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# Optimal Egg Size in Marine Invertebrates: Theory and Phylogenetic Analysis of the Critical Relationship between Egg Size and Development Time in Echinoids

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ABSTRACT: Life-history models for marine invertebrate larvae generally predict a dichotomy in egg size in different species: eggs should be either minimal in size or large enough to support development fully without larval feeding. This prediction is contradicted, however, by the empirical observation of wide, continuous variation in egg size between these extremes. The prediction of dichotomy rests on the assumption of a negative linear relationship between egg size and development time. Here, I present a simple model in which development time is inversely proportional to egg size. Incorporating this relationship into an optimality model produces predictions of intermediate rather than extreme egg size. Modeled variations in mortality, food availability, fertilization rates, and temperature all produce continuous shifts in the value of the intermediate optimal size, in direct contrast to those produced by previous models, which predict shifts between two extreme optima. Empirical data on echinoid egg size and development time strongly support the model's assumption of an inverse proportional relationship between egg size and development time. A composite phylogeny is constructed of the 37 species for which egg size, development time, water temperature, and phylogenetic relatedness are known. Independent contrasts are made of the evolutionary changes in egg size and development time. This analysis indicates that evolutionary shifts in development time are correlated with the inversely proportional shifts in egg size assumed in the model. The assumption of a negative linear relationship used in previous models is rejected. This model provides a potential explanation for intraspecific variation in egg size along environmental gradients, sympatric differences in egg size among species, and biogeographic trends in egg size and development mode across taxa.

*Keywords:* comparative method, development time, echinoids, egg size, life-history theory, phylogeny.

In 1973, Vance presented a model to explain differences in reproductive strategies among marine invertebrates. That model was the first in a rapid proliferation of studies on the evolution of offspring size in a variety of both marine and terrestrial taxa (reviewed in Roff 1992). Despite the large number of articles examining selection on egg size and reproductive strategies in marine invertebrates (reviewed in Strathmann 1985; Havenhand 1995), the most basic aspects of these questions remain unresolved. A striking example is that these models (Vance 1973*a*, 1973*b*; Christensen and Fenchel 1979; Podolsky and Strathmann 1996) predict selection for an extreme dichotomy in egg size among species (but see Levitan 1993, 1996*b*, 1996*c*; McEdward 1997), in stark contrast to the empirical evidence to the contrary (noted by Herrera et al. 1996; Levitan 1996*b*; McEdward 1997; illustrated in fig. 1).

Predictions for a dichotomy, rather than continuous variation, in egg size are founded on an assumption made by Vance (1973*b*) and followed by others (e.g., Podolsky and Strathmann 1996; McEdward 1997) that there is a negative linear relationship between egg size and development time. Vance's (1973*b*) concept of the energetics of larval development (and others that followed, reviewed in Strathmann 1985; Havenhand 1995) was that the energy in the egg ($S$) varied from 0 to 1, where 0 indicates that all energy for development must be gathered through larval feeding and 1 indicates that all energy for development is present in the yolk. The consequence of this formulation is a prediction of selection for either a size 0 or size 1 egg, dependent on the degree of planktonic mortality. This prediction fit nicely with the idea that species that produce feeding larvae (planktotrophs) tend to have small eggs and species that produce nonfeeding larvae (lecithotrophs) tend to have larger eggs.

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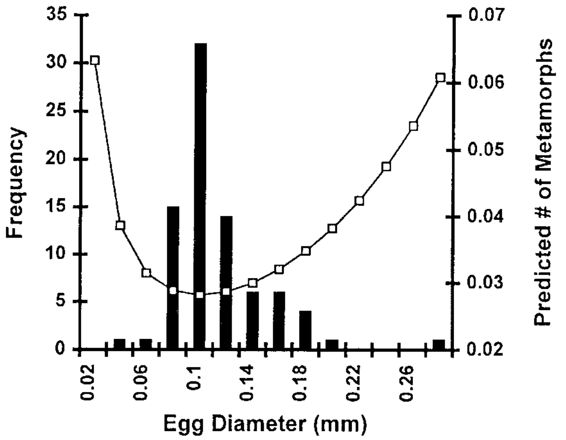

**Figure 1:** Empirical data on egg size and predicted egg sizes for echinoids with feeding larvae. Empirical data from Emlet et al. (1987). Prediction from equation (5) (from Vance 1973*b*) with $m = 0.8$, $p = 70$, $\ell = 35$, and $C = 1$ (from Havenhand 1995). Echinoids eggs at a size of 280 mm can be facultative feeders (Emlet 1986) and are here considered to have $s = 1$; the theoretical and empirical scales are adjusted accordingly. Although different parameter values alter the predicted estimates quantitatively, local optima at 0 and 280 mm ($s = 0$ and 1) are always predicted.

More recent empirical work has demonstrated, however, that the large yolk-filled eggs of lecithotrophs contain much more energy than is needed for development and that this excess is probably important in postmetamorphic processes that were not considered in Vance's model (Emlet and Hoegh-Guldberg 1997). In addition, the eggs of planktotrophic species can range up to size 1 (Herrera et al. 1996) and, in contrast to Vance's predictions, have a bell-shaped distribution over that size range—one dominated by species with intermediate egg size (fig. 1). These recent findings suggest that a new theoretical framework is needed for investigation of variation in egg size in marine invertebrates.

Two current models attempt to explain variation in intermediate egg size in marine invertebrates. The first is that the relationship between egg size and development time may be curvilinear rather than linear. If a negative but diminishing relationship between egg size and development time exists, then intermediate optima are predicted (Levitan 1996*b*, 1996*c*). In principle, this is the notion suggested by Smith and Fretwell (1974) as a general explanation for variation in offspring size, which has been largely overlooked in the marine larval literature. Although nonlinearities in fitness functions have been suggested as a mechanism leading to selection for intermediate strategies in marine invertebrates (Caswell 1981), they are usually only mentioned briefly (Strathmann 1985; Podolsky and Strathmann 1996; McEdward 1997), if at all, before an explicit model based on a linear assumption is evaluated (but see Levitan 1996*b*, 1996*c*). Previous models using a curvilinear relationship between egg size and development time were based on scant empirical evidence and lacked a causal mechanism for that relationship (Levitan 1996*c*). No first-principle model has been developed that uses a nonlinear fitness function to explain variation in marine invertebrate larvae.

