OFFSPRING SIZE VARIATION WITHIN BROODS AS A BET-HEDGING STRATEGY IN UNPREDICTABLE ENVIRONMENTS

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Abstract. Offspring size is strikingly variable within species. Although theory can account for variation in offspring size among mothers, an adaptive explanation for variation *within* individual broods has proved elusive. Theoretical considerations of this problem assume that producing offspring that are too small results in reduced offspring viability, but producing offspring that are too large (for that environment) results only in a lost opportunity for increased fecundity. However, logic and recent evidence suggest that offspring above a certain size will also have lower fitness, such that mothers face fitness penalties on either side of an optimum. Although theory assuming intermediate optima has been developed for other diversification traits, the implications of this idea for selection on intra-brood variance in offspring size have not been explored theoretically. Here we model the fitness of mothers producing offspring of uniform vs. variable size in unpredictably variable environments and compare these two strategies under a variety of conditions. Our model predicts that producing variably sized offspring results in higher mean maternal fitness and less variation in fitness among generations when there is a maximum and minimum viable offspring size, and when many mothers under- or overestimate this optimum. This effect is especially strong when the viable offspring size range is narrow relative to the range of environmental variation. To determine whether this prediction is consistent with empirical evidence, we compared within- and among-mother variation in offspring size for five phyla of marine invertebrates with different developmental modes corresponding to contrasting levels of environmental predictability. Our comparative analysis reveals that, in the developmental mode in which mothers are unlikely to anticipate the relationship between offspring size and performance, size variation within mothers exceeds variation among mothers, but the converse is true when optimal offspring size is likely to be more predictable. Together, our results support the hypothesis that variation in offspring size within broods can reflect an adaptive strategy for dealing with unpredictably variable environments. We suggest that, when there is a minimum and a maximum viable offspring size and the environment is unpredictable, selection will act on both the mean *and* variance of offspring size.

Key words: egg size; environmental variation; life history; marine invertebrates; maternal effect; offspring size–fitness; optimality; reproductive strategy; seed size; unpredictable environments.

INTRODUCTION

For over 50 years, biologists have sought to understand the remarkable variation in offspring size among species (Lack 1947, Bagenal 1969), and the study of offspring size has become an important branch of life-history research (Stearns 1992). The resources available to mothers are finite, so they can produce either many small or fewer, large offspring. Larger offspring typically have higher fitness than smaller offspring, thereby offsetting any decrease in fecundity. Smith and

Fretwell (1974) produced one of the first theoretical examinations of how mothers optimally balance the size and number of offspring they produce. Their classic study has formed the basis for most theory on offspring size/number trade-offs, and most models published since share a number of features with their original work. These models typically derive the best maternal allocation strategy assuming a trade-off between offspring size and number and a positive correlation between offspring fitness and offspring size (e.g., Vance 1973, Smith and Fretwell 1974, Sargent et al. 1987). The general prediction from this work is that, under constant environmental conditions (and thus a constant offspring size–fitness relationship), a single offspring size will be optimal. However in nature, offspring sizes are extremely variable within populations, and offspring size can be correlated with a number of maternal factors such as body size or nutrition (Turner and Lawrence 1977).

While the earliest models could not account for such variation, more recent models incorporating the effects of maternal phenotype on the natal environment successfully predict the observed variation in offspring sizes among different mothers (e.g., Parker and Begon 1986, Hendry et al. 2001, Sakai and Harada 2001). Empirical evidence supports these models. For example, in species of fish where the maternal phenotype can affect the offspring size–fitness relationship, offspring size variation within populations is relatively high (Einum and Fleming 2002). Similarly, Fox et al. (1997) showed that when mothers can detect the likely environment of their offspring, they adjust the size of their offspring accordingly, suggesting that interindividual variation in offspring size represents an adaptive maternal effect.

Although theory can now account for variation in offspring size among mothers, explaining variation in the size of offspring from the same mother remains problematic. Offspring size shows remarkable variation within individual broods in many taxa (Turner and Lawrence 1977, Williams 1994, Fox and Czesak 2000, Kudo 2001, Marshall et al. 2003). There are numerous verbal arguments for producing offspring that vary in size (e.g., Capinera 1979, Crump 1981, Lips 2001). In such considerations, within-brood variation is viewed as a form of bet-hedging in which females ensure that at least a few offspring approach the optimum in some unpredictable future environment (Koops et al. 2003). However, the few formal models of within-brood offspring size variation do not support such an adaptive explanation for this variation (McGinley et al. 1987, Einum and Fleming 2004b, but see Geritz [1995] for a rare exception using a game theoretic approach). In most instances, producing a single offspring size within each brood is predicted to be optimal (note that Vance [1973] and similar models predict two optima, but one of these is simply a product of infinitely small offspring retaining some fitness: an unrealistic situation). In the few cases where producing variably sized offspring within broods is favored in these models, it is under restrictive and improbable conditions. For example, McGinley et al. (1987) found that producing offspring of variable size was only advantageous when mothers could strictly control the dispersal of their offspring. Similarly, Einum and Fleming (2004b) found that within-brood offspring size variation (described as diversified bet-hedging) was a less effective strategy than producing very large offspring (described as conservative bet-hedging) for coping with environmental uncertainty. Consequently, within-brood variation in offspring size is increasingly viewed as a product of physiological constraints that prevent mothers from producing offspring of identical size, rather than as an adaptive strategy (Fox and Czesak 2000, Einum and Fleming 2004b). In their review of offspring size effects in insects, Fox and Czesak (2000:358) concluded that "... some authors have suggested that at least some of

the variation within families is an adaptive response to living in a variable environment. At this time however, there are few experimental studies and too little theoretical work to generalize." Thus, despite the intuitive appeal of intra-clutch variation in offspring size as a mechanism for coping with environmental heterogeneity, theoretical support for the concept remains elusive.

