

A Model for Optimal Offspring Size in Fish, Including Live-Bearing and Parental Effects

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Submitted September 9, 2010; Accepted January 2, 2011; Electronically published March 25, 2011

ABSTRACT: Since Smith and Fretwell's seminal article in 1974 on the optimal offspring size, most theory has assumed a trade-off between offspring number and offspring fitness, where larger offspring have better survival or fitness, but with diminishing returns. In this article, we use two ubiquitous biological mechanisms to derive the shape of this trade-off: the offspring's growth rate combined with its size-dependent mortality (predation). For a large parameter region, we obtain the same sigmoid relationship between offspring size and offspring survival as Smith and Fretwell, but we also identify parameter regions where the optimal offspring size is as small or as large as possible. With increasing growth rate, the optimal offspring size is smaller. We then integrate our model with strategies of parental care. Egg guarding that reduces egg mortality favors smaller or larger offspring, depending on how mortality scales with size. For live-bearers, the survival of offspring to birth is a function of maternal survival; if the mother's survival increases with her size, then the model predicts that larger mothers should produce larger offspring. When using parameters for Trinidadian guppies *Poecilia reticulata*, differences in both growth and size-dependent predation are required to predict observed differences in offspring size between wild populations from high- and low-predation environments.

Keywords: growth rate, life-history evolution, live-bearing, maternal effects, mortality, offspring size.

Introduction

There is large variation in the size of offspring that animals produce. For example, while fish with pelagic development produce eggs that range from 0.5 to 5.5 mm in diameter (Ahlstrom and Moser 1980), the coelacanth *Latimeria chalumnae*, a deep-sea fish, produces eggs that are 90 mm in diameter and develop inside the mother to become 35–38 cm at birth (Balon 1991). In volume, the coelacanth egg is almost 6 million times larger than the smallest pelagic eggs. It is also interesting to note that a majority of fish species produce eggs that are of intermediate size

(Ahlstrom and Moser 1980) and that there seems to be no correlation between mother's size and offspring size across species (Ware 1975). For example, the ocean sunfish *Mola mola* (up to 2,300 kg and 310 cm) and sprat *Sprattus sprattus* (maximum 27 g and 16 cm) both produce eggs that are around 1 mm in diameter (Froese and Pauly 2008). That many fish species produce eggs of similar size despite large variation in other traits points toward some shared ecological mechanism that underlies the evolution of offspring size.

To date, several theoretical models for the evolution of offspring size have been presented. Common to most of these is the fact that mortality is the central mechanism that shapes the evolution of offspring size, and many models also predict that offspring should be as small or as large as possible but not in between (e.g., Vance 1973a, 1973b; Shine 1978; Christiansen and Fenchel 1979; Parker and Begon 1986). A second line of theory derives from Smith and Fretwell's (1974) seminal article, which incorporated an intuited assumption that offspring needed to be of a minimum size to be viable and that an increase in size above this minimum would increase offspring fitness but with diminishing returns. Graphically, the assumption represents a sigmoid relationship between offspring size and offspring fitness. The tangent to this curve that passes through the origin identifies the optimal offspring size (Smith and Fretwell 1974). The sigmoid shape is notable because it predicts that the optimal strategy is to produce offspring of intermediate size. Many subsequent models have repeated this assumption and used it as a base from which to consider how factors such as environmental conditions or competition between offspring might impact the evolution of optimal offspring size (e.g., Parker and Begon 1986; Sargent et al. 1987; Winkler and Wallin 1987; Kindsvater et al. 2010). However, making an assumption many times does not make it true (see also Bernardo [1996], who reviews the basis for other assumptions in the Smith and Fretwell model). Deriving the sigmoid curve from first principles is therefore an important task because

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it might reveal ecological conditions under which there is likely to be selection on offspring size.

To our knowledge, the sigmoid curve has been derived for only four different ecological mechanisms. These are reviewed below.

First, Brockelman (1975) showed that intraspecific competition during early life stages may cause a sigmoid relationship between offspring size and offspring fitness. The model is consistent with empirical findings. For example, in a field experiment on Atlantic salmon *Salmo salar*, in which eggs of varying sizes were compared in the same stream environment, offspring survival was described by a sigmoid function of egg size (Einum and Fleming 2000). A similar relationship has been found in bryozoa (Marshall et al. 2006; Marshall and Keough 2008). In both these species, offspring develop in a limited habitat (a section of a stream or on a limited surface) where intracohort competition is likely; the mechanisms of Brockelman's (1975) model may therefore contribute to the sigmoid relationship in these species. Marshall et al. (2006) and Marshall and Keough (2008) used the observed sigmoid relationship as input to an optimality model that consequently predicted intermediate optimal offspring size, but similar to the Smith and Fretwell (1974) model, the sigmoid shape itself was not derived from first principles. Parker and Begon (1986) extended the Brockelman model and further showed that intrabrood competition among siblings could lead to maternal effects, whereby females with large reserves should produce larger offspring (see also Kindsvater et al. 2010). Many species of fish, however, spawn in a vast pelagic habitat, so it is unlikely that intracohort competition among offspring is a ubiquitous factor shaping offspring evolution. Yet they still produce offspring of intermediate size. One would therefore expect that mechanisms other than intrabrood competition also could lead to the sigmoid relationship between offspring size and offspring fitness.

The second mechanism was proposed by Levitan (1993), who modeled fertilization kinetics in broadcast spawning marine invertebrates (echinoderms). In short, a larger egg is an easier target for sperm, which enhances fertilization probability. If the egg is too big, however, fertilization from multiple sperm cells becomes harder to avoid, thus reducing egg fitness at larger sizes. The result is a sigmoid relationship between egg size and fertilization success. Optimal egg size also depends on sperm concentration (Levitan 1996), and model predictions fit between-species patterns (Levitan 1993).

The third mechanism involves an effect of egg size on development time (Levitan 2000). If development is faster within the egg than when the larvae has to feed on its own, then a larger egg can sustain rapid yolk-driven development longer, and total development time will thus

be shorter. By further assuming a constant mortality rate so that faster development translates to higher survival, Levitan (2000) derived a model that predicted a sigmoid relationship between offspring size and offspring fitness and compared it favorably with data from echinoderms. However, comparisons of laboratory and field observations have revealed that pelagic fish larvae often grow close to their physiological maximum after hatching (Folkvord 2005), which suggests that the mechanism proposed by Levitan (2000) may have limited applicability for marine fishes.

The fourth mechanism elaborates on mortality and combines it with offspring growth rate. Mortality can vary in magnitude and is often size dependent, typically decreasing with increasing body size (McGurk 1986; Fox et al. 1997; Sogard 1997). McGurk (1986) also noted that pelagic fish eggs and larvae have significantly higher mortality than other aquatic organisms of the same size, with mortality declining more rapidly with size compared with other groups. Some earlier theories have incorporated size-dependent mortality (e.g., Christiansen and Fenchel 1979). When mortality is size dependent, one has to account for how mortality changes as the offspring grow. Growth rate is affected by food availability and temperature, so several studies have suggested that temperature and food also play a role in offspring size evolution (Ware 1975; Perrin 1988; Azevedo et al. 1996). For example, Ware (1975) noted that several fish species tend to produce large eggs in winter, while they often spawn smaller eggs toward spring and summer, when temperature and growth conditions are more favorable. Similarly, in butterflies, optimal offspring size is larger when temperatures are lower and growth conditions are poorer (Fischer et al. 2003). Sargent et al. (1987) incorporated both size-dependent mortality rate and growth by adapting the life-history model of Taylor and Williams (1984) to study optimal offspring size. However, they followed Smith and Fretwell (1974) and assumed the sigmoid shape between offspring size and offspring fitness. This approach was taken one step further by Kiflawi (2006), who showed that the combination of size-dependent mortality and growth leads to the emergence of a sigmoid relationship between offspring size and offspring fitness. In the model by Kiflawi, mortality was not effective on the egg stage, which yielded an extra benefit for large egg sizes since eggs were not depredated before hatching. In this article, we include predation on the egg stage and show that the Smith and Fretwell sigmoid curve emerges for a wide region of parameter space. Consequently, our model predicts intermediate offspring sizes for a range of ecological scenarios that are likely to be encountered in the wild.