The second idea is to modify Vance's model by including facultative feeding (McEdward 1997). A facultatively feeding larva can feed but does not need to feed to undergo metamorphosis. This model uses a conditional approach, dependent on the value of $S$. If $S$ is $<1$, then increases in $S$ result in increased offspring survival through reduced development time by relating egg size to development time by means of the negative linear relationship assumed by Vance. Under these conditions, optimal $S$ is either 0 or 1. At values of $S > 1$, increasing $S$ confers no fitness benefits because development time is already at some minimum. The model assumes that increases in the value of $S$ beyond 1, which would result in increases in the energy reserves of metamorphs, do not influence fitness; metamorphs of different sizes have the same fitness. Because both conditional formulas contain the fitness cost of reduced egg number with increased egg size, $S$ reaches a peak fitness value at $S = 1$ and then decreases at greater values of $S$ because the benefits remain constant while the costs of reduced egg number increase. The model predicts intermediate optimal values of $S < 1$ by incorporating facultative feeding. Facultative feeding allows larvae to accumulate energy and to reach a value of $S = 1$ with an investment in egg material less than $S = 1$. Once larvae reach $S = 1$ through facultative feeding, only the costs of increased $S$ are considered (reduction in egg number) and not the benefits (increased energy reserves at metamorphosis). The critical assumption of this model, that fitness is independent of the energy state at metamorphosis, is not supported by the evidence. Metamorphs with increased energetic reserves are larger, grow faster, and survive better than conspecifics with fewer reserves (Emlet and Hoegh-Guldberg 1997). Although incorporating facultative feeding into life-history models is an important step in understanding the evolution of larval strategies, the current formulation of this model leaves explanations for intermediate optima unresolved.

Here, I introduce a new model of selection on egg size in marine invertebrates, one based on the assumption that development time is inversely proportional to egg size. In the model, I vary mortality, food availability, sperm availability, and water temperature and produce predictions of continuous variation in intermediate optimal egg size. I then confirm the assumption of the model using empirical data on echinoid egg size and development time. Finally, I construct a composite phylogeny from the literature and use the comparative method to reveal that the relationship between egg size and development noted in extant species reflects the evolutionary changes in egg size and development time. These results contradict long-standing views on selection on egg size in marine invertebrates and provide a simple theoretical framework for understanding the evolution of egg-size differences among species and biogeographical patterns in egg size and developmental mode.

## A Brief Review of Vance's Model

Vance's (1973*b*) goal was to determine which environmental conditions would result in the evolution of three reproductive strategies in marine invertebrates: larvae that feed in the plankton, larvae that develop but do not feed in the plankton, and nonfeeding larvae that develop directly within an egg mass or brooded by the parent. Vance calculated the number of metamorphic individuals ($N_T$) as

$$N_T = (C/S)e^{-MT}, \tag{1}$$

where $C$ is the total amount of material allocated to egg production, $S$ is the amount of material in each egg, $M$ is the planktonic mortality rate, and $T$ is the time from fertilization to metamorphosis. In order to evaluate selection for different reproductive strategies, Vance divided $T$ into two components: $\lambda$, the time spent as a nonfeeding larva, and $\rho$, the time spent feeding during development, where $\ell$ and $p$ are constants that represent the time required to develop if nutrition is derived entirely from yolk ($\ell$) or feeding ($p$). Egg size ($S$) in this model varies from 0 to 1, where 0 indicates that all energy for development must be gathered through larval feeding and 1 indicates that all energy for development is present in the yolk. The key to Vance's analysis is the negative linear relationship between egg size and development time such that

$$\lambda = \ell S \tag{2}$$

and

$$\rho = p(1 - S). \tag{3}$$

This linear relationship allows the components of development time to be a simple function of egg size and the total development time ($T$) to be

$$T = p - (p - \ell)S. \tag{4}$$

The number of metamorphs becomes

$$N_T = (C/S)e^{-M[p-(p-\ell)S]}. \tag{5}$$

This equation was evaluated by Vance, who found that only extremes in egg size ($S = 0$ or 1) were stable.

## The Model

### Basic Model

Here, I present a simple alternate model, also confined to the life stage between egg and metamorphosis. The rationale for restricting the model to this stage is that, in planktotrophic echinoids, size at metamorphosis is independent of egg size (see "Assumption of the Independence of Egg Size and Size at Metamorphosis"; Emlet et al. 1987). Further, in some genera with highly divergent interspecific egg sizes, size at metamorphosis is conserved (Emlet et al. 1987; Sinervo and McEdward 1988), so selection for divergent egg size probably occurs before metamorphosis, when these size differences diminish or are eliminated. This is not to say that size at metamorphosis is unimportant to fitness; it simply means that, in taxa where size at metamorphosis is independent of egg size, the influence of premetamorphic factors on selection on egg size can be analyzed without the confounding effects of postmetamorphic factors.

As in previous models, planktonic survival is a function of development time:

$$N_T = (C/S_\mathrm{a})e^{-MT}, \tag{6}$$

where $S_\mathrm{a}$ is the absolute egg volume, as opposed to $S$, which in Vance's model is a relative value between 0 and 1. Egg volume appears to be a good surrogate of egg energy content across species. Jaeckle (1995) reviewed the available data and notes that the relationship between log of energy content and log of egg volume has a slope of 1 ($R^2 =$ 0.98) across echinoderm species.