While offspring size theory has struggled to account for within-brood variation in offspring size, parallel developments in the more general theory of bet-hedging have long predicted a selection advantage for producing offspring with variable phenotypes. Cohen's (1966) classic model and others since have shown that when the environment varies unpredictably, mothers should produce offspring with a range of phenotypes either in a single reproductive bout (Gillespie 1977, Bull 1987, Simons and Johnston 2006) or across multiple reproductive bouts (Cooper and Kaplan 1982). Thus, we face the puzzling situation where general theory predicts a selection advantage for variation in offspring traits, but specific theory for offspring size typically does not.

The nature of optimality models may be partly responsible for the prevalence of theory showing that within-brood offspring size variation is not adaptive. Most optimality models use highly asymmetrical offspring fitness functions whereby, as offspring size increases, offspring fitness increases with diminishing returns, or levels off at a constant maximum value (Smith and Fretwell 1974, McGinley et al. 1987, Einum and Fleming 2000, 2004b). In contrast, more general models of bet-hedging assume a symmetrical, curvilinear relationship between offspring phenotype and fitness such that there are fitness penalties at each end of the offspring phenotype continuum (e.g., Cohen 1966, Cooper and Kaplan 1982). We suggest that offspring size models using an asymmetrical function are unrealistic and underestimate the benefits of a diversified bet-hedging strategy in unpredictable environments while overestimating the benefits of a conservative bet-hedging strategy (i.e., producing offspring of a constant, large size).

The use of a Smith-Fretwell fitness function is problematic because it assumes that above a certain size, larger offspring (including infinitely large offspring) have equal fitness. Therefore, the only fitness cost to mothers of producing large offspring is a reduction in fecundity. In nature, however, offspring exceeding a certain size will have lower fitness due to physiological or anatomical constraints (Strathmann and Chaffee 1984, Congdon and Gibbons 1987, Kaplan 1992, Strathmann 1995, Bernardo 1996), increased predation risk (Dibattista et al. 2007), or an increased risk of polyspermy (Styan 1998, Marshall et al. 2002). Thus, offspring are likely to suffer a direct fitness cost if they are too small *or too large* for their environment. If the environment varies unpredictably, then a conservative bet-hedging strategy (i.e., simply producing larger

offspring) is unlikely to insulate mothers from this unpredictability because excessively large offspring will suffer reduced fitness. Furthermore, with direct fitness costs on both sides of an optimum, the benefits of producing variably sized offspring may be increased in unpredictable conditions. The benefits of within-brood offspring size variation have not been modeled under the assumption that both very small and very large offspring suffer reduced fitness.

Here, we compared the fitness of mothers employing contrasting reproductive strategies: (1) an "invariant" strategy where all offspring (or eggs) within a brood are of equal size, and (2) a "variable" strategy where offspring within broods vary in size. Like previous authors, we found that this problem precludes a tractable analytic solution, and opted for a simulation approach (Einum and Fleming 2004a). However, our approach differed from previous studies in that we used a fitness function that penalizes offspring that are too large as well as those that are too small for that environment. Recent empirical work has shown that optimal offspring sizes can vary twofold over very small spatial scales within similar habitats (Marshall and Keough 2006, Marshall et al. 2006), so the chances of mothers producing the "wrong" offspring size for any particular environment are probably high. Therefore, we varied the probability that mothers will produce offspring of a size that is not optimal for that environment (i.e., make "errors"), and examined the relative fitness of the variable and invariant reproductive strategies. Our simulation analysis suggested that, when mothers are likely to make large errors with regard to optimal offspring size and viable offspring sizes are bounded by a minimum and a maximum, within-brood variation in offspring size increases maternal fitness. We then examined whether species that were less able to predict the natal environment produced more variably sized broods through a comparative analysis of offspring size variation among marine invertebrate species that differ in their capacity to predict the environment of their offspring (i.e., direct developers without dispersive young vs. indirect developers with highly dispersive young). A direct test of the predictions of our model requires verifying the presumed causal link between a maximum viable egg size and selection on the variable strategy: a challenging problem. Our comparative analysis did not constitute such a direct test. Nonetheless, the comparative analysis enabled us to determine whether the empirical evidence was consistent with our model's predictions.

MATERIALS AND METHODS

Model

Following traditional offspring size models (e.g., Smith and Fretwell 1974), we assumed that there is a function linking egg fitness to egg size (m), a minimum viable egg size (m_{min}), and a trade-off between the mean size of the eggs that a female produces and the number of eggs that she can produce (Smith and Fretwell 1974).

However, unlike previous authors, we also assumed that egg fitness decreases when egg size exceeds an optimum, so that there is a maximum viable egg size (m_{max}). Thus, the fitness of an individual egg, $\phi(m)$, is zero when egg size is less than m_{min} or greater than m_{max}. In the viable range between m_{min} and m_{max}, egg fitness is given by

$$\phi(m) = \frac{\left(1 - \frac{m_{min}}{m}\right)\left(1 - \frac{m}{m_{max}}\right)}{m} \qquad (1)$$

where m is the size of an individual egg. This represents a convex function relating egg fitness to egg size (see Appendix A: Fig. A1).

We assumed that all females have an equal quantity of resources, R, to invest in reproduction, and that there is a trade-off between the mean size of a female's eggs (brood mean, μ), and the number of eggs that she can produce. Thus, the number of eggs, $N(\mu)$, produced by a female with a brood-mean egg size μ is

$$N(\mu) = R\left(\frac{M}{\mu}\right) \qquad (2)$$

where M is the mean egg size in the population (equal to the optimum egg size and the expected value of the distribution of μ). Consequently, females whose mean egg size (μ) is smaller than the population average (i.e., $\mu < M$) produce more eggs than the population average egg number (i.e., $N(\mu) > N(M)$), whereas females whose mean egg size is greater than the population average (i.e., $\mu > M$) produce fewer eggs than the population average (i.e., $N(\mu) < N(M)$), such that total reproductive output (the sum of the sizes of all eggs produced by a female) is equal for all females.