Sargent et al. (1987) considered the whole life history from birth to death and predicted that species should

spend their life history in the size region where growth rate is higher than the mortality rate. Growth and mortality are often hard to quantify across the whole size range of an organism and, if quantified, the mathematical relationships may be awkward to solve and communicate. We move beyond this limitation by noting that conceptually, offspring size can be studied in isolation from traits later in the life history (see also Kiflawi 2006). For example, for a fish or fish larvae that is 15 mm long, one can separate the optimal strategy for its future from the optimal strategy it used to obtain the size of 15 mm. The same logic underlies dynamic programming (Houston and McNamara 1999; Clark and Mangel 2000), and it has the advantage that quantifying survival and growth for such a narrow size range is feasible empirically, and solving the math is easier conceptually and numerically.

Our model makes specific reference to fishes, but the mechanisms are general and can be extended to other taxa. We emphasize fishes in our work because they occupy a larger parameter space than many other taxa, as defined by variation in offspring size versus offspring number. A contribution of this article is also that we consider maternal and paternal effects arising from parental strategies that modify mortality during the egg or juvenile stages or from adaptations that reduce egg mortality relative to the rate predicted by size dependence alone. For example, the positioning of eggs in sheltered habitats can make them harder to prey on (DeBlois and Leggett 1991). We also include egg guarding, where parental presence can reduce egg mortality, and live-bearing, where the embryos develop inside the mother. In these latter cases, the mortality rate of developing offspring is contingent on the survival of the live-bearing mother or guarding parent. Because optimal offspring size may then depend on the parent's state, this introduces a potential role for parental effects. We do not extend the model to include mouth brooding or post-hatching parental care, such as the provisioning or sheltering of feeding young. Doing so would require more extensive modifications of the basic model.

We examine the optimal offspring size using a broad parameter space and then provide a specific test based on field and lab data from live-bearing Trinidadian guppies *Poecilia reticulata*. Guppies are an interesting case study because their environments on the island of Trinidad can be classified as either high predation (lower segments of streams) or low predation (higher up in the stream, where few predators co-occur). The low-predation sites usually have higher densities of guppies, which leads to more intense resource competition and slower growth rates. Growth and mortality are thus correlated among populations of guppies, and with the model we show that patterns in offspring size can be predicted with knowledge of both these factors.

Our model can offer basic predictions for the effects of offspring mortality and growth on the optimal offspring size. More complex processes are likely to modify our predictions, including intra- and interspecific competition (Brockelman 1975; Parker and Begon 1986; Bashey 2008), fertilization kinetics (Levitan 1993), ontogenetic patterns of growth rate (Levitan 2000), further parental effects (Berkeley et al. 2004), parental care (Shine 1978), and bet-hedging strategies due to, for example, patchy food resources (Winemiller and Rose 1993) or effects of repeated exposure to size-selective mortality (Tian et al. 2007).

Model Description

We model the evolution of offspring size by considering events that span from fertilization of the egg, through hatching or birth, to the attainment of some critical size during the juvenile stage. Events during this period can shape the evolution of offspring size because egg size has implications for the condition of the juvenile at hatching while simultaneously putting constraints on the number of babies that a mother can produce.

Our model allows for different egg versus hatchling mortality rates. Declining size-dependent mortality is a typical pattern in aquatic systems (e.g., Peterson and Wroblewski 1984; McGurk 1986; Rijnsdorp and Jaworski 1990; Sogard 1997; Einum and Fleming 2000), so we generally model hatchling mortality rate as a declining function of size (fig. 1). In principle, mortality may also increase with size in some juvenile fish, so we also consider positive size-dependent mortality. It has been shown that egg fitness does not necessarily depend on egg size alone but that other investments in nutrients or quality can affect fitness (Moran and McAlister 2009). In this article, we assume that egg size or offspring size at hatch is the only variable trait.

Maternal Fitness

The optimal offspring size is determined by the amount of resources invested in each offspring that maximizes the fitness of the mother. Larger offspring often have higher survival because they are less vulnerable to size-dependent mortality (Conover and Schultz 1997). Because the mother typically has limited energy for reproduction, increased investment in each offspring necessarily comes at a cost to the number of offspring produced. The mother's dilemma is therefore centered on how this trade-off between offspring size and offspring number is resolved.

We consider the optimal offspring size from the time of fertilization onward. How offspring size is defined depends on the mode of reproduction. For fish with external fertilization, where fertilization normally coincides with

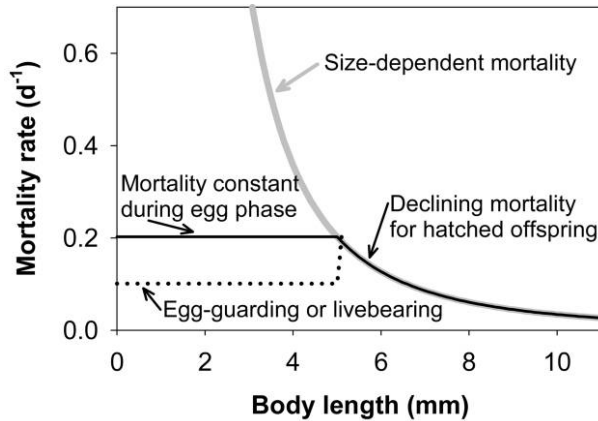


Figure 1: Daily mortality rate is assumed to be a declining allometric function of body length. *Gray line*, mortality for pelagic fish eggs and larvae from McGurk (1986). *Solid black line*, mortality trajectory for an offspring that is 5 mm at hatching; mortality is constant during the egg development phase. *Dotted black line*, adaptations such as egg guarding or live-bearing may lower the mortality during the egg phase. The scaling relationship was recalculated for length by assuming $c = 1.3 \times 10^{-5}$, $q = 3$, and that wet weight is five times dry weight.

the release of eggs into the external environment, we define offspring size as the size at hatching, given either as body mass or as the corresponding body length. For fish with internal fertilization, embryos develop inside the mother either through a lecithotrophic mode of reproduction, in which resources are provided in the egg, or through a matrotrophic mode of reproduction, whereby the developing embryo is continually nourished by the mother through a placenta-like structure (Reznick et al. 2002). In these cases of internal development, we define offspring size as the size at birth. Although mothers may change the composition of nutrients that they provision their offspring (Moran and McAlister 2009), for example, the amount of carotenoids or lipids, we assume no such stoichiometry but consider only how a homogeneous resource is divided between several identical offspring. Furthermore, we do not consider that fish eggs take up water and swell before spawning in marine environments (e.g., Fyhn et al. 1999).

We follow Smith and Fretwell (1974) and argue that it is reasonable to see the question of optimal offspring size independently from how much the parent should invest in reproduction in total. There might be exceptions when clutch size is very low, such that the choice is not necessarily between two eggs or only one egg of twice the size (Ricklefs 1968), which might affect the model's applicability to, for example, sharks and rays. If the female has a total gonad mass of G (in grams) that can be divided

among a certain number of eggs, each of which has a mass of w_0 (in grams), then her fitness f , defined as the total number of surviving offspring, is given by

$$f = s(w_0) \times \frac{G}{w_0}, \quad (1)$$

where $s(w_0)$ is the survival probability that an egg of weight w_0 has from fertilization onward (Smith and Fretwell 1974). The mother should thus produce offspring of a size that maximizes f . Since we use optimization, a prerequisite for the optimal offspring size to actually evolve is that there is sufficient genetic variation and that evolution is not constrained by linkages with other traits under selection.

Offspring Survival

Under size-dependent mortality, the survival probability of offspring depends on both their size at hatch and how quickly they grow from one size class to the next. Offspring that grow fast can experience higher survival because they spend less time in size ranges or life stages associated with high mortality rates (Sogard 1997), but fast growth may also increase the risk of predation (Lankford et al. 2001; Dmitriew 2011). For a given growth rate, offspring that hatch at a smaller size will grow and eventually assume the same growth trajectory as offspring that hatch at a larger size. Thus, the difference in survival between offspring that hatch at different sizes can be traced back to the daily mortality risk associated with the size classes a smaller offspring must grow through and the time required to reach that size.

Because body length increases approximately linearly with time during the early stages of life (e.g., Quince et al. 2008), we recast the equations in terms of offspring length rather than mass. For this conversion, we assume a length-weight relationship whereby egg mass w_0 is a function of offspring length at hatch l_h (in mm):

$$w_0(l_h) = cl_h^q, \quad (2)$$

where c and q can be fitted to observed data. The optimization problem outlined in equation (1) can then be solved by finding the l_h that corresponds to the maximum maternal fitness f^* :

$$f^* = \max_{l_h} \left(s(l_h) \times \frac{G}{w_0(l_h)} \right) = G \times \max_{l_h} \left(\frac{s(l_h)}{w_0(l_h)} \right), \quad (3)$$

where $s(l_h)$ is the survival probability of offspring as a function of l_h . Because G is assumed constant, it can be moved outside the parenthesis, and the optimization problem becomes independent of it.