It is worth noting that one of the studies in Jaeckle's (1995) review, the one by Strathmann and Vedder (1977), suggested that egg energy content scaled at a fractional power (0.75) of egg volume in echinoids. In an unreported analysis, I used an extreme scaling factor of 0.67 and found results qualitatively similar to those of this analysis. So although using a scaling factor of 1 is supported by the overall data, the qualitative predictions of the model do not hinge on this assumption.

Unlike that in previous models, the relationship between egg size and development time is not linear but proportional:

$$T = (S_\mathrm{fp}/S_\mathrm{a} - 1) + T_\mathrm{fp}, \tag{7}$$

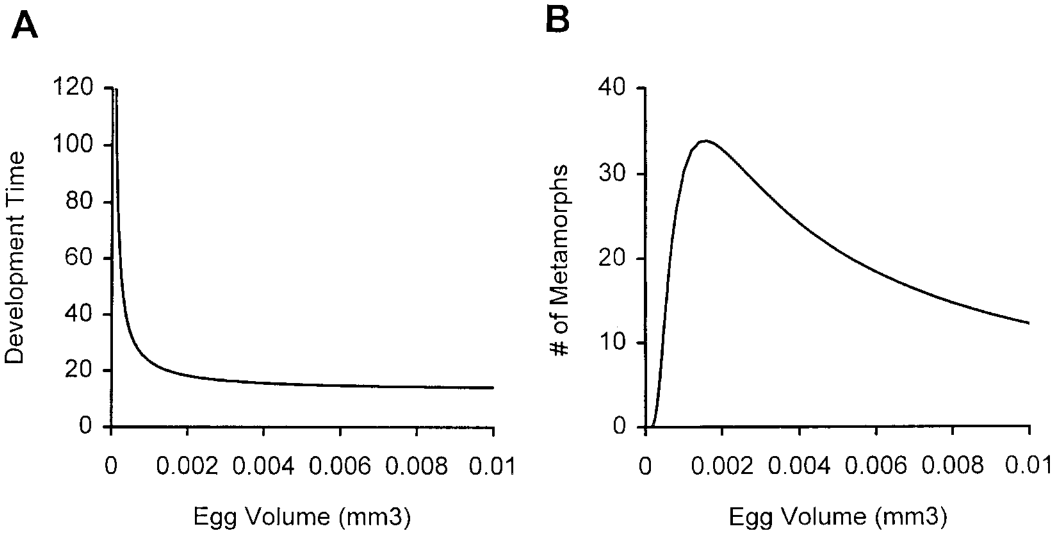

**Figure 2:** Consequences of an inverse proportional relationship between egg volume and development time. *A*, Plot of equation (7) using an egg volume of 0.0103 mm$^3$ for $S_{fp}$ and a development time of 14 d for $T_{fp}$ (at 20°C). See appendix for empirical data on the facultative planktotroph *Clypeaster rosaceus*. *B*, Plot of equation (6) using the inverse proportional relationship between egg size and development time, $C = 1$, and $M = 0.15$. Note the contrast between this humped curve and the U-shaped curve plotted in figure 1 on the basis of a negative linear relationship.

where $S_{fp}$ is the volume of egg needed to provide enough energy for a facultative planktotroph larva to develop, to complete metamorphosis, and to survive, all without feeding, until it can feed as a metamorph, and $T_{fp}$ is the development time of that larva. Note that, when $S_a = S_{fp}$, $T = T_{fp}$. Thus, this model assumes that it takes a certain time period to build a larva ready to undergo metamorphosis ($T_{fp}$) and that any deficiency in the energy needed to develop and to grow must be filled from feeding in a proportional fashion.

Smaller eggs might take longer to develop through metamorphosis than larger eggs for at least three reasons. First, as the amount of yolk decreases, the larvae are required to feed for longer periods in the plankton to make up the deficit, even when food is abundant. It takes time to capture, to handle, and to process phytoplankton even when food is not limiting. Second, smaller eggs produce smaller larvae and smaller arms for filtering food (see, e.g., Sinervo and McEdward 1988; Aslan et al. 1999). Smaller larval arms clear phytoplankton more slowly (Hart and Strathmann 1994; Hart 1995), so smaller larvae cannot feed as efficiently as larger ones. The resulting lower rate of energy acquisition should increase development time. Finally, in planktotrophic echinoids, egg size is independent of size at metamorphosis (see "Assumption of the Independence of Egg Size and Size at Metamorphosis"; Emlet et al. 1987). Species that produce smaller eggs must grow more and develop longer to reach metamorphosis than do species that produce larger eggs (Sinervo and McEdward 1988; Herrera et al. 1996).

Here, I use the development time and egg volume of *Clypeaster rosaceus* for $S_{fp}$ and $T_{fp}$. *Clypeaster rosaceus* has the smallest reported egg size of any echinoid facultative planktotroph and, thus, provides the best available estimate of the minimal echinoid egg size needed for development without feeding. The key difference from Vance's model (1973*ba*) and its modifications (reviewed in Havenhand 1995) produced by the proportionality assumption is that it produces a curvilinear relation between egg size and development time (fig. 2*A*).

Substituting equation (7) into the model (eq. [6]) produces a humped fitness curve with an intermediate optimal egg size (fig. 2*B*). This result contrasts with the U-shaped fitness curve predicted by Vance's model (fig. 1).

## *Shifts in Optimal Egg Size Based on Environmental Conditions*

Planktonic mortality (Rumrill 1990), food availability (Strathmann 1987*b*; Olson and Olson 1989; Fenaux et al. 1994), water temperature (Emlet et al. 1987; Emlet 1995), and fertilization rates (Levitan 1995; Levitan and Petersen 1995) have been shown to influence either development time or the survivorship of eggs and larvae. Below, I model the effect of each of these factors on egg size and compare the sensitivities of the factors over a fivefold range typical of natural variation noted in the field.