The fitness of a particular mother, W, is thus equal to the summed fitnesses of all her eggs:

$$W = \sum_{}^{N(\mu)} \phi(m) \qquad (3)$$

where m is the size of a particular egg produced by a female with mean egg size μ.

To determine whether the variable strategy could yield higher fitness than the invariant strategy in unpredictably variable environments, we simulated different degrees of environmental variability, and examined their consequences for the relative fitnesses (i.e., recruitment rates) of two populations of 500 females; one population pursuing an invariant reproductive strategy (no variation in egg size within broods), and the other population pursuing a variable reproductive strategy (within-brood variation in egg size). We used populations, rather than a single individual, to represent each strategy within each generation because this approach seemed more biologically relevant, corresponding, for example, to a situation where clonal populations of marine invertebrates or plants pursue contrasting reproductive strategies. Simulating populations also greatly diminishes the probability of genotype extinction, enabling us to analyze variation

in strategy fitness within and across generations as a continuous variable. Environmental variability (CV_E) was a proxy for mothers' abilities to predict the optimum brood-mean egg size: on average, the magnitude of maternal "errors" (i.e., deviations from the optimum) increased with increasing environmental variability. Note that we manipulated mean egg size for a population of females rather than manipulating environmental parameters. This approach is functionally equivalent to modeling environmental variation because the distribution of mismatches between maternal mean egg size and environment are the same in each case. Our approach has the advantage of allowing manipulation of variation in the mean distance from an optimum independently of changes in minimum and maximum viable egg size. In each simulation (representing a generation or reproductive bout), a brood-mean egg size, μ, was generated randomly for each of 500 mothers. The distribution of μ was log-normal, and its expected value, M, always corresponded to the optimum egg size (i.e., the egg size that maximizes maternal fitness). This assumes that the population mean is centered at the fitness optimum, but that individuals within the population may over- or underestimate the optimum egg size. The coefficient of variation of this distribution, CV_E, represented environmental variability. We examined six degrees of environmental variability: $CV_E = 0.3, 0.6, 1.0, 1.15, 1.3, 2.1$. The biological significance of these values of CV_E can be appreciated by inspecting their consequences for reproductive failure rate and among-generation variation in fitness (see *Results* and Appendix A), which can be compared directly with parameters measured in real populations. Indeed, empirical studies strongly suggest that reproductive failure rates due to producing offspring of the "wrong" size can be even higher than those generated in our simulations (Marshall and Keough 2007).

For each of the 500 brood-mean egg sizes, μ, we then randomly generated $N(\mu)$ individual egg sizes, m, distributed normally about μ with standard deviation σ. Although some eggs could thus have negative sizes, we assumed that egg size as measured on an arbitrary scale, and negative sizes simply yield zero fitness because they are less than m_{min}. For a given female with brood-mean egg size μ, maternal fitness was then calculated in two ways. First, maternal fitness under the invariant strategy, W_{inv}, was calculated based on $N(\mu)$ eggs of size μ. Second, maternal fitness under the variable strategy, W_{var}, was calculated based on $N(\mu)$ eggs of different sizes, m. The arithmetic mean fitness of each strategy within each generation (or reproductive bout) was then calculated from the fitnesses of the 500 females, and the relative fitness of the variable strategy (fitness differential, ΔW) within a generation was calculated as

$$\Delta W = \frac{\left(\sum W_{var} - \sum W_{inv} \right)}{\sum W_{inv}} \qquad (4)$$

where $\sum W_{var}$ and $\sum W_{inv}$ are the summed fitnesses of the 500 females based on the variable and invariant strategies. Thus, $\Delta W < 0$ indicates higher fitness for the invariant strategy, whereas $\Delta W > 0$ indicates higher fitness for the variable strategy within a generation or reproductive bout.

To examine how the magnitude of within-brood variance in egg size affects maternal fitness, we simulated different coefficients of within-brood variation, CV_B (defined as σ/μ). We examined values of CV_B ranging from 0.01 to 0.5 because these values encompass those observed in nature (Marshall and Keough 2007, Kohn and Perron 1994). The value of σ was adjusted for each female so as to maintain a constant CV_B despite variation in μ.

To investigate how the shape of the function relating egg fitness to egg size affects the performance of the variable strategy, we simulated every combination of CV_E and CV_B for three different egg fitness functions varying 16-fold in the width of the viable egg size range (see Fig. 2). For each parameter combination, we conducted 500 simulations, with different random distributions of μ and m generated in each simulation, and tested the null hypothesis $\Delta W = 0$ by t test. Where ΔW was not significantly different from zero, we conducted up to 2000 additional simulations. Appendix A: Fig. A1 illustrates the performance of females under the variable and invariant strategy for several parameter values. We checked our model for systematic bias by setting CV_B to very small values, and confirming that ΔW approaches zero as CV_B approaches zero.

As an additional index of relative performance, we compared the coefficients of variation of $\sum W_{var}$ and $\sum W_{inv}$ over multiple simulations, assuming that the strategy exhibiting less variation in mean fitness across generations enjoys a long-term advantage (Roff 1992). Simulations were conducted in Mathcad Plus 6.0 Professional Edition (MathSoft 1995).

Comparative analysis

Marine invertebrates are an ideal group to examine offspring size variation across species because they are taxonomically diverse with a wide range of offspring dispersal modes. Many marine invertebrate lineages exhibit a range of developmental modes, indicating repeated, independent evolution of different developmental modes (Hart et al. 2003), and multiple dispersal modes are present within some populations of the same species (Krug 1998). Importantly, offspring size consistently has fitness consequences in marine invertebrates and can be important at each life-history stage, sometimes in a conflicting manner (Hart 1995, Levitan 1996, Moran and Emlet 2001, Marshall and Keough 2003, Marshall et al. 2003).