We consider the probability that the offspring survives

from fertilization until it reaches a certain size that we will call boundary size l_b (in mm). The boundary size should be chosen to be above the largest potential egg size we want to investigate (i.e., $l_b > l_h$) but below the size at which the species begins to mature.

We assume that offspring have the same future expectation for fitness regardless of when they reach size l_b (there is thus no seasonality in this model) and that all offspring experience the same environment until size l_b . From size l_b onward, offspring can vary with respect to behavior, life-history strategies, environmental exposure, and phenotypic plasticity, without consequences for the predictions from this model.

Offspring survival is considered for two periods, first during the egg stage s_e (from fertilization until hatching) and thereafter during the larval/juvenile stage s_j (from hatching until size l_b). Both of these stage-specific survival probabilities depend on egg size: the egg survival (s_e), because eggs of different sizes might have different predation probabilities, and the juvenile survival (s_j), because smaller eggs yield smaller hatchlings that need to grow for a longer period to reach the boundary size l_b . Thus, total survival s from fertilization to size l_b is

$$s(l_h) = s_e(l_h) \times s_j(l_h). \quad (4)$$

Below we consider these two stage-specific survival probabilities in more detail. Note that we do not explicitly consider metamorphosis from larvae to juveniles but will, for simplicity, refer to offspring between hatch and the boundary size as juveniles.

Egg Survival

We begin by focusing on the simplest case in which there is no postfertilization parental involvement. This includes species with pelagic spawning and many other egg layers. We then extend the model to consider cases in which egg mortality might be modified by parental adaptations associated with live-bearing, egg guarding, or sheltered or armored eggs. Survival probability is related to mortality rate m as $s = e^{-m}$, and all mortality rates are given in units day^{-1} .

No Postfertilization Parental Involvement. In this case, egg survival s_e depends on both the egg's mortality rate $m_e(l_h)$ and its development time d (in days):

$$s_e(l_h) = \exp(-m_e(l_h) \times d(l_h)). \quad (5)$$

Note that we follow the observations of McGurk (1986) that the same size-dependent scaling relationship seems to hold for both eggs and larvae, although this assumption can easily be relaxed if other data are available. We therefore assume that egg mortality scales with the size of the

offspring at hatch, l_h , since all the material to produce the hatchling needs to be present in the egg from fertilization onward. This assumption is illustrated by the horizontal trajectories in figure 1, where mortality is constant at the value of $m(l_h)$ while the offspring develop inside the egg. For simplicity, we assume that the offspring grow in length at the same rate g (in mm day^{-1}) inside the egg as they do after hatching, so that development time is a function of the length at hatch and can be written as

$$d(l_h) = l_h g^{-1}. \quad (6)$$

We justify this simplification by noting that growth and development are tightly linked through the physiological effects of temperature and that marine larvae often seem to grow at their temperature-dependent maximum despite variation in food abundance (Folkvord 2005). More sophisticated relationships exist for egg development time in, for example, marine fish (Pauly and Pullin 1988; Brown et al. 2004). With this simplification, the model will illustrate general predictions, but parameters might need to be more carefully chosen if one is to investigate relationships in a particular species.

Live-Bearing and Egg Guarding. Parents can reduce egg mortality rates through live-bearing or egg guarding. For live-bearers, the developing offspring by all practical means have the same mortality rate as the mother m_m until their birth:

$$s_e = \exp(-m_m(L) \times d(l_h)). \quad (7)$$

Here the mother's mortality rate m_m may depend on her size L (in mm), which introduces a potential role for maternal effects. For egg guarding, the $m_m(L)$ would need to be replaced with the mortality rate the eggs suffer while guarded by the parent, $m_g(L)$, which may also be a function of parental traits such as body size.

Sheltered Egg Development. Egg survival can be improved through deposition of fertilized eggs in sheltered or safe habitats or through tougher membranes that protect the eggs from predation, fungus, or disease. One example is the capelin *Mallotus villosus*, which spawns on intertidal beaches during wintertime, where the exposure to low air temperatures requires special adaptations in the egg. Despite some amphipods at high tide, predation in this spawning habitat is presumably lower compared with eggs spawned in demersal habitats (DeBlois and Leggett 1991). We model this by multiplying egg survival s_e by a constant.

Size-Dependent Juvenile Survival

Several large-scale empirical comparisons (McGurk 1986; Savage et al. 2004) as well as theoretical derivations (Pe-

tersen and Wroblewski 1984; Brown et al. 2004; Andersen and Beyer 2006) strongly suggest an allometric scaling relationship between body size and instantaneous mortality rate:

$$m_j(l) = a \times l^b, \quad (8)$$

where m_j is the instantaneous mortality rate for a juvenile, l (in mm) is juvenile body length (which is continuously increasing due to growth), and a and b are parameters that can be fitted to data.

While size determines mortality rate, growth determines how much time is spent in a given size class and thus for how long mortality is accumulated. Juvenile length from length at hatch l_h onward is assumed to be proportional with time since hatching t (in days; t is thus days post-hatch) with a growth rate g that is assumed constant in a given environment:

$$l(t) = l_h + gt. \quad (9)$$

Unlike survival probabilities, mortality rates are additive. To find the total mortality during the juvenile stage, we can therefore integrate the mortality rate along the growth trajectory from hatch at time $t = 0$ until l_b is reached at time t_b (by inserting eq. [9] into eq. [8]):

$$\int_0^{t_b} m_j(l(t))dt = \int_0^{t_b} a(l_h + gt)^b dt = \frac{a(l_b^{b+1} - l_h^{b+1})}{g(b+1)}. \quad (10)$$

Juvenile survival from hatching until the boundary size is therefore

$$\begin{aligned} s_j(l_h) &= \exp\left(-\int_0^{t_b} m_j(l(t))dt\right) \\ &= \exp\left(\frac{-a(l_b^{b+1} - l_h^{b+1})}{g(b+1)}\right). \end{aligned} \quad (11)$$

Thus, survival across both the egg and the juvenile stage under no parental care is

$$s(l_h) = \exp\left[-m_e(l_h) \times d(l_h) - \frac{a(l_b^{b+1} - l_h^{b+1})}{g(b+1)}\right]. \quad (12)$$

By combining both egg and juvenile mortality rates under no parental care, we can then derive the expression that finds maximum maternal fitness as

$$f^* = G \times \max_{l_h} \left\{ \exp\left[-m_e(l_h) \times d(l_h) - \frac{a(l_b^{b+1} - l_h^{b+1})}{g(b+1)}\right] \frac{1}{w_0(l_h)} \right\}. \quad (13)$$

To find the maximum maternal fitness with postferti-

zation parental involvement, all that is needed is to replace $m_e(l_h)$ in equation (13) with the mother's mortality rate $m_m(L)$, in the case of live-bearing, or $m_g(L)$, in the case of egg guarding, or to add a multiplicative constant in the case of sheltered egg development.

We first illustrate the relationship between juvenile length and mortality using equation (8) (fig. 1). Using equation (13), we then find the optimal offspring size at hatch under conditions with no parental care and where mortality in both the egg and juvenile stage is size dependent. Beginning with an example to illustrate the nuts and bolts of the model, we continue with an exploration of parameter space under different mortality-size scaling relationships and explore optimal offspring size under both negative and positive size-dependent mortality. For a particular scaling relationship, we then illustrate how growth rate influences optimal offspring size. Thereafter, we explore how live-bearing and egg guarding can alter the optimal offspring size through its effects on egg mortality. Finally, we parameterize the model for guppies to test the combined effects of growth and mortality regime on the evolution of offspring size. Optimal offspring size was found by an exhaustive search programmed in Fortran.