*Variation in Planktonic Mortality.* Estimates of daily planktonic mortality among echinoids range from 0.0625 to 0.2658 ($\bar{X} = 0.1615$; Rumrill 1990). Initially, I used the assumption of constant daily mortality that is independent of larval size, shape, and age. The model indicated that, as mortality increased, predicted optimal egg size shifted from intermediate to larger sizes. A 400% increase in mortality ($M = 0.05$–$0.25$) resulted in a 420% change in optimal egg volume (fig. 3*A*).

Because larval size may influence mortality rate (Rumrill et al. 1985; Pennington et al. 1986), I also modeled a functional relationship between egg size and mortality, such that the size-dependent mortality rate ($M_s$) is inversely related to egg size,

$$M_s = M(S_{\mathrm{fp}}/S_{\mathrm{a}}). \qquad (8)$$

A 400% increase in mortality ($M = 0.0005$–$0.0025$, resulting in $M_s = 0.0005$–$0.116$) resulted in a 178% change in optimal egg volume. This result changes the quantitative predictions but not the qualitative conclusion that selection on egg size shifts between various intermediate optima. This prediction is fundamentally different from that of Vance, that optimal egg size alternates between two extreme states (Vance 1973*b*).

*Variation in Food Availability.* The rate of gathering energy is likely to depend on the concentration of food resources in the water. Laboratory and field experiments have documented that low food availability can increase development times (Strathmann 1987*b*; Olson and Olson 1989; Fenaux et al. 1994). The effect of food availability was modeled on the assumption that the proportion of available resources ($R = 0$–$1$) was equivalent to proportionate reduction of egg volume in its effect on development time

$$T_R = [(S_{\mathrm{fp}}/S_{\mathrm{a}} - 1)/R] + T_{\mathrm{fp}}. \qquad (9)$$

Like variation in mortality rate, variation in food limitation results in continuous variation in optimal egg size (fig. 3*B*). When daily mortality was held constant at 0.15, a 400% increase in food availability ($R = 0.2$–$1.0$) resulted in a 406% change in optimal egg volume.

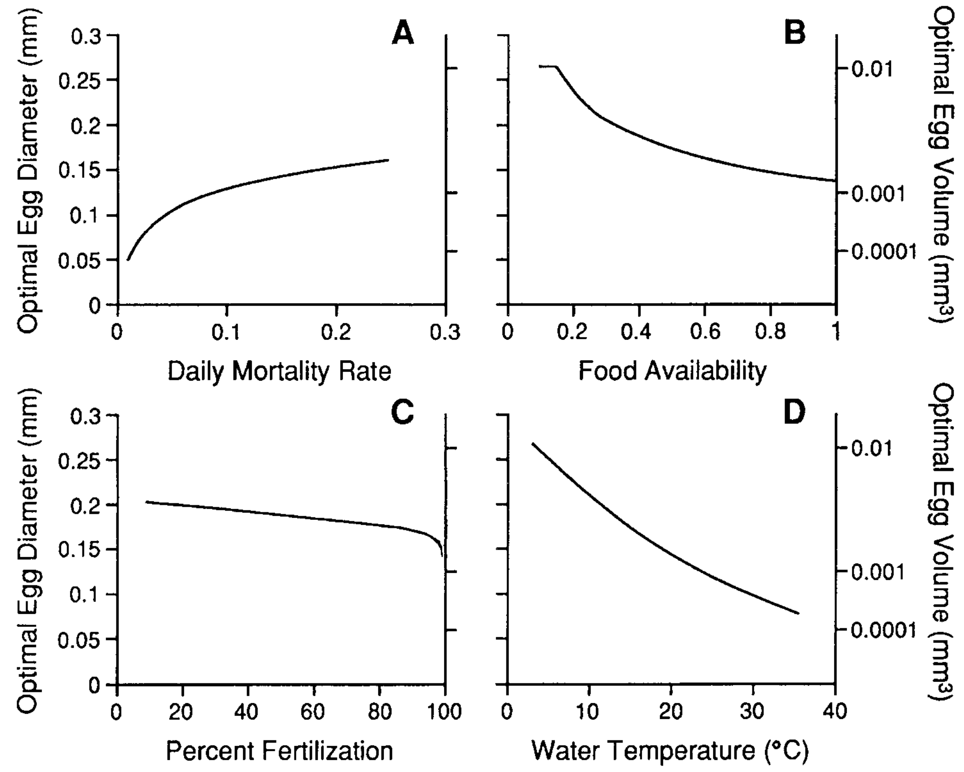

**Figure 3:** Modeled variation in parameters influencing optimal egg size. *A*, Variation in daily mortality rate. *B*, Variation in food availability. *C*, Variation in fertilization success. *D*, Variation in water temperature.

*Variation in Fertilization Rates.* Fertilization rates of broadcast-spawning invertebrates and echinoids in particular are highly variable (Levitan 1995). In addition, fertilization rates are directly correlated with egg size within individuals, species, and genera of sea urchins (Levitan 1993, 1996*b*, 1996*c*, 1998). The proportion of eggs fertilized ($F$ ) was modeled with Vogel et al.'s (1982) fertilization kinetics:

$$F = 1 - \exp\left[-\beta S_0/\beta_0 E_0(1 - e^{-\beta_0 E_0 t})\right], \tag{10}$$

where $\beta$ is the fertilization constant (mm$^3$/s), $\beta_0$ is the sperm-egg collision constant (mm$^3$/s), $E_0$ is the egg concentration ($n/\mu$L), $t$ is the sperm-egg contact time ($s$). Egg size enters into the model in the calculation of the collision constant, where $\beta_0$ is the product of sperm velocity (mm/s) and egg cross-sectional area (mm$^2$).