Marine invertebrates can be divided into distinct developmental groups: direct development, indirect development with no feeding, and indirect development with feeding. Direct developers (D) typically produce
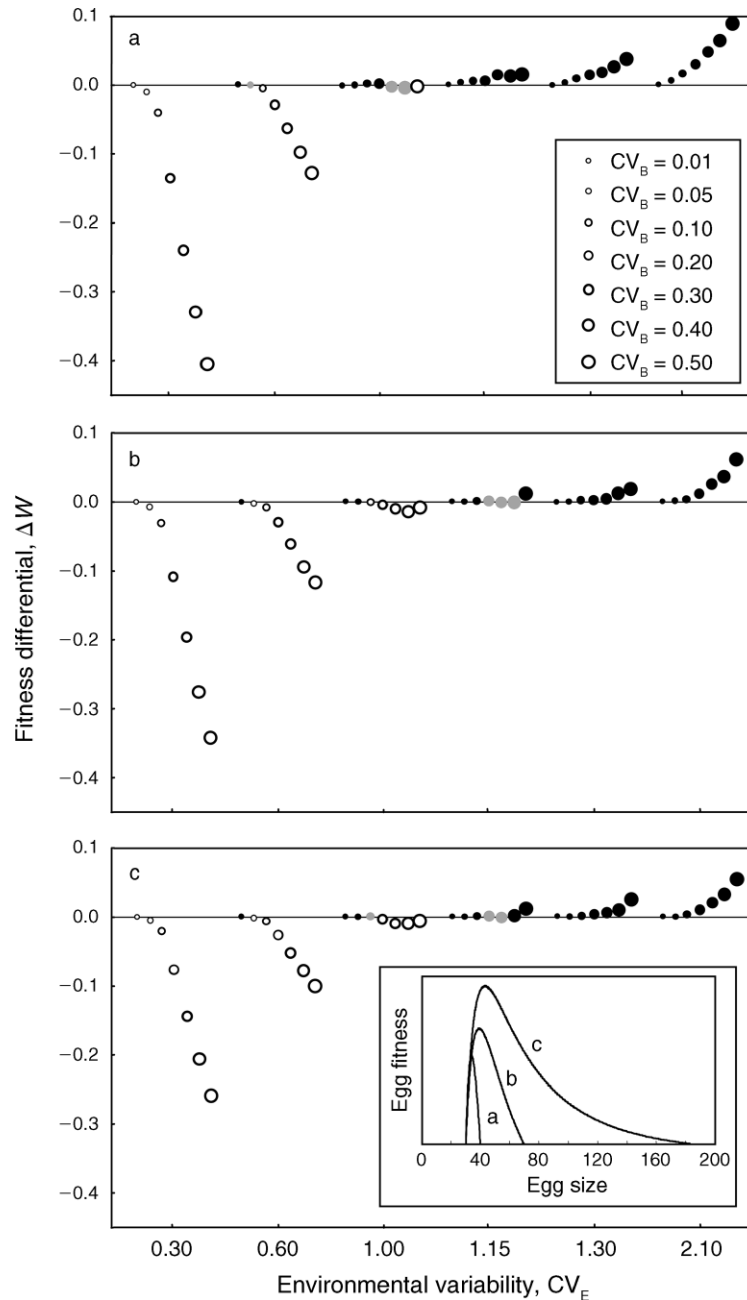
FIG. 1. Fitness differentials (ΔW), representing the relative fitness of mothers producing offspring of variable size within broods (variable strategy), shown for varying levels of environmental variability (CV_E) and within-brood variability (CV_B) for three egg fitness functions varying 16-fold in the viable egg size range: a, $m_{min} = 30$, $m_{max} = 40$; b, $m_{min} = 30$, $m_{max} = 70$; c, $m_{min} = 30$, $m_{max} = 190$ (see inset in panel c). Each point represents mean ΔW for at least 500 simulation runs (equivalent to generations or reproductive bouts) for a given combination of parameters, with each simulation comprising 500 females pursuing each of the two strategies: open circles denote $\Delta W < 0$ (invariant strategy advantage), and solid circles denote $\Delta W > 0$ (variable strategy advantage) based on one-sample t tests ($t > |2.01|$, $P < 0.05$); gray circles represent parameter combinations where ΔW was not significantly different from zero ($P > 0.05$) after 2500 simulation runs. The horizontal line represents equal fitness for the two strategies ($\Delta W = 0$). The 95% confidence limits are narrower than the smallest symbol.

relatively large offspring that either emerge from the adult as a fully developed juvenile or emerge from an egg capsule as a juvenile. There is extremely little dispersal during development and fertilization in usually internal. Non-feeding, indirect developers (NF) typically produce

"medium" sized offspring that are released from the adult as eggs (in the case of external fertilizers) or larvae (in the case of internal fertilizers or brooders). The larvae typically have no feeding structures, rely on maternal provisioning, and spend minutes to a few days

in the plankton before encountering a suitable habitat whereupon they metamorphose and begin adult life (Havenhand 1995). Feeding, indirect developers (F) produce small eggs that are either externally or internally fertilized and spend days to months feeding in the plankton. They may go through several larval stages while in the plankton before metamorphosing and becoming an adult. Thus, there is a clear ranking in the dispersal capabilities of D, NF, and F offspring, with D being the least dispersive and F being the most dispersive.

