. 2008. Hypoxia impairs embryo development and survival in black bream (*Acanthopagrus butcheri*). *Mar. Pollut. Bull.*, **57**: 302–306.
- Heath, D.D. and Blouw, D.M. 1998. Are maternal effects in fishes adaptive or merely physiological side effects? In *Maternal Effects as Adaptations* (T.A. Mousseau and C.W. Fox, eds.), pp. 178–201. Oxford: Oxford University Press.
- Hendry, A.P. and Day, T. 2003. Revisiting the positive correlation between female size and egg size. *Evol. Ecol. Res.*, **5**: 421–429.
- Hendry, A.P., Day, T. and Cooper, A.B. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *Am. Nat.*, **106**: 387–407.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Ca. Entomol.*, **91**: 385–398.
- Hughes, G.M. 1984. Measurement of gill area in fishes: practices and problems. *J. Mar. Biol. Assoc. UK*, **64**: 637–655.
- Jones, J.C. and Reynolds, J.D. 1999. Costs of egg ventilation for male common gobies breeding in conditions of low dissolved oxygen. *Anim. Behav.*, **57**: 181–188.
- Kaufman, L.S., Chapman, L.J. and Chapman, C.A. 1997. Evolution in fast forward: haplochromine fishes of the Lake Victoria region. *Endeavour*, **21**: 23–30.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.
- Lowe-Jinde, L. and Niimi, A.J. 1983. Influence of sampling on the interpretation of haematological measurements of rainbow trout, *Salmo gairdneri*. *Can. J. Zool.*, **61**: 396–402.
- Magnhagen, C. and Heibo, E. 2001. Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. *Funct. Ecol.*, **15**: 754–762.
- Martinez, M.L., Chapman, L.J. and Rees, B.B. 2009. Population variation in hypoxic responses of the cichlid *Pseudocrenilabrus multicolor victoriae*. *Can. J. Zool.*, **87**: 188–194.
- McGinley, M.A. 1989. The influence of positive correlation between clutch size and offspring fitness on the optimal offspring size. *Evol. Ecol.*, **3**: 150–156.
- Muir, B.S. 1969. Gill dimensions as a function of fish size. *Fish. Res. Board Can.*, **26**: 165.
- Neal, D. 2004. Predation. In *Introduction to Population Biology*, pp. 300–307. Cambridge: Cambridge University Press.
- Nilsson, G.E. and Östlund-Nilsson, S. 2008. Does size matter for hypoxia tolerance in fish? *Biol. Rev.*, **83**: 173–189.
- Nilsson, P.A. and Bronmark, C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, **88**: 539–546.
- Oppen-Berntsen, D.O., Boggsnes, A. and Walther, B.T. 1990. The effects of hypoxia, alkalinity and neurochemicals on hatching of Atlantic salmon (*Salmo salar*) eggs. *Aquaculture*, **86**: 417–430.
- Parker, G.A. and Begon, M. 1986. Optimal egg size and clutch size: effects of environmental and maternal phenotype. *Am. Nat.*, **128**: 573–592.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung*, **28**: 251–282.
- Randle, A.R. and Chapman, L.J. 2004. Habitat use by the air-breathing fish *Ctenopoma muriei*: implications for costs of breathing. *Ecol. Freshwater Fish*, **13**: 37–45.
- Reardon, E.E. 2009. Fish in extreme environments: reproduction and energetics under hypoxia. PhD dissertation, McGill University, Montreal.

- Reardon, E.E. and Chapman, L.J. 2009. Hypoxic stress and reproduction: life history variation in the mouth brooding cichlid, *Pseudocrenilabrus multicolor*. *J. Fish Biol.*, **75**: 1795–1815.
- Reardon, E.E. and Chapman, L.J. in press a. Effects of hypoxia on the energetics of an African cichlid: interdemic and developmental effects. *Physiol. Biochem. Zool.* (DOI: 10.1086/651100).
- Reardon, E.E. and Chapman, L.J. in press b. Hypoxia and energetics of mouth brooding: is parental care a costly affair? *Comp. Physiol. Biochem. A* (DOI: 10.1016/j.cbpa.2010.03.007).
- Reznick, D.N. 1991. Maternal effects in fish life histories. In *Proceedings of the IVth International Congress of Systematic and Evolutionary Biology* (E. Dudley, ed.), pp. 780–793. Portland, OR: Dioscorides Press.
- Robb, T. and Abrahams, M.V. 2003. Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small? *J. Fish Biol.*, **62**: 1067–1081.
- Rodd, F.H. and Reznick, D.N. 1997. Variation in the demography of guppy populations: the importance of predation and life histories. *Ecology*, **78**: 405–418.
- Roff, D.A. 1992. *The Evolution of Life Histories*. London: Chapman & Hall.
- Schael, D.M., Rudstam, L.G. and Post, J.R. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Can. J. Fish. Aquat. Sci.*, **48**: 1919–1925.
- Schofield, P.J. and Chapman, L.J. 1999. Interactions between Nile perch, *Lates niloticus*, and other fishes in Lake Nabugabo, Uganda. *Environ. Biol. Fish.*, **55**: 343–358.
- Sloman, K.A., Wood, C.M., Scott, G.R., Wood, S., Kajiumura, M., Johannsson, O.E. et al. 2006. Tribute to R.G. Boutilier: the effect of size on the physiological and behavioural responses of oscar, *Astronotus ocellatus*, to hypoxia. *J. Exp. Biol.*, **209**: 1197–1205.
- Smale, M.A. and Rabeni, C.F. 1995. Hypoxia and hypothermia tolerances of headwater stream fishes. *Trans. Am. Fish. Soc.*, **124**: 698–710.
- Smith, C.C. and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.*, **108**: 499–506.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Truemper, H.A. and Lauer, T.E. 2005. Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items. *J. Fish Biol.*, **66**: 135–149.
- West, G.B., Brown, J.H. and Enquist, B.J. 1997. A general model for the origin of allometric scaling laws in biology. *Science*, **276**: 122–126.
- Wourms, J.P. and Lombardi, J. 1992. Reflections on the evolution of piscine viviparity. *Am. Zool.*, **32**: 276–293.
- Wu, R.S.S. 2009. Effects on fish reproduction and development. In *Hypoxia in Fishes* (J.G. Richards, A.P. Farrell and C.J. Brauner, eds.), pp. 80–81. San Diego, CA: Elsevier.
- Zanuy, S. and Carrillo, M. 1985. Annual cycles of growth, feeding rate, gross conversion efficiency and hematocrit levels of sea bass (*Dicentrarchus labrax* L.) adapted to different osmotic media. *Aquaculture*, **44**: 11–25.