I varied sperm concentration to find the optimal egg size in the model. The ratio of sperm-egg collisions to fertilizations ($\beta/\beta_0$) was held constant at 0.05117 (Levitan 1993), the egg concentration ($E_0$) at 0.01/$\mu$L (Levitan 1996*b*, 1996*c*), sperm velocity at 0.13 mm/s (Levitan 1993), and sperm-egg contact time ($t$) at 10 s (Levitan 1996*b*, 1996*c*). Fertilization success was inserted into the model as

$$N_T = [F(C/S_a)]e^{-MT}. \tag{11}$$

When daily mortality ($M = 0.15$) and resource availability ($R = 1.0$) were held constant, varying sperm concentration to cause a 400% increase in fertilization success of 0.270 mm eggs (20%–100%) resulted in a 163% change in optimal egg volume (fig. 3*C*).

*Variation in Water Temperature.* Development time in echinoids is inversely related to water temperature (Emlet et al. 1987; Strathmann 1987*b*; Emlet 1995). Assuming a $Q_{10}$ value of 3 (Emlet 1995), I calculated the adjusted developmental rates ($T_2$) over a range of typical seawater temperatures using the formula

$$T_2 = \{(1/Q_{10})^\wedge[(Z_2 - Z_1)/10]\} + T_1, \tag{12}$$

where $T_1$ is the predicted development time from equation (7), $Z_1$ is a baseline water temperature of 20°C, and $Z_2$ is the modeled water-temperature shift.

When daily mortality ($M = 0.15$), resource availability ($R = 1.0$), and fertilization success ($F = 1.0$) were held constant, a 400% increase in water temperature (2.5°–25°C) resulted in a 788% change in optimal egg volume (fig. 3*D*).

## Relationship between Egg Size and Development Time

The model suggests that, if the relationship between egg size and development time is proportional rather than linear, intermediate egg sizes are optimal, rather than extremes in egg size. The humped rather than U-shaped fitness curve is critical because, in the former, the optimal value shifts continuously with variation in the model's parameters. This result provides a potential explanation for the continuum of egg size noted among planktotrophic species (e.g., fig. 1). When the fitness function is U-shaped, the selection gradient against intermediate optima is too great to result in anything but extremes in egg size, regardless of the parameter values (see, e.g., Podolsky and Strathmann 1996). Because the functional relationship between egg size and development time has such critical implications for these life-history models, it is important to evaluate this relationship with empirical data. This is not a trivial task for two reasons. The first is that, even under controlled conditions in the laboratory, variation in water temperature, food quality and quantity, and laboratory protocols can introduce wide variation in development times. The second is that, without a good understanding of the phylogenetic relatedness across taxa, patterns may arise that do not reflect the true evolutionary association of these two traits. Below, I address both these issues.

### *Empirical Data from the Laboratory*

Comparisons of development time across taxa spread over a large geographic area are difficult because developmental rates depend greatly on temperature. Emlet et al. (1987) could not detect a significant effect of egg size on development time in planktotrophic echinoids. The lack of significance was a result of high variance in temperature, which is negatively correlated with development times (Emlet et al. 1987). Emlet (1995) did not find a significant effect of egg size on development time over a wide geographic range of planktotrophic echinoid species until he adjusted the development times for temperature. He noted that $Q_{10}$ values ranged from 3.0 to 3.6 in echinoids (Cameron et al. 1985; McEdward 1985) and found a significant negative correlation of egg size with development time over this range, but he did not consider the shape of this negative relationship. Previously, I (Levitan 1996*c*) reported data for a small group of temperate and tropical echinoids analyzed separately and found a negative curvilinear relationship in each case. Here, I use a much larger data set collected from the literature (appendix) and adjust the development time by temperature using $Q_{10}$ values. In situations where more than one datum was available for a species, the temperature adjustment was made first, and then the average value was used in the analysis. Values of $Q_{10}$ were first set at 3.0 and 3.6, and then, because empirically derived $Q_{10}$ values may vary among species, I used randomly assigned $Q_{10}$ values between 3.0 and 3.6 for each species in 10 independent iterations (table 1). The results are similar whether constant or randomly assigned $Q_{10}$ values are used. There is a strong negative curvilinear relationship between egg size and development time. The shape of this relationship is described by the inverse proportional relationship of equation (7) (fig. 4).

These data may be confounded by species differences in culturing protocols, but a curvilinear relationship is also apparent in smaller analyses from single laboratories (Levitan 1996*c*). Some of the variation around the regressions may be caused by variation in laboratory protocols, but there is no reason to suspect that these protocols are biased as a function of egg size.

One caveat is that, when asteroid species are reared at extreme temperatures, $Q_{10}$ values decrease at relatively high temperatures and increase at relatively low temperatures (Hoegh-Guldberg and Pearse 1995). These are not absolute temperature effects but relative to the species' ambient developmental temperature. The $Q_{10}$ values, but not developmental rates (which also are lower at lower temperatures), are similar at ambient temperature for warm- and cold-water species. This result suggests the existence of adaptation of the physiological processes characterized by the $Q_{10}$ to a particular temperature regime. The validity of assuming moderate $Q_{10}$ values across a large range of temperatures may hinge on how quickly the processes characterized by $Q_{10}$ can adapt to different temperature regimes, relative to egg-size evolution.

The proportional relationship for planktotrophic species also describes the patterns of egg size and development time in lecithotrophic echinoid species with larger eggs (fig. 4). As egg size increases, development time of obligate and then facultatively feeding larvae asymptotically approaches the development time of yolk-filled, nonfeeding larvae. A potential explanation for this pattern is that once egg size reaches the energetic threshold where feeding is facultative, development time may be at a constrained minimum dictated by the time needed to build a juvenile (McEdward 1997). The additional egg investment found in lecithotrophs is reflected in an increased size and energetic content at metamorphosis, consistent with the observation that lecithotrophic species often produce larger metamorphs than do planktotrophic species (Emlet and Hoegh-Guldberg 1997).