There are clear differences in the ability of mothers with directly and indirectly developing offspring to predict the relationship between offspring size and overall performance (and thus the optimal offspring size that should be produced). Because indirectly developing offspring are far more dispersive and can pass through multiple life-history stages: (1) The natal habitat (defined as the habitat in which offspring become independent from maternal nutrition sources and begin to feed) is unlikely to be assessed by mothers, (2) the natal habitat is unlikely to be affected by maternal phenotype, and (3) there can be conflicting selection pressures on offspring size among stages (Marshall et al. 2002). These three factors all suggest that mothers with F offspring have a lower chance of optimally provisioning individual offspring. In contrast, mothers with D offspring should be better able to predict their offspring's environment. Because directly developing offspring are released into the maternal environment, there is at least the potential for mothers to assess the environmental conditions and adaptively adjust the size of their offspring (e.g., Fox et al. 1997, Einum and Fleming 2002). Moreover, because direct developing offspring are relatively weak dispersers, sibling competition and maternal phenotype are more likely to affect the quality of the natal environment (i.e., essentially make it more predictable; Parker and Begon 1986, Hendry et al. 2001). Finally, there is less potential for conflicting selection pressures on offspring size in direct developers because they have fewer life-history stages, making the relationship between offspring size and performance more likely to be predictable. If environmental unpredictability favors the production of variably sized offspring, then we should see higher levels of variation *within broods* of F species than D species. Similarly, if the offspring environment of D species is more predictable, we should see more variation *among mothers* in D species than F species. It is important to note that for all the developmental groups, we expect there to be a minimum and maximum offspring size that will be viable although the underlying causes of the upper constraints will probably differ among the developmental modes. For example, physiological constraints probably limit the maximum offspring size in direct developers but polyspermy effects limit offspring size in broadcast spawners (Marshall and Keough 2007). Thus, while our theoretical analysis
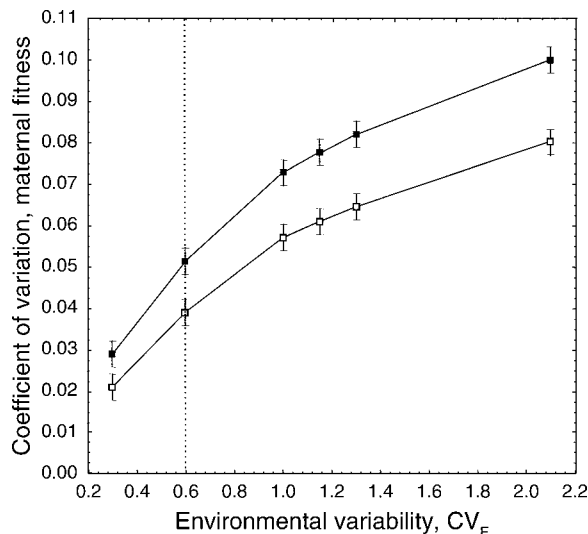

Fig. 2. Coefficients of variation (mean and 95% confidence limits) in maternal fitness of the variable (open squares) and invariant (solid squares) reproductive strategies at varying levels of environmental variability (CV_E). Each coefficient of variation was based on mean fitness values from 100 generations or reproductive bouts. For the variable strategy, data are pooled for seven levels of within-brood variation (CV_B). Data are based on an egg fitness function with $m_{min} = 30$ and $m_{max} = 70$; other functions (see Appendix A) yielded similar patterns (not shown). The dotted vertical line represents the lowest CV_E that yielded a significant within-generation advantage for the variable strategy ($\Delta W > 0$).

considered the effects of environmental predictability on fitness under the assumption that offspring can suffer fitness costs if they exceed an optimum size, our comparative analysis examined the relationship between environmental predictability and components of variation in offspring size in order to test our model's predictions. To determine whether the empirical evidence was consistent with the predictions arising from our simulations, we compiled data on variation in offspring size among and within marine invertebrate mothers from the available literature and from unpublished data of our own (see Table 1). For more detailed methods on our comparative analysis, see Appendix B.

RESULTS

Model

Our simulations suggest that, in unpredictably variable environments, mothers producing offspring of variable size within each brood (variable strategy) have higher mean fitness within generations, as well as lower variance in fitness across generations, than mothers producing offspring of uniform size (invariant strategy). This is because the production of offspring of different sizes insures that, for some females whose brood-mean egg size falls outside the viable egg size range, some offspring are nonetheless able to survive.

Within generations, the invariant strategy yields higher mean fitness when a large proportion of females

TABLE 1. Summary table of within- and among-brood variation in offspring size for marine invertebrates.

Phylum, Class	Order	Family	Species
Annelida, Polychaeta	Sabellida	Serpulidae	*Galeolaria caespitosa*
Mollusca, Gastropoda	Mesogastropoda	Calyptraeidae	*Crepidula adunca*
	Patellogastropoda	Lottiidae	*Lottia pelta*
	Archaeogastropoda	Fissurellidae	*Diadora aspersa*
Mollusca, Opisthobranchia	Sacoglossa	Stiligeridae	*Alderia modesta* (F)
	Sacoglossa	Stiligeridae	*Alderia modesta* (NF)
Bryozoa, Gymnolaemata	Cheilostomata	Bugulidae	*Bugula neritina*
Echinodermata, Asteroidea	Spinulosida	Asterinidae	*Meridiastra occidens*
	Spinulosida	Asterinidae	*Meridiastra calcar*
	Spinulosida	Asterinidae	*Parvulastra parvivipara*
	Spinulosida	Asterinidae	*Meridiastra gunnii*
	Spinulosida	Echinoasteridae	*Echinaster modestus* (D)
	Spinulosida	Echinoasteridae	*Echinaster modestus* (NF)
	Forcipulatida	Asteriidae	*Uniophora granifera*
	Forcipulata	Asteriidae	*Asterias forbesi*
	Platyasterida	Luidiidae	*Luidia clathrata*
Echinodermata, Echinoidea	Clypeasteroida	Clypeasteridae	*Clypeaster rosaceus*
	Clypeasteroida	Dendrasteridae	*Dendraster exentricus*
	Clypeasteroida	Mellitidae	*Encope aberrans*
	Temnopleuroida	Toxopneustidae	*Lytechinus variegatus*
	Echinoida	Strongylocentrotidae	*Strongylocentrotus droebachiensis*
Chordata: Ascidia	Stolidobranchia	Pyuridae	*Pyura stolonifera*
	Stolidobranchia	Pyuridae	*Pyura fissa*
	Stolidobranchia	Styelidae	*Styela plicata*
	Phlebobranchia	Cionidae	*Ciona intestinalis*

Note: In the development column, F refers to species with indirect development and feeding larvae; NF refers to species with indirect development and non-feeding larvae; and D refers to species with direct development (see *Methods: Comparative analysis*).