Parameters

We first use parameters derived from marine fish and pelagic eggs and larvae and thereafter consider the specific case of optimal offspring size in a live-bearing Poeciliid, the Trinidadian guppy. For marine fish, we set the boundary size at $l_b = 15$ mm because this size is larger than the size at hatch but smaller than the size at maturity characteristic of most fish species. This is an arbitrary choice but has little influence on the model's predictions beyond setting an upper limit on offspring sizes considered. In the relationship between egg weight and length at hatch (eq. [2]), we assume isometric growth ($q = 3$) and a Fulton's condition factor of 1.3 so that $c = 1.3 \times 10^{-5}$. We assume that the relationship between length at hatch and egg weight is the same as the relationship between juvenile weight and length during the rest of development. We examine growth rates between 0.0 and 0.8 mm day⁻¹, since these rates are typical for fish larvae during their early stages of life (Houde 1989). For size-dependent mortality (eq. [8]), we use estimates of a and b for marine adult fish and for pelagic marine fish eggs and larvae from McGurk (1986; see table 1).

Since guppies rarely become sexually mature at lengths below 13 mm (Reznick and Endler 1982), for guppies we set $l_b = 13$ mm. This length is also larger than the largest observed size at birth. From the large laboratory assay of guppy life histories underlying Reznick et al. (2004), the

Table 1: Parameters for the allometric scaling of mortality used in this article

Situation	Description	Coefficient a	Exponent b	Reference
1	Marine adult fish	.131	-.75	McGurk 1986
2	Pelagic marine fish eggs and larvae	12.3	-2.55	McGurk 1986
3	Guppies, high-predation site	26.1	-2.71	Reznick et al. 1996
4	Guppies, low-predation site	184	-3.74	Reznick et al. 1996

Note: Mortality m (day^{-1}) is related to length l (mm) as $m = al^b$.

parameters for the length-weight relationship are estimated to be $c = 1.61 \times 10^{-5}$ and $q = 3.128$. Survival probabilities for different sizes were reported by Reznick et al. (1996). By doing a linear regression of $\ln(m)$ on $\ln(l)$, we obtain the a and b of equation (8) (for values, see table 1). We assume that the drop in survival for the largest size class is because some individuals die from old age, and this data point was omitted from the regression. High growth and high predation often co-occur in nature for guppies (Reznick et al. 2001). The growth rates we use were taken from (1) the lab experiments by Reznick (1983), where the high and low growth rates are the mean growth rates of the three highest (0.31 mm day^{-1}) and three lowest (0.19 mm day^{-1}) food treatments, and (2) field measurements reported by Reznick et al. (2001), where the high growth rate (measured in high-predation sites) was 0.15 mm day^{-1} and the low growth rate (observed in low-predation sites) was 0.083 mm day^{-1} .

Guppies are lecithotrophic live-bearers, meaning that they yolk a clutch of eggs that become internally fertilized, and the embryos then develop inside the mother until they are born. They bypass the larval life stage and are born as juveniles. On the basis of unpublished data, we found that interbrood intervals are significantly related to offspring length at hatch in guppies; we thus used the relationship $d(l_h) = 3.404 + 3.214 \times l_h$ to describe egg development times (S. K. Auer and D. N. Reznick, unpublished data). For the mother's length, we used $L = 25$ mm.

Results

Smith and Fretwell Revisited

By incorporating the combined effects of mortality rate and growth rate in shaping the evolution of optimal offspring size, the model predicts relationships that correspond to assumptions in the seminal model of Smith and Fretwell (1974). First, the model yields a sigmoid relationship between offspring size and offspring fitness (fig. 2A). This shape was first assumed through a verbal argument by Smith and Fretwell (1974; see their fig. 2a) and has formed the basis for many later models of optimal offspring size. The lack of a mechanistic basis for this initial model has been pointed out in the past (e.g., Sargent et

al. 1987), and several articles, including this one, have derived the sigmoid shape for special or general mechanisms that may act simultaneously (Brockelman 1975; Levitan 1993, 2000; Kiflawi 2006). Size-dependent mortality implies that mortality during small egg and juvenile stages is so high that a little extra investment in offspring size drastically increases survival because it allows one to skip the smallest and most vulnerable size classes. For large offspring, there is only a small increase in survival for each marginal increase in offspring size, which explains the diminishing returns assumed by Smith and Fretwell (1974; see also Kiflawi 2006).

Since our model generates the sigmoid relationship between offspring size and offspring fitness, it also yields the same relationship between offspring size and maternal fitness illustrated by Smith and Fretwell (1974). By considering the marginal value of a further investment in offspring size, the intersection of the tangent in Smith and Fretwell's (1974) model corresponds to peak maternal fitness (see fig. 2A). The fitness function for the mother can also be calculated as the survival of each offspring multiplied by the number of offspring produced, which is the inverse of the mass of each offspring (eq. [3]). Figure 2B shows how the relationship between offspring size and offspring survival integrates with the number of eggs that are produced to yield our estimate of maternal fitness (see also fig. 2B in Smith and Fretwell 1974). Finally, we rescale maternal fitness to offspring length rather than offspring weight to make it easier to interpret the equations alongside the figures (fig. 2C). Because length is proportional to the cube root of weight, the fitness curve in terms of offspring length looks somewhat different but has the same characteristics. A consequence of this rescaling is that the early acceleration in maternal fitness as a function of offspring size becomes more visible. In conclusion, our model duplicates the assumed relationships and key results of Smith and Fretwell (1974), but here they emerge from explicit mechanisms of growth and mortality rather than as a consequence of assumed relationships.

Beyond Smith and Fretwell: Effects of the Relationship Scaling Mortality with Size

The sigmoid offspring fitness curve assumed by Smith and Fretwell (1974) arises only in a subset of parameter space:

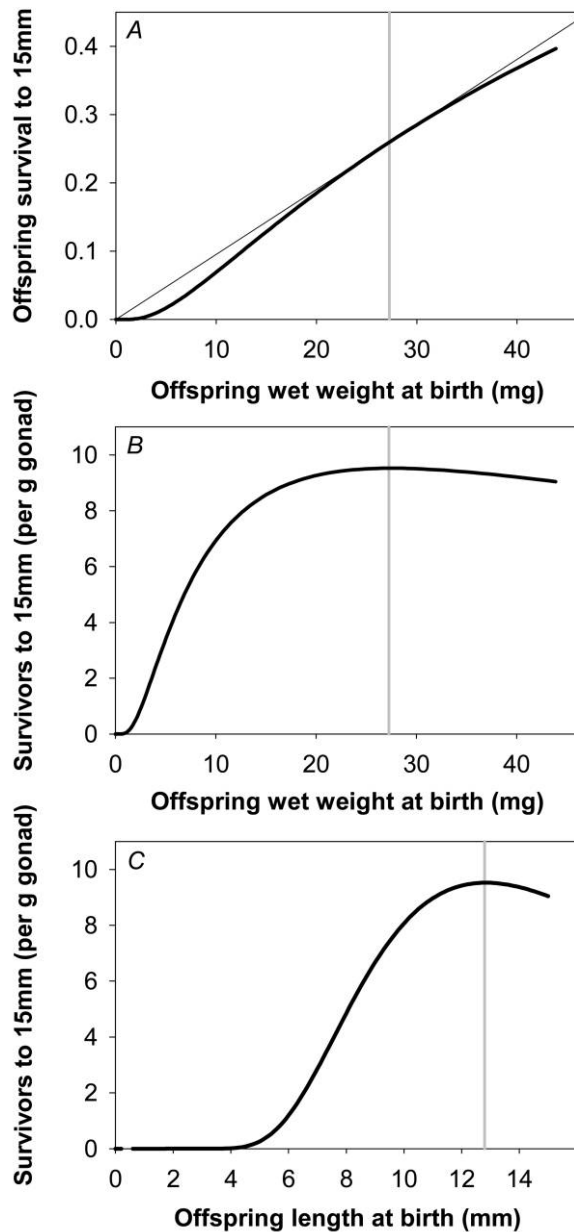


Figure 2: Every big fish starts out small, and its survival during early life stages has consequences for fitness. *A*, The offspring's perspective on fitness is its survival probability, here evaluated until it reaches a length of 15 mm (*thick black line*). The probability that an offspring reaches 15 mm increases with size at birth; the bigger the better. Mother's perspective on fitness: mothers have to trade the survival of each offspring against the total number of offspring she can make. Following Smith and Fretwell (1974), the intersection between the tangent (*thin black line*) through the origin and the survival curve is the point that maximizes the mother's fitness. *B*, The location of maximum maternal fitness is easier to visualize by dividing by offspring weight, since the result becomes the number of surviving offspring per unit of maternal gonads. *C*, Same as in *B* but rescaled

when the scaling exponent for the size-dependent mortality (b in eq. [8]) is sufficiently steep. When the scaling is less steep, the offspring size–offspring fitness curve can be either concave down or concave up, depending on whether mortality is low or high, respectively (fig. 3; the panels in this figure are actually four different versions of fig. 2A in different regions of parameter space). Only when the curve is sigmoid (fig. 3B) does the model predict an intermediate optimal offspring size; otherwise, the model predicts that offspring should be either the smallest (fig. 3A, 3D) or the largest (fig. 3C) size, as defined by the model limits.