### *Phylogenetic Analysis*

Comparisons of the functional relationships between two or more traits across taxa can be confounded by failure to adjust for their phylogenetic relatedness (Felsenstein 1985). If, for example, small eggs evolved once and the clade having small eggs happened to have large variation in development time, but the clade having large eggs had small variation in development time, then plotted on the same graph the two clades might produce a curvilinear relationship. To determine whether the inversely proportional relationship between egg size and development time noted in extant species represents the evolutionary relationship between egg size and development time in echinoids, I used the comparative method (Harvey and Pagel 1991).

**Table 1:** Regression estimates of the relationship between developmental time and egg size (log egg size [$\text{mm}^3$] + 4) using a $Q_{10}$ temperature adjustment

| $Q_{10}$ values | *c* | *b* | $r^2$ |
|---|---|---|---|
| Constant: | | | |
| 3.0 | 23.70 | −.67 | .45 |
| 3.6 | 23.47 | −.75 | .44 |
| Variable (iteration): | | | |
| 1 | 23.54 | −.73 | .45 |
| 2 | 23.75 | −.73 | .47 |
| 3 | 23.45 | −.72 | .44 |
| 4 | 23.03 | −.70 | .44 |
| 5 | 23.57 | −.72 | .43 |
| 6 | 23.20 | −.72 | .44 |
| 7 | 23.54 | −.71 | .44 |
| 8 | 23.69 | −.72 | .44 |
| 9 | 23.65 | −.72 | .45 |
| 10 | 23.59 | −.72 | .45 |
| $\bar{X}$ | 23.59 | −.72 | .45 |
| SE | .068 | .003 | .004 |

Note: A value of $Q_{10}$ between 3.0 and 3.6 was assigned randomly to each species. The data were fit by means of a power equation ($y = cx^b$). Values of *c*, *b*, $r^2$ are presented for each iteration as well as the mean and standard error (SE).

A composite phylogeny was constructed that included all planktotrophic species for which data were available on egg size, development time, ambient temperature, and phylogenetic relatedness. The foundation of the tree was based on that of Littlewood and Smith (1995). Where additional phylogenies could be unambiguously spliced into that tree, they were simply added. Congeners were assumed to be sister taxa in the absence of contradictory evidence, and if more than two congeners were represented by life-history data but without a phylogenetic hypothesis, a polytomy was constructed. I was able to construct a phylogeny using 37 species with only four nodes unresolved (fig. 5).

Lecithotrophic development in echinoids is generally thought to be a derived condition (Strathmann 1978*a*;

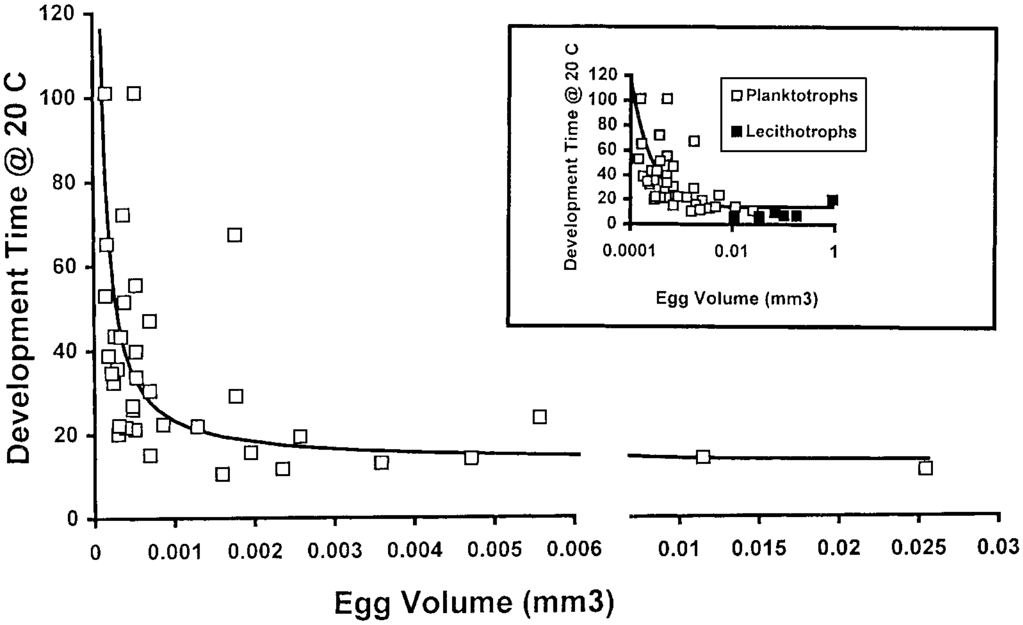

Figure 4: Model prediction and empirical relationship between egg volume and development time at 20°C. Curved line is a plot of equation (7). Open square symbols are temperature-adjusted empirical data from the appendix. A linear relationship fits the data poorly (development time = $-1668.5$ egg volume $+ 38.656$; $R^2 = 0.107$) compared to equation (7) (see fig. 6*a* and table 2 for fit of model to data with an $R^2 = 0.509$). Note the break in the scale between the egg sizes of 0.006 and 0.01. Inset shows how model fits both planktotrophic (*open symbols*) and lecithotrophic (*solid symbols*) species. Lecithotrophic data from Emlet (1995).