† Measurements for offspring size for diameter are in μm, and those for volume are in millions of $μm^3$.

are able to produce mean egg sizes near the optimum, since all the eggs produced by invariant strategy females have high fitness. However, when many females produce mean egg sizes that deviate substantially from the optimum, the variable strategy tends to do better on average because fewer females suffer total reproductive failure, and many females produce some eggs of near-optimum size, even if their brood-mean egg size deviates from the optimum. When environmental variability is moderate (e.g., $CV_E = 0.6$), a small degree of within-brood variability in egg size (e.g., $CV_B = 0.01$) nonetheless results in significantly higher mean maternal fitness than an invariant strategy, although higher levels of within-brood variability are disadvantageous (Fig. 1; Appendix C: Table C1). For example, egg fitness function "c" in Fig. 1 yields a significant advantage for the variable strategy (with $CV_B = 0.01$) at $CV_E = 0.6$, which corresponds to a reproductive failure rate (i.e., probability of having no surviving offspring) of 24% for invariant-strategy females. When environmental variability is high (e.g., $CV_E \geq 1.3$, resulting in reproductive failure for >50% of invariant strategy females), maternal fitness increases with the degree of within-brood variability (CV_B). At intermediate levels of environmental variation (e.g., $CV_E = 1.0–1.15$), a complex transition occurs where selection on CV_B appears to be disruptive.

We investigated how the strength of stabilizing selection on egg size affects the relative advantage of the variable strategy by examining three egg fitness functions differing 16-fold in the viable egg size range.

The narrowest egg fitness function (function "a" in Fig. 1), representing the strongest stabilizing selection on egg size, results in the greatest advantage for the variable strategy in variable environments (Appendix A: Fig. A2). However, the difference between the two wider egg fitness functions (functions "b" and "c" in Fig. 1) is less pronounced. This is because, given the trade-off between egg size and number, females with large brood-mean egg sizes have few offspring and, thus, little influence on mean fitness.

In addition, the variable strategy always results in lower variation in fitness across generations (Fig. 2; Appendix C: Table C2), and this represents an additional advantage of the variable strategy (see Roff 1992 and *Discussion*).

The fitness advantages of the variable reproductive strategy, both in terms of higher mean fitness within generations and lower coefficients of variation in fitness across generations, partly reflects lower rates of complete reproductive failure (Appendix A: Fig. A3). For females pursuing the variable egg size strategy, reproductive failure rate declines with increasing within-brood variability (CV_B; Appendix C: Table C3) and, even with the smallest degree of within-brood variability ($CV_B = 0.01$), the variable strategy yields a significantly lower reproductive failure rate than the invariant strategy (sign test: $N = 12\,500$ simulation runs, $Z = 111.66$, $P < 0.0001$). Reduced rates of reproductive failure thus moderate the effects of environmental unpredictability.

Table 1. Extended.

Study	Development	Measurement	Offspring size†	CV within	CV among
Marshall and Keough (2003); D. J. Marshall (*unpublished data*)	F	diameter	80.15	11.56	1.99
Collin (2000)	D	diameter	2200	6.04	25.71
Hadfield and Strathmann (1996)	NF	diameter	135.8	8.6	2.4
Hadfield and Strathmann (1996)	NF	diameter	173	12.9	4.9
Krug (1998)	F	volume	0.16	13.70	11.75
Krug (1998)	NF	volume	0.63	9.78	12.37
D. J. Marshall (*unpublished data*)	NF	diameter	271	6.5	6.9
M. Byrne (*unpublished data*)	NF	diameter	398	4.24	4.42
M. Byrne (*unpublished data*)	NF	diameter	412.9	3.85	3.87
M. Byrne (*unpublished data*)	D	diameter	810	5.92	7.16
M. Byrne (*unpublished data*)	NF	diameter	434	4.14	5.07
Turner and Lawrence (1977)	D	diameter	239.16	12.23	16.21
Turner and Lawrence (1977)	NF	diameter	199.1	10.39	8.27
D. J. Marshall (*unpublished data*)	NF	diameter	521	7.86	6.3
Turner and Lawrence (1977)	F	volume	1.477	22.91	16.31
Turner and Lawrence (1977)	F	volume	2.44	15.53	8.52
Emlet (1986)	NF	diameter	280.3	1.67	2.74
Podolsky (2002)	F	diameter	129	3.5	3.5
Turner and Lawrence (1977)	F	volume	3.19	15.26	11.17
Turner and Lawrence (1977)	F	Volume	0.59	10.01	9.05
Turner and Lawrence (1977)	F	volume	2.01	9.04	4.96
Marshall et al. (2000)	NF	diameter	269	7.9	9.18
Marshall and Keough (2003)	NF	diameter	175.78	4.89	5.21
Marshall and Keough (2003)	NF	diameter	163	3.9	7.9
Marshall and Keough (2003)	NF	diameter	145	4.5	5.17

Comparative analysis

The comparative data are consistent with the hypothesis that within-brood offspring size variation reflects an adaptive maternal bet-hedging strategy in unpredictable environments. The principal source of variation in offspring size strongly depends on the development type of that species (Table 2). For direct developers (where mothers have the greatest ability to predict offspring environment), most of the variation in offspring size is at the among-mother level (Fig. 3), whereas for indirect developers with feeding larvae (where mothers have little ability to predict offspring environment), most of the variation is at the within-mother level (Fig. 3). The indirect developers with non-feeding larvae are intermediate to the two other groups, with equal levels of variation within and among mothers. This pattern is maintained regardless of the taxonomic level at which it is tested (scale of variation $\times$ development type interaction, family level, $F_{2,18} = 7.05$, $P = 0.0055$; order level, $F_{2,15} = 6.11$, $P = 0.0011$; class level, $F_{2,8} = 6.11$, $P = 0.0245$; Fig. 3). Examining within-mother variation in offspring size alone, there was a significant difference among development types ($F_{2,22} = 5.54$, $P = 0.011$), and within-mother variation was highest in indirect developers with feeding larvae (Dunnett's test: F vs. NF, $P < 0.001$; F vs. D, $P = 0.04$).