With regard to maternal fitness, the model can be solved for different values of the parameters in the mortality-size scaling relationship, the a and the b of equation (8). Figure 4 illustrates optimal offspring size from the mother's perspective for different regions of parameter space. To make the figure easier to interpret, the Y-axis is scaled so that an offspring of 8-mm length has the same mortality along each horizontal line. As the absolute value of the scaling exponent increases (toward the right), smaller sizes will have higher mortality, while larger offspring will have lower mortality. Figure 4 can be divided into three regions. There is one region for positive scaling exponents b and slightly negative exponents b when mortality is low; in this region, the optimal offspring size approaches 0. This corresponds to the situation in figure 3A. There is also a region for intermediate scaling exponents and high mortality in which the optimal offspring size increases asymptotically; in this region, mortality is so high for most size classes that it becomes optimal for the mother to shield her offspring from this mortality by making sure they are large at birth. This corresponds to the situation in figure 3C. For more negative exponents b , the fitness curve is sigmoid, as in the study by Smith and Fretwell (1974) and our figure 3B, and in this region optimal offspring size is intermediate and variable.

Effects of Growth Rate

Growth rate is important for fitness during early life stages because it determines the duration of time juveniles must spend in the more vulnerable smaller size classes. Faster growth means that the high mortality rates need to be sustained over a shorter time interval. Consequently, as growth rate goes up, the optimal offspring size goes down (fig. 5A). In contrast, if growth conditions worsen, the

to offspring length at birth (mm) on the X-axis. The gray vertical lines indicate the optimal solution. Parameters: $a = 12.3$, $b = -2.55$ (situation 2 in table 1; mortality as in McGurk 1986 for pelagic fish eggs and larvae), $c = 1.3 \times 10^{-5}$, $q = 3$, $g = 0.2$, $l_0 = 15$.

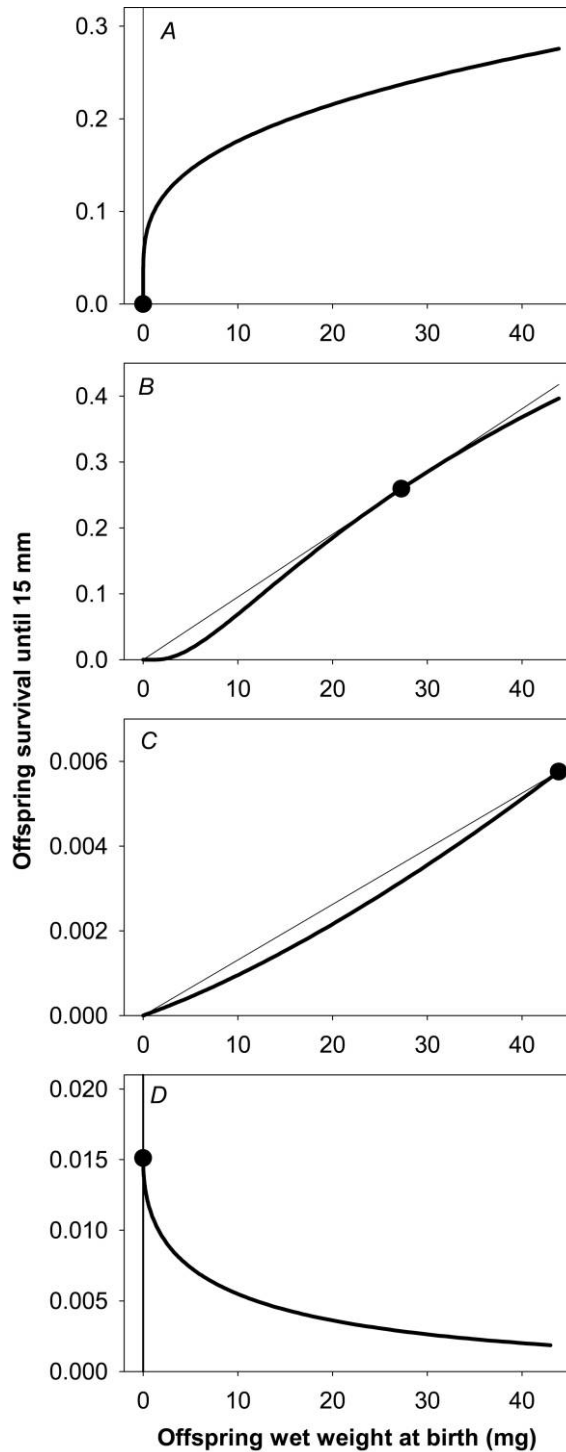


Figure 3: Different outcomes of the function for offspring fitness (defined as the probability of survival until 15 mm). The shape of the survival curve (thick black line) depends on parameters a and b of the mortality scaling relationship. *A*, For positive scaling exponents b and slightly negative b with low values of a , offspring fitness is

mother can offset the increased time her juveniles spend in these smaller size classes by giving birth to larger offspring. Although she would then be able to make fewer offspring, the advantage in terms of survival outweighs the cost in terms of number of offspring.

For example, at a biologically reasonable growth rate of 0.2 mm day^{-1} (Houde 1989), the optimal strategy is to produce offspring that are 12.8 mm at hatch, but if growth is twice as fast, the optimal offspring size is reduced to 8.2 mm (fig. 5A). In mass, this corresponds to a reduction from 27 to 7 mg, which has large consequences for the number of eggs that can be produced per unit weight of gonad tissue and thus for the overall fecundity of the mother. This extends the perspective of the match-mismatch hypothesis (Cushing 1990), which predicts best recruitment if spawning matches peak production of food for offspring. Because of the strong influence of growth on optimal offspring size, there is also a need for egg sizes to match expected offspring growth rates.

Egg Guarding and Live-Bearing

The model predicts a larger optimal offspring size when the egg-guarding parent or the live-bearing mother is larger (fig. 5B). We will interpret this pattern with respect to live-bearing, but the logic is the same for egg-guarding strategies. The instantaneous mortality of the egg is determined not by its own size but by that of its mother. The egg stage thus becomes safer as the size of the mother increases and her mortality risk subsequently decreases. For large mothers, it is therefore beneficial to produce large eggs that take longer to develop but do so in a safer environment. In contrast, a small mother represents a riskier environment for developing young, so there is a greater advantage to producing smaller eggs that then take less time to develop. This reasoning is in line with the logic of the safe harbor hypothesis (Shine 1978), where higher mortality during the egg stage (small mothers) should translate to less time during that phase and consequently

concave down. From the parent's point of view, the optimal offspring size (black circle) is small ($a = 0.131$, $b = -0.75$; corresponding to situation 1 in table 1 and fig. 4). *B*, When the scaling relationship is steeper, it is optimal for the mother to produce offspring of intermediate size ($a = 12.3$, $b = -2.55$; pelagic fish eggs and larvae; situation 2 in table 1 and fig. 4). *C*, If mortality is high but the scaling less steep, the fitness function becomes concave up. In this case, large offspring are optimal from both the parent's and the offspring's point of view ($a = 0.524$, $b = -0.75$; same scaling but mortality four times as high as in situation 1). *D*, If mortality is positively size dependent, survival may be highest if offspring are born small because mortality during the egg stage is lower ($a = 0.0216$, $b = 0.5$; same mortality at 8 mm as in situation 2 but with positive scaling). Thin black lines are tangents as in figure 2. Other parameters as in figure 2.