Emlet et al. 1987), and those species were not included in the analysis. The evolutionary transition to, and among, lecithotrophic species involves great changes in egg volume but little or no change in development time (fig. 4). This pattern is consistent with the use of this excess egg material in postmetamorphic processes (Emlet and Hoegh-Guldberg 1997) and is beyond the scope of the current model. A potential reason for including these species would be to increase the accuracy of the calculated ancestral character states used for the independent contrasts. However, because the rate of evolutionary change during the transition to lecithotrophy may be greater than among planktotrophic species (Wray and Raff 1991; Hart 1996), the inclusion of lecithotrophs could have a misleading effect on ancestral character states. For example, under the punctuational model of evolution used in the analysis of contrasts (see below), a planktotrophic ancestor that gave rise to a clade of planktotrophic and lecithotrophic species would be estimated to have transitional life-history traits. Given an accelerated rate of evolution during transition (Wray and Raff 1991), it may be more likely that this ancestor had planktotrophic life-history traits. This is an interesting line of research, worth pursuing, but without more data on the life history, the phylogenetic placement, and especially the evolutionary rates during the transition to lecithotrophy, evaluating it would be premature. The consequences of not including those data in the present context is not likely to be great because the model predicts the relationship between egg size and development time in the few extant lecithotrophic species for which there are life-history data.

### *Independent Contrasts*

Independent contrasts (Felsenstein 1985) represent the evolutionary change, between sister taxa, across each branch point, in two or more traits. Because the difference in trait values between sister taxa represents a unique evolutionary event, each contrast is independent of all other events, avoiding the problem of pseudoreplicating the analysis of character evolution. Unbiased examination of the pattern of evolutionary correlation of traits can then be conducted from a plot of the contrast in one trait (development time) against the contrast in another (egg size) across all ancestral and terminal branch points. If the slope of this plot is positive or negative and the intercept passes through the origin, then evolution in the first trait is associated with evolution in the second. The slope of the relationship indicates the functional relationship between the two traits as they have coevolved.

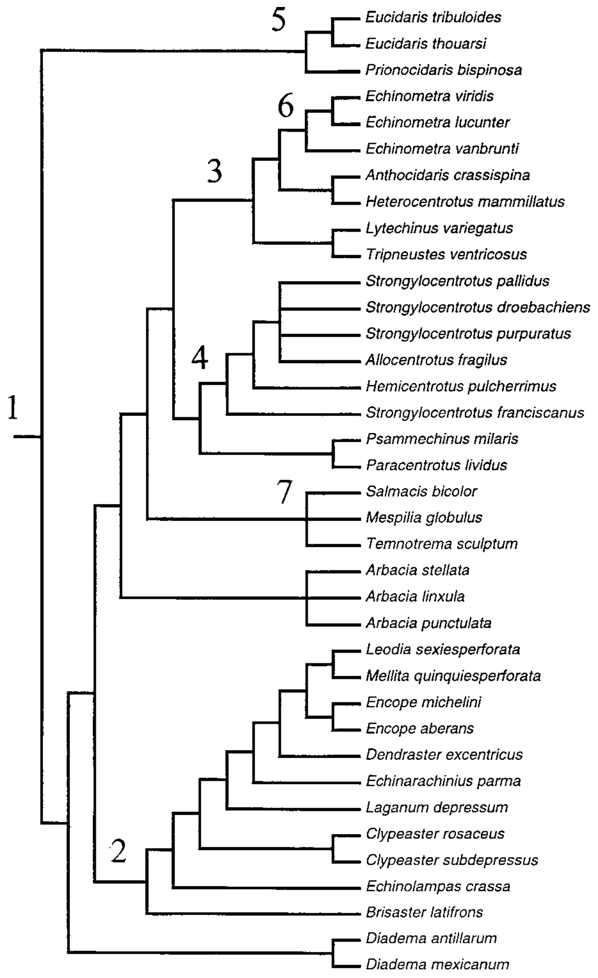

**Figure 5:** Phylogeny of echinoid taxa. Numbers indicate reference for justification for that node and all descendant branch points until the next number is reached. 1 = Littlewood and Smith (1995); 2 = Mooi (1987, 1990); 3 = Smith (1988); 4 = Biermann (1998); 5 = *Prionocidaris bispinosa* is the only remaining species in the subclass Cidaroidea and is placed as a sister to the *Eucidaris* species; 6 = McCartney (unpublished data) mitochondrial sequences; 7 = *Temnotrema sculptum* is the only remaining species in the order Temnopleuroida and is placed with the other two genera in that order.

The first step in this analysis was to transform the data to make the relationship between egg size and development time linear (natural log and inverse transforms, respectively; fig. 6*A*) because, if the true relationship is curvilinear, then the degree of change on one axis depends on the absolute value of that on the other. Specifically, at a large egg size, small changes in size are not predicted to have a large effect on development time, but at small egg sizes, a similar change would have a drastic effect on development time. The result would be a plot of comparisons that could have either a positive or a negative slope dependent on the distribution of samples. If the data are transformed to a linear relationship, however, a change on one axis should be correlated with a constant and proportional change on the other axis, regardless of the distribution of data along one axis.

The second step was to calculate the ancestral character states for each node on the phylogeny for each trait. I did so using MacClade (Maddison and Maddison 1992) with Maddison's (1991) algorithm for squared-change parsimony, a method capable of calculating ancestral character states when polytomies are present.