Discussion

We found that when environments are unpredictable (such that mothers are likely to produce offspring of a mean size that deviates from the optimal size) and offspring fitness is maximized at an intermediate size, mothers producing a range of offspring sizes within a brood (variable strategy) are likely to have higher fitness than mothers producing offspring of identical size within broods (invariant strategy). Typically, the benefit of producing variably sized offspring is assumed to be a reduction in among-generation variance in fitness (Seger and Brockman 1987, Simons and Johnston 1997, Lips 2001, Laaksonen 2004), and our analysis supports this view. This represents an advantage for the variable strategy because genotypes pursuing such a strategy will face a lower risk of extinction resulting from low population size in some generations, and will have a higher net growth rate over multiple generations (i.e., they will have a higher *geometric* mean fitness: For a detailed description of why geometric mean fitness may be more important for selection, see Roff 1992, Orr 2007). This reduction in among-generation variation in fitness (yielding a higher geometric mean) forms the basis of bet-hedging theory: bet-hedgers don't necessarily do best all the time, but they perform most consistently and are therefore favored by selection (Cohen 1966, Roff 1992). However, our simulations show that mean fitness *within* generations is also higher for mothers that produce offspring of variable size when the environment is sufficiently variable (i.e., a higher *arithmetic* mean fitness): a novel finding. Together, these findings represent a large potential fitness advantage for the variable strategy in some environments.

The finding that a variable strategy can attain higher fitness within generations reflects the fact that the variable strategy outperforms the invariant strategy

TABLE 2. Analysis of the effect of development type and the scale of variation (within or among mothers) in offspring size in marine invertebrates with direct or indirect development.

Source	df	MS	F	P
Species	22	27.44	2.84	0.009
Development type	2	13.31	1.37	0.273
Scale of variation	1	15.16	1.57	0.223
Interaction	2	83.30	8.62	0.002
Error	22	9.65		

when brood-mean egg size is displaced from the egg size optimum. Thus, the net relative fitness of the variable strategy within generations reflects the average displacement of brood-mean egg size from the egg size optimum, and a net advantage for the variable strategy can arise if the mode of the distribution of brood-mean egg sizes is displaced from the egg size optimum. In our simulations, the expected value of the brood-mean egg size distribution always coincides with the optimum egg size, but the mode of the distribution is to the left of the egg size optimum (as a consequence of the shape of the log-normal distribution), yielding a net advantage within generations for the variable strategy under some parameter combinations. We suggest that, in natural populations, the mode of the distribution of offspring size may often be shifted to the left of the optimum as a result of resource limitation, or classic bet-hedging, whereby genotypes that produce a greater number of small offspring may outperform those that produce fewer, larger offspring when optimum egg size is difficult to predict.

Our findings provide some of the first compelling theoretical support for the idea that the production of heterogeneous broods, so often observed in nature, can reflect an adaptive reproductive strategy that yields higher fitness within generations (see Kudo [2001] for an interesting empirical example). Our results suggest that whenever there is a minimum and a maximum viable offspring size, there are two ecological conditions under which producing offspring of variable size may be favored: highly unpredictable environments and narrow fitness functions. There is good evidence suggesting that optimal offspring sizes can vary considerably, even over small spatial and temporal scales due to a range of physical (e.g., desiccation stress on either side of a surge channel; Moran and Emlet 2001) and biological factors (Bervan and Chadra 1988, Marshall et al. 2006), but what conditions are likely to result in narrow fitness functions? Obviously, constraints on maximum size will result in narrowed fitness functions (Strathmann and Chaffee 1984, Congdon and Gibbons 1987, Strathmann 1995). But there are factors other than functional constraints that penalize offspring that are too large. For example, in the frog *Bombina orientalis*, tadpoles from larger eggs can have lower performance than tadpoles from smaller eggs (Kaplan 1992). For marine broadcast spawners, there is likely to be a narrow range

of offspring sizes that results in the optimal fertilization of eggs because fertilization is dependent on egg size. Smaller eggs face sperm limitation and larger eggs may suffer from polyspermy (Marshall et al. 2002). In species with non-feeding larvae, egg size is *positively* correlated with development time and, as such, larger eggs will remain in the plankton for longer (reviewed in Marshall and Keough 2007). Given that mortality rates in the plankton can be very high, increasing offspring size in species with non-feeding larvae may reduce rather than increase offspring fitness. As a result of such factors, only a narrow range of offspring sizes may be viable. In species such as these, we suggest that even a small level of environmental unpredictability may result in variable strategies being favored (for a more detailed review of the negative effects of increasing offspring size see Bernardo 1996). We should note that we do not suggest that *all* within-brood variation in offspring size is necessarily adaptive, merely that there is an adaptive element to this variation when environments are unpredictably variable and production of offspring that are too large or too small results in direct fitness costs. Our results are robust to a 16-fold difference in the viable egg size range. However, it would be interesting to investigate the consequences of altering the shape of the egg fitness function in a variety of other ways (e.g., disruptive selection on egg size).
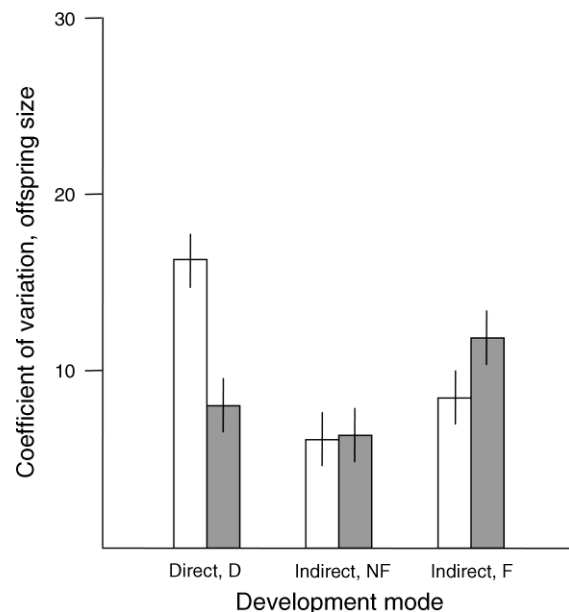