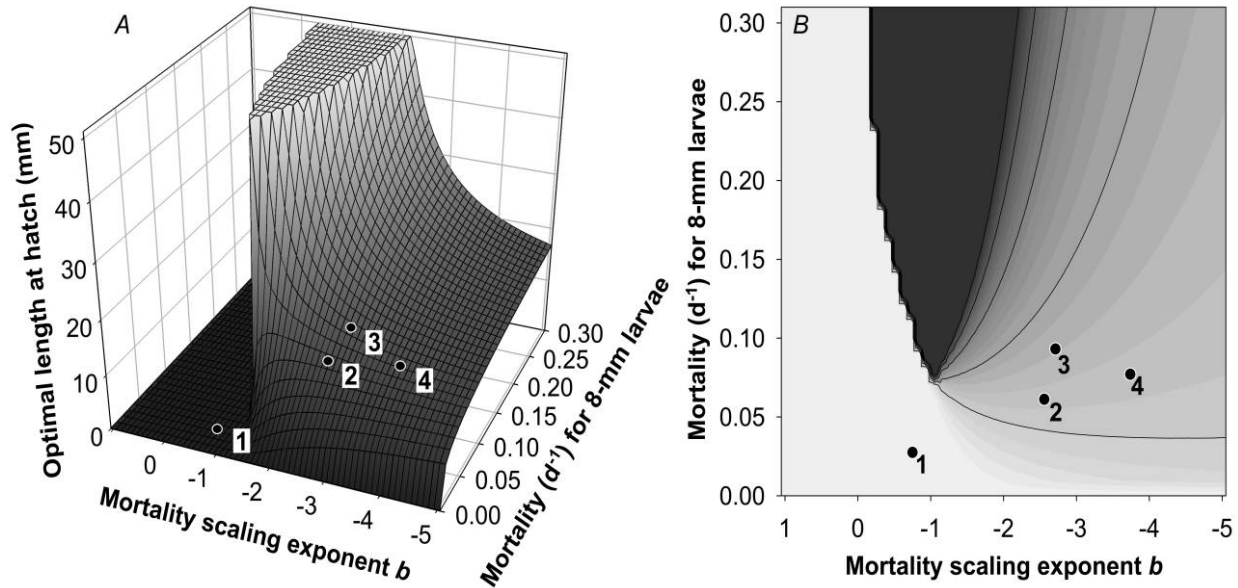


Figure 4: Optimal offspring size (mm) for fish eggs as it varies with exponent b of the allometric relationship that scales mortality with body size and with the daily mortality rate $m_{8\text{mm}}$ for a larvae of $l = 8$ mm. Coefficient a can be found as $a = m_{8\text{mm}} \times 8^{-b}$. *A*, Three-dimensional surface plot of optimal offspring size. *B*, Same as *A* but viewed directly from above as a contour plot. The plateau is a region of parameter space where it is optimal to produce a few very large offspring. The points are coefficients and exponents for the mortality scaling of (1) adult and juvenile marine fish (McGurk 1986), (2) marine fish eggs and larvae (McGurk 1986), (3) high-predation guppies, and (4) low-predation guppies. Parameters as in figure 2 except $l_0 = 50$ to show more dynamics.

a smaller offspring size at birth. Interestingly, the model of Parker and Begon (1986) also predicted that larger mothers should produce larger eggs, but for a different reason: sibling competition within a brood. When the same phenomenon can be produced by several distinct mechanisms, it is essential to be aware of the causal relationships in order to understand, interpret, or manipulate nature.

Adaptations That Reduce Egg Mortality

Next we consider parental strategies that reduce egg mortality without the continued presence of a parent, such as armored morphology or positioning of eggs in particularly sheltered habitats. In such cases, egg survival $s_e(l_h)$ depends both on the duration of egg development and, in contrast to cases of egg guarding or live-bearing considered above, on the size-dependent mortality rate of the egg. With the assumptions in our model, the total accumulated mortality during the egg stage is the product of the mortality rate and the duration of development and therefore depends on length at hatch as $m_e(l_h) \times d(l_h) \propto l_h^{b+1}$. Mortality during the egg stage is therefore independent of length at hatch if $b = -1$ and will decrease with l_h if $b < -1$. With the McGurk (1986) parameters for pelagic fish eggs and larvae,

$b = -2.55$ such that the total mortality during the egg stage scales as $l_h^{-1.55}$. From the offspring's perspective, a larger size at hatch therefore decreases the total mortality accumulated in the egg stage. In other words, when $b < -1$, producing a larger egg has an advantage in lowering the size-dependent mortality rate on the egg that more than outweighs the disadvantage of prolonged development times.

Predictions for how adaptations that reduce egg mortality will affect optimal offspring size therefore depend on the scaling exponent b (fig. 5C). In the case of $b = -1$, egg mortality does not depend on egg size, adaptations that reduce egg mortality will not change the shape of the curve, and the optimal offspring size is independent of the level of egg mortality. When $b < -1$, smaller offspring size is optimal (fig. 5C). This is because the mother's perspective on fitness is different from that of the offspring. When eggs are not protected by parental strategies, mothers must accept the cost of producing larger offspring partly because it reduces mortality during the egg stage. However, when size-dependent egg mortality is reduced by sheltered habitats or protective armor, she can produce more eggs that are smaller but still have the same survival as unprotected eggs. At first glance, this is seemingly in contrast to the effect of live-bearing and egg guarding

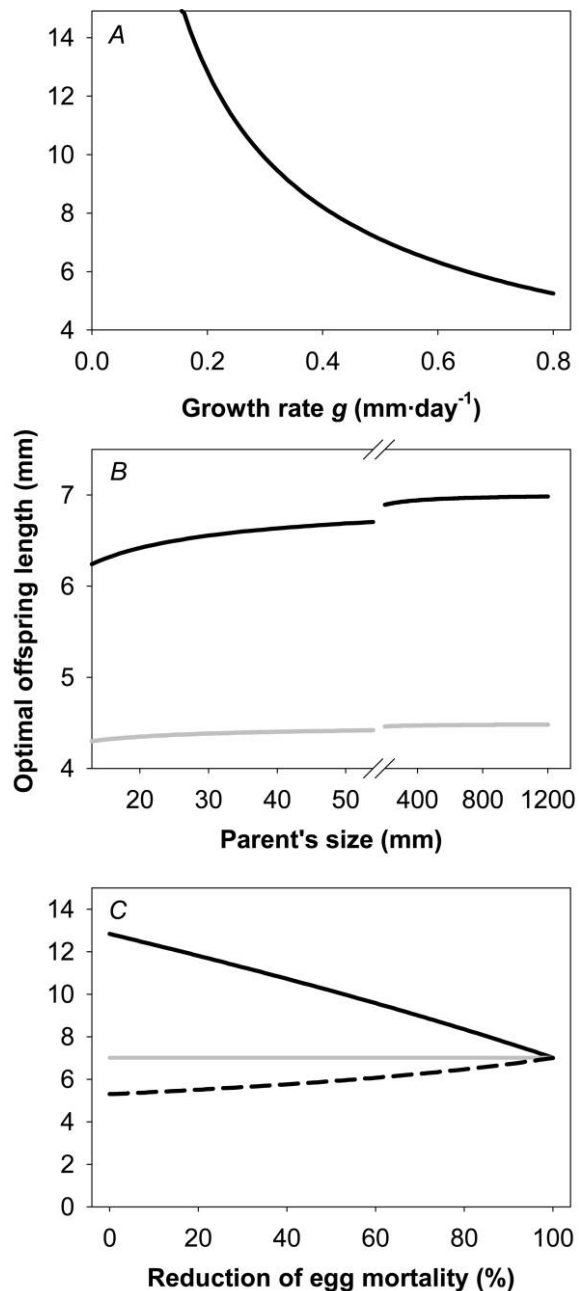


Figure 5: A, Effect of growth rate on optimal offspring size at birth. When growth conditions are better, it becomes optimal for the mother to produce more numerous but smaller-sized offspring (mortality as in situation 2 in table 1). B, For live-bearers or species that guard their eggs, the eggs have the same mortality rate as the mother or the guarding parent, respectively. Here it is assumed that free-living juvenile mortality follows McGurk's (1986) relationship for pelagic fish eggs and larvae (situation 2 in table 1), while the parent's mortality scales as the general scaling relationship for fish (McGurk 1986; situation 1 in table 1). Results for two growth rates are shown: $g = 0.2$ mm day⁻¹ (black line) and $g = 0.4$ mm day⁻¹ (gray line).

above, where larger parents have lower mortality rates and should produce larger offspring. However, the difference lies in the fact that with independent eggs, the mortality rate is set by egg size, whereas for live-bearing, it is the mother's size that defines the mortality rate during the egg stage (within the mother, an egg can be any size and still have the same mortality rate). When total mortality during the egg stage increases with egg size, as was the focus of Sargent et al. (1987) and in our model happens when $b > -1$, then adaptations that reduce the overall egg mortality will make the optimal offspring size increase (fig. 5C).

Although we have included predictions for live-bearing and adaptations that reduce egg mortality rates, there are several forms of parental care that we have not considered. For example, we have omitted care that affects juvenile feeding rate, since that would require relatively extensive modifications of our model. This means that we exclude, for example, the guarding of foraging offspring by a mouth brooder. Another example of parental care that we have omitted is fanning and cleaning for the purpose of avoiding fungal and parasite infections or to achieve adequate oxygenation (Green and McCormick 2005). In that case, egg survival depends partially on the survival of the parent, as with live-bearers above, but also on factors that are independent of the parent, as in the predictions in figure 5C. Our two modeled scenarios are thus endpoints of a continuum where species that fan and clean eggs lie somewhere in between.

Optimal Offspring Size in Guppies

Guppies are an interesting test case because mortality is size dependent (Reznick et al. 1996), but mortality rates in nature are confounded by systemic variation in growth rates (Reznick et al. 2001). Guppy populations are effectively thinned in high-predation environments, and the per capita food availability is high. Low-predation environments have low mortality rates, but because guppy densities are higher, they also have lower growth rates compared with guppies from high-predation sites.

Using parameters for guppies, the model predicts the two main patterns also found with the general parameterization: (1) for any given growth rate, guppies from

C, Effect of reduced egg mortality on optimal offspring size depends on the scaling relationships. With $b < -1$, adaptations that reduce egg mortality (moving along the X-axis) make it optimal for the mother to produce smaller offspring (solid black line; situation 2 in table 1). With $b > -1$, the relationship is the opposite, and the model predicts that reduced egg mortality would lead to larger offspring size ($b = 0$; dashed black line). For $b = -1$, egg mortality is inconsequential for the evolution of offspring size (gray line).

high-predation sites should produce larger offspring (except for the very highest growth rates), and (2) offspring should be smaller when growth is faster (fig. 6). Mortality differences alone would thus predict that low-predation guppies should produce smaller offspring, yet in nature they produce larger offspring: offspring in low-predation fish can be as much as 65%–70% heavier at birth than those from high-predation sites (Reznick and Endler 1982). Because growth and mortality covary in nature, their combined effect is that guppies from low-predation sites (with slow growth) should produce larger offspring than guppies from high-predation sites (where growth is faster; fig. 6). This conclusion holds qualitatively when we use both laboratory (Reznick 1983) and field (Reznick et al. 2001) estimates of growth rate, but the exact prediction of size at birth depends on the growth characteristics. It thus appears that growth rate and mortality rate both have shaped the evolution of offspring size in guppies.

General Discussion

A reproducing female can in theory produce more offspring by reducing the size or quality of each of them. Whether this would actually lead to more descendants and a positive effect on fitness depends on the future prospects of each of the offspring. Since the life-history decision of how to partition reproductive investment lies with the

female, the offspring size that is favored by natural selection is the one that maximizes her fitness, the optimal offspring size from the mother's perspective often being very different from the one that is best for each of her offspring. The evolutionary consequences of this trade-off have been studied in numerous models, with most of them derived from or built upon the work of Smith and Fretwell (1974). Although these models have provided great insights into factors that influence the evolution of offspring size (e.g., Brockelman 1975; Parker and Begon 1986; Kiflawi 2006), a main weakness was that Smith and Fretwell (1974) based their model on a sigmoid curve for offspring fitness that was substantiated only by a verbal argument; it was not linked explicitly to quantifiable or observable ecological mechanisms. Repeating an assumption many times does not make it true, so in this article we derive the sigmoid curve from first principles by focusing on size-dependent mortality and growth rate. With these mechanisms, we show how the Smith and Fretwell curve emerges in a relatively wide region of parameter space. As often happens when a mechanism is included directly, we can extend predictions to new domains such as live-bearing, egg guarding, and adaptations that reduce mortality during the egg stage. Some of these predictions align with earlier models, whereas some seem counterintuitive at first glance.

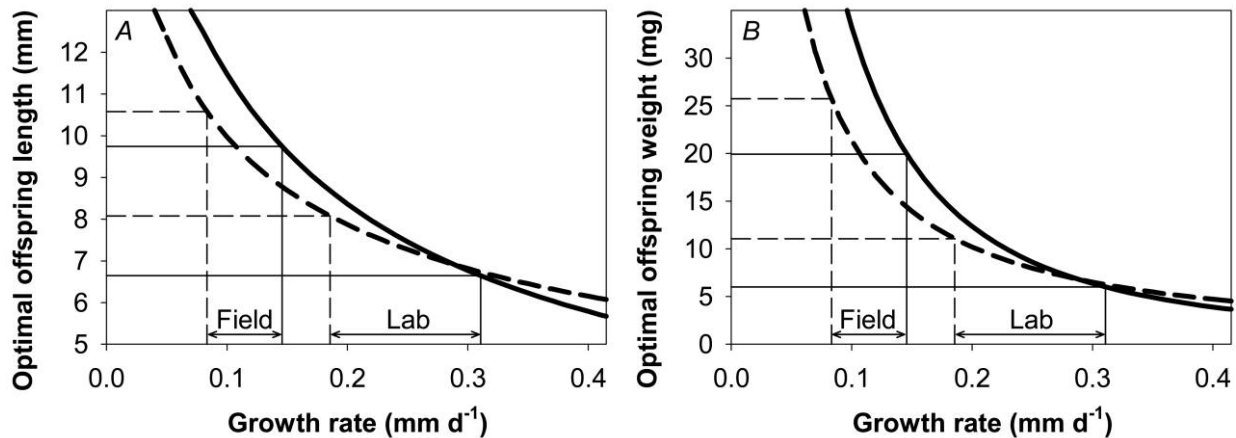


Figure 6: Optimal offspring length at birth (A) and weight at birth (B) for guppies from high-predation (*solid lines*) and low-predation (*dashed lines*) environments. The thin lines illustrate observed growth rates in high-predation (*solid lines*) and low-predation (*dashed lines*) environments and the corresponding optima for offspring size, given for both lab (Reznick 1983) and field (Reznick et al. 2001) estimates of growth rate (*arrows*). Conditions for growth and predation are confounded in nature so that high-predation guppies also experience the highest growth rates. For this reason, high-predation guppies are here predicted to produce smaller offspring than low-predation guppies, although the optimum is to produce offspring of larger size if they were in the same growth environment (except for the very highest growth rates, where the lines cross). For comparison, observations of offspring in the field are in the range 4.3–6.7 mg wet weight (6.0–6.9 mm) in high-predation localities and 7.3–10.4 mg wet weight (7.1–7.9 mm) in low-predation localities. Parameters: $c = 1.61 \times 10^{-5}$, $q = 3.128$, $l_b = 13$ mm, $L = 25$ mm.

From Static to Size-Dependent Mortality

Mortality rates and their distribution across early life stages played a central role in earlier models of life-history evolution. Williams (1966) identified mortality as an important factor because early life stages generally suffer higher mortality rates. He noted that successful strategies, when viewed in a whole life cycle perspective, minimize the time spent in the stages with highest mortality. Shine (1978) formalized the relationship between mortality rate and time spent in each life stage in his safe harbor hypothesis. Although Shine's model was designed to explain the positive correlation between offspring size and parental care, the main effect of parental care was assumed to be increased offspring survival. Assuming fixed mortality rates for the egg and the juvenile stage, he predicted that optimal strategies would produce either no investment or maximum investment, depending on which stage had the higher mortality rate, but nothing in between.

All organisms need to grow and survive, and survival during early life stages is the key portal to future fitness. Our model is centered on the widespread observation that mortality declines with size and often rapidly so for early life stages (McGurk 1986). This implies an important role for growth, since individuals that grow fast will also reduce their mortality rates quickly. Our model aligns with that of Kiflawi (2006), since both include ubiquitous and measurable ecological relationships to arrive at quantitative predictions. In this article, we also take it a step further and predict consequences of reproductive strategies that modify survival during the egg stage, which may lead to parental effects.

Lessons from Guppies

Guppies from high-predation streams consistently produce smaller offspring relative to guppies from areas with fewer predators. Field data and common garden laboratory experiments have demonstrated that differences in offspring size between populations in these different environments are genetically determined and have evolved repeatedly across multiple drainages (Reznick 1982; Reznick and Bryga 1996). When we model the effects of predation alone, our model predicts that high-predation guppies should produce larger, rather than smaller, offspring. It is only when we add in differences in juvenile growth rate that our model predicts that guppies from low-predation environments should produce larger offspring. This result is an example of the more general property of our model. Predicting optimal offspring size just on the basis of the trade-off between egg size and fecundity, as done by Smith and Fretwell (1974), falls short of capturing the true complexity of the interactions that shape the evolution of off-

spring size. One must also consider the mode of reproduction, the risk of mortality before birth/hatching, and the risk of mortality after birth/hatching. A benefit from including the mechanisms of predation and growth directly is that the underlying relationships can be measured in the field, which allows one to move from qualitative to quantitative predictions.