FIG. 3. Coefficient of variation in offspring size among different developmental modes: direct (D) and indirect (F refers to species with feeding larvae; NF refers to species with non-feeding larvae) of marine invertebrates. See *Methods: Comparative analysis* for more details. Open bars indicate mean among mothers, and solid bars indicate mean within mothers. Note that the appropriate error for this figure is the $\sqrt{MS_{error}}$ as shown in Table 2. For a description of why this error term is appropriate, see Quinn and Keough (2002:506).

The theoretical finding that within-brood variation in egg size can represent an adaptive form of diversified bet-hedging in highly unpredictable environments accords with comparative empirical evidence, which shows that within-brood variation in offspring size is relatively low in species where mothers have greater opportunity to anticipate the relationship between offspring size and performance (i.e., direct developers), but high in species where this relationship is likely to be unpredictable (i.e., indirect developers with feeding larvae). Based on the key assumption that offspring fitness is maximized at an intermediate size, our theoretical analysis suggests that the observed relationship between environmental predictability and within-brood variation in offspring size in marine invertebrates reflects adaptive variation in reproductive strategies. The converse pattern was observed for variation among mothers. The high level of among-mother variation in offspring size for direct developers is predicted to occur only if mothers can adjust the size of their offspring according to local conditions. If mothers can produce offspring that are close to the optimal size, then fitness will be higher under an invariant strategy. While adaptive plasticity in offspring size has been demonstrated in insects (Fox et al. 1997), we know of no study that has demonstrated this in marine direct developers.

Previous studies have examined variation in offspring size in more or less predictable environments, but they did not partition variation into among- and within-mother levels (Poulin and Hamilton 2000, Einum and Fleming 2002, Dziminski and Alford 2005). Our findings in both the simulations and the comparative analysis highlight the fact that selection will act very differently on these two sources of variation, suggesting that they should be considered separately. Environmental unpredictability should select for increased among-mother variation for species that can predict the environment that their offspring will encounter, whereas it should select for increased within-brood variation for species that cannot predict the conditions that their offspring are likely to experience.

Both non-feeding and feeding indirect developers had much lower levels of among-mother variation in offspring size than direct developers, but only the indirect developers with feeding larvae had high levels of within-brood variation. This accords with our model's predictions: Most indirect developers with feeding larvae spend weeks to months in the plankton, passing through multiple life-history stages, and disperse to habitats far removed from the maternal habitat. The different developmental modes differed not only in their dispersal, but also the number of life-history stages at which offspring size could affect performance. For example, fertilization was external in most of the indirect developers, and other studies have shown that egg size can affect fertilization kinetics in external fertilizers (Levitan 1996, Marshall et al. 2002). Thus, we would expect that the relationship between offspring size and performance would be least predictable in this group and, accordingly, high levels of offspring size variation within-broods should be favored. It should be noted that the species within the different developmental modes vary across a range of different life-history traits, all of which have the potential to affect offspring size variation. For example, all of the direct developing species have a mobile adult stage, but many of the indirect developers were sessile as adults. Thus, we cannot rule out other factors that may also affect the differences in offspring size variation observed in this study.

An alternative explanation for the high levels of variation in offspring size *among* mothers in direct developers is that maternal phenotype and the natal environment are linked. Larger mothers typically produce more offspring and, in weakly dispersing species, this may result in higher levels of sibling competition. McGinley et al. (1987) suggest that larger mothers may therefore provision their offspring with more resources (i.e., make them larger) to deal with the increased levels of sibling competition, thus producing a correlation between maternal and offspring size. In many marine invertebrates, offspring size is correlated with maternal size (Marshall et al. 2000, Marshall and Keough 2003), but it is, as yet, unclear whether this relationship is more common in direct developers.

Overall, our theoretical and comparative analyses support the view that within-brood variation in offspring size, like mean offspring size, is under selection. When environment is unpredictably variable, and the range of viable offspring sizes is relatively narrow, selection is likely to favor production of offspring of variable sizes within broods. In contrast, stable environments and a large range of viable offspring sizes will generally favor a constant offspring size within broods. One component that theoretical considerations of offspring size, including our own, fail to incorporate is the physiological cost of producing offspring of uniform size. We agree with the suggestion of Fox and Czesak (2000) that at least some of the within-brood variation in offspring size may reflect the cost associated with the production of uniformly sized offspring, or physiological constraints against uniform offspring size. Nevertheless, it is clear that systematic differences in the level of within-brood variation occur among organisms with different life-history strategies and we suggest that these differences may be adaptive.

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APPENDIX A

Figures showing the among- and within-generation benefits of a variable offspring size strategy (*Ecological Archives* E089-140-A1).

APPENDIX B

Literature compilation and data analysis (*Ecological Archives* E089-140-A2).

APPENDIX C

Additional model analyses (*Ecological Archives* E089-140-A3).