On the Evolution of Live-Bearing

Although live-bearing (viviparity) is found in ~2%–3% of bony and ~55% of cartilaginous fishes (Wourms and Lombardi 1992), Turner (1947, p. 508) observed, "There seems to be no relation between the development of viviparity and ecological conditions." During live-bearing, the parental mortality rate also applies to the developing brood as they would die together with the mother. This suggests that both the growth and the mortality of the offspring need to be evaluated together with the mortality rate of the mother to quantify when live-bearing could confer a selective advantage and that a demographic perspective may be a different and productive way to consider why live-bearing has evolved so many times in fishes but under such a diversity of ecological settings.

From the perspective of our model, one advantage of live-bearing is that the developing embryos experience a lower mortality rate inside the mother than if placed somewhere in the external environment. This may be more important if the developmental phase before hatching or birth is long. One might, therefore, expect that the ecological conditions that favor large offspring in our model might also favor live-bearing. As noted by Wourms and Lombardi (1992), live-bearing also confers advantages to the young in terms of osmoregulation, excretion, respiration, and immune defense, and these factors may of course act on top of the effects of predation and growth on which we focus in this article. To this list, one could also add that live-bearing may allow the developing offspring to experience a different temperature regime. For example, in temperate waters, embryos may develop faster inside a mother that can be in warm waters close to the surface, as opposed to eggs deposited in colder bottom waters.

Plasticity to Environmental Signals

Organisms often exhibit plasticity in offspring size and development time in response to variation in both growth conditions and mortality risk. With regard to growth conditions, many species are known to increase their investment in offspring size when conditions worsen (Bashey 2006). For example, Reznick et al. (1996) observed that lecithotrophic species (provisioning to the egg provided

before fertilization) responded to reduced food availability by producing larger eggs, in accordance with our model. Mothers are also known to modify the developmental period of their offspring in response to predation risk. For example, female guppies responded to increased predation risk by releasing their offspring earlier (Evans et al. 2007). Although we did not model this explicitly, this result is consistent with the maternal effect on offspring size in live-bearers (fig. 5C), where smaller mothers (suffering higher mortality) give birth to smaller offspring after shorter development times.

Seasonal Variation

That eggs should be smaller as productivity or temperature increases also corresponds to Ware's (1975) observation that many marine species produce larger eggs in winter, while eggs become progressively smaller toward spring and summer. It is worth noting, however, that seasonality can also provide strong constraints on when it is favorable for the offspring to be born or when it is favorable for the parent to reproduce (e.g., Reznick et al. 2006; Varpe et al. 2007). In particular, peaks in productivity can give rise to especially fruitful windows for offspring growth and development, which may lead parents to reproduce at times or in manners that are not ideal for their own needs (Varpe et al. 2007). Such parent-offspring conflicts may shift the optimal offspring size away from the optimum predicted by our model or lead to additional types of seasonal variation in optimal offspring size.

A Restricted Potential for Parental Effects

There is evidence for parental effects in some commercial fish stocks, where larger or older mothers have better-quality offspring (Berkeley et al. 2004). Our model predicts that the parent's mortality rate has consequences for optimal offspring size if there is live-bearing or guarding of eggs/offspring involved. When we parameterized parent survival with the general relationship obtained for adult and juvenile fish by McGurk (1986), the effect of parent size was most pronounced for small fish. For parents smaller than ~10 cm, one could expect size-dependent parental effects. One such small live-bearing species is the northern shrimp *Pandalus borealis*, which may reach a maximum length of 12 cm; females carry the developing eggs for 236 days at 2°C, a typical temperature in their environment (Brillon et al. 2005). For larger parents, however, huge size differences translate to only minor differences in optimal offspring size, meaning that parental effects would be rare or even unlikely by the mechanisms in our model alone. Consequently, the mechanisms investigated in this article fall short of explaining why there

are parental effects in larger-bodied fish. Some parental effects may arise when different habitats have different optima for offspring size (Hendry et al. 2001). In salmonids, oxygen limitation may reduce survival, particularly for large eggs. There are differences between habitats in water flow, and larger mothers tend to obtain better territories. Due to such a chain of events, it can be optimal for larger mothers to produce larger eggs. This type of habitat-mediated effect is also likely to be at play for larger fish.

Further Factors Affecting Offspring Size

When confronting a topic as complex as the evolution of offspring size, it is important to acknowledge the many ecological mechanisms that affect it and consequently make only humble claims in support of a simplified theoretical approach. Several processes not discussed above may further influence the evolution of offspring size. First, competition among young is often size-dependent in favor of large individuals (Brockelman 1975), particularly in stream fish such as salmonids (Einum and Fleming 2000) and guppies (Bashey 2008). Bashey (2008) demonstrated that size differences at birth within wild populations of guppies were not only maintained but were also amplified under higher competition during the juvenile life stage. This effect was strongest in populations from low-predation environments, which usually have higher densities of guppies and more intense resource competition. Similar conclusions were reached for a marine colonial invertebrate (Allen et al. 2008). Although differences in growth and size-dependent mortality may be sufficient to explain the direction and magnitude of offspring size in guppies, there may be additional consequences of intraspecific competition that modify the predictions of our model. Specifically, low-predation populations of guppies often have a higher density and more intense competition for food, which could favor larger offspring over and beyond the effects of growth and mortality that we modeled. Second, Winemiller and Rose (1993) showed that small eggs are adaptive when conditions for growth or survival are correlated on relatively large spatial scales, which is often the case in pelagic systems where productive patches can be separated by less productive stretches of the ocean. McGurk (1986) arrived at similar conclusions. This patchiness basically acts as a lottery, where the number of tickets increases the chance of winning. Such a lottery favors bet-hedging strategies, where parents that produce a high quantity of young may produce the lucky winners, but the provisioning to each one of them is of less importance. Tian et al. (2007) demonstrated a similar effect resulting from size-dependent mortality acting repeatedly throughout ontogeny. With individual-based simulations, they

showed that the surviving larvae from a cohort of pelagically spawned eggs were the ones that by chance had good conditions for growth early in life. Bet-hedging strategies have also been shown to favor diversity in offspring size within a brood (Crean and Marshall 2009). Third, fertilization kinetics may influence optimal offspring size, particularly in broadcast-spawning species (Levitan 1993, 1996). Fourth, offspring size may also be subject to constraints on egg buoyancy, especially where pelagic dispersal at the egg stage favors eggs with oil globules or high water content to obtain low gravity (Kjesbu et al. 1992). Each of these mechanisms may act on top of the mechanisms of growth and mortality included in our model, but in no case is fitness independent of growth and mortality. This is why we argue that our model can be perceived as a baseline for making predictions and that cases where it makes the wrong predictions may be as enlightening as cases where the model makes predictions closer to observations.

Acknowledgments

We thank F. Bashey and reviewers for comments that improved the manuscript. C.J. thanks the Research Council of Norway for funding to stay at University of California–Riverside and the members of the Reznick lab and their colleagues for a stimulating scientific and social environment. S.K.A. was funded by a Nordic Research Opportunity grant from the National Science Foundation (NSF) and the Research Council of Norway. D.N.R. was supported by grants DEB0416085 and EF0623632 from the NSF.

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Associate Editor: Peter D. Taylor
Editor: Mark A. McPeck



Top, photo shows a pair of guppies *Poecilia reticulata* in their native stream habitat on the island of Trinidad, West Indies. Above is a colorful male, below is a pregnant female. Guppies are live-bearers, meaning that they have internal fertilization, after which the female carries the offspring as they develop, attached to a placenta-like structure. Size at birth varies between guppy populations, and in this article it is argued that the growth environment and the size-specific scaling of predation mortality both contribute to predict the optimal offspring size. Photograph by Paul Bentzen (all rights reserved). *Bottom*, this larva of the Atlantic cod *Gadus morhua* hatched 1 day earlier, after about 2 weeks of development inside the egg. At a length of only 5 mm, it will now begin a free-living phase in the vast pelagic, hunting for zooplankton to feed on as it drifts with the currents. Photograph by Arild Folkvord (all rights reserved).