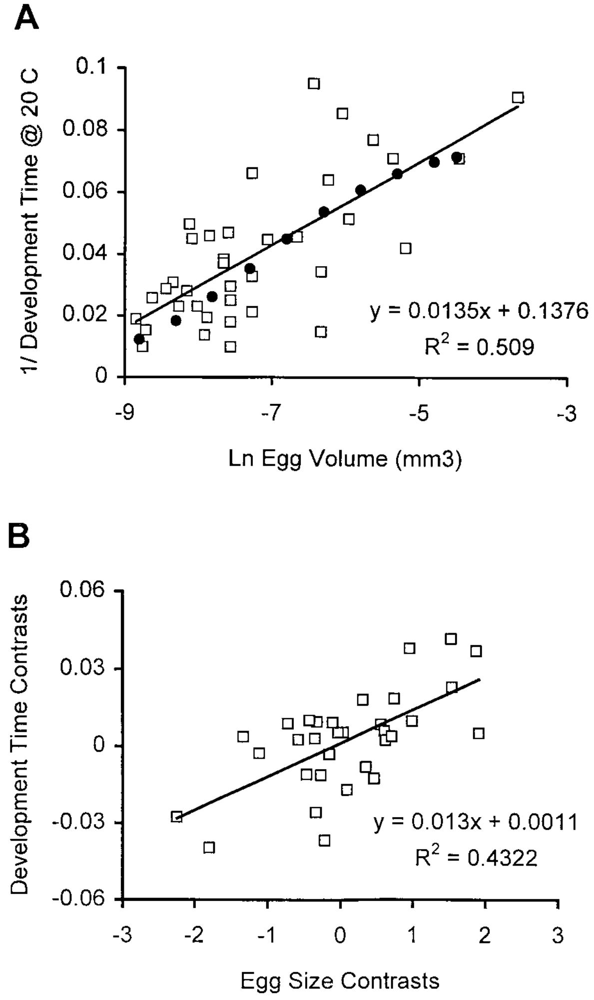

**Figure 6:** Inverse and natural log transformed relationship between development time and egg volume using extant species and phylogenetic relationships. *A*, Extant species relationship (*open squares*) and prediction of equation (7) (*solid circles*). Regression equation and $R^2$ of empirical data shown. Linear approximation of equation (7) (*solid circles*) is $y = 0.0145x + 0.1408$. Linear approximation of linear relationship of untransformed data is $y = 0.0043x + 0.0595$. *B*, Plot of independent contrasts of transformed development time and egg size from phylogenetic reconstruction of ancestral character states.

**Table 2:** Tests of hypotheses comparing the intercept (0.001135, SE = 0.002604) and slope (0.012993, SE = 0.002719) from the regression of development time contrasts (inverse transformation) as a function of egg size contrasts (natural log transformation)

| Hypothesis | *t* value | *P* value |
|---|---|---|
| 1. Intercept = 0 | .436 | >.5 |
| 2. Slope = 0 | 4.779 | <.0001 |
| 3. Slope = .135 (extant-species relationship) | .186 | >.5 |
| 4. Slope = .147 (approximation of proportional model) | .039 | >.5 |
| 5. Slope = .0043 (approximation of linear model) | 3.197 | <.01 |

Note: Student's *t*-test of intercept versus (1) zero and of slope versus (2) zero, (3) the extant-species relationship, (4) a linear approximation of the proportional model after a similar transformation, and (5) a linear approximation of the untransfromed linear relationship in the extant-species relationship (after a similar relationship). See fig. 6*A*.

The third step was to calculate the difference in trait values across each branching point on the tree. In the absence of information on branch lengths, I assumed a punctuational model of evolution and assigned equal branch lengths between nodes (Harvey and Pagel 1991). Where polytomies were present, differences were calculated by the method of Pagel and Harvey (1989; Harvey and Pagel 1991). This technique first divides members of a polytomy into two groups—those above and those below the mean value for that trait—and then weights each member by multiplying the trait value by the inverse of the number of members in each group. Those members above the mean are given a positive sign, those below are given a negative sign, and then all are summed to yield an estimate of the difference.

All the contrasts across each node were calculated for both traits and then plotted (fig. 6*B*). Regression analysis (table 2) indicates that the intercept is not significantly different from 0, and the slope is not significantly different from either the slope of the absolute values of the extant species or a linear approximation of the model assumption (eq. [7]). However, the slope is significantly different from an approximation of a negative linear relationship like that assumed by Vance (1973*b*) and others (e.g., Podolsky and Strathmann 1996; McEdward 1997). Egg size and development time in planktotrophic echinoids coevolved in the proportional manner illustrated in figure 4.

Emlet (1988) suggested, on the basis of morphological features noted in photographic plates from McPherson's (1968) study, that McPherson, although purportedly rearing *Eucidaris tribuloides*, might inadvertently have been rearing a species of either *Echinometra* or *Tripneustes*. I reanalyzed the independent contrasts without including *Eucidaris tribuloides*, and the results are nearly identical to those of the full analysis. Regression of the independent contrasts of the reanalyzed data yields the equation $y = 0.014x + 0.0014$ ($R^2 = 0.4642$; see fig. 6*B* for comparison). This controversy has no bearing on the present analysis.

### *Assumption of the Independence of Egg Size and Size at Metamorphosis*

To test the assumption that size at metamorphosis is independent of egg size, I created an abridged phylogeny including only the 25 species for which size at metamorphosis was reported (see appendix). In this subsample of 25 species, the coefficient of variation is 199% for egg volume and 78% for size at metamorphosis; much of the initial variation in offspring size is eliminated at settlement. Interestingly, plots of the extant species values indicate that size at metamorphosis is weakly but negatively related to egg size (fig. 7*A*). This apparent dependence disappears when the influence of phylogeny is considered. Using the phylogeny and extant species values, I estimated the independent contrasts for egg size (natural log transformed) and size at metamorphosis (fig. 7*B*). Regression analysis indicates that size-at-metamorphosis contrasts are independent of egg-size contrasts ($P = .68$, $R^2 = .008$); the evolution of size at metamorphosis is independent of the evolution of egg size.

## Discussion

Vance's assumption that the relationship between egg size and development time is linear had a profound influence on his predictions and the subsequent literature on marine reproductive life-history theory (Vance 1973*b*; Strathmann 1985; Havenhand 1995). When this assumption is replaced by a proportional relationship, optimality models predict intermediate egg sizes that shift continuously in response to a variety of environmental variables. Every environmental factor modeled resulted in the same qualitative conclusion; extremes in egg size were never predicted.

### *Model Assumptions*

The critical assumption of this model, that egg size and development time are inversely and proportionately related, is confirmed by the analysis not only of the extant species relationship but also of the pattern of evolutionary changes in planktotrophic echinoids. Shifts in egg size have commonly occurred through time, and they are concurrent with proportional shifts in development time.

Development times of experimentally reduced eggs have also been studied in the echinoid *Strongylocentrotus droe-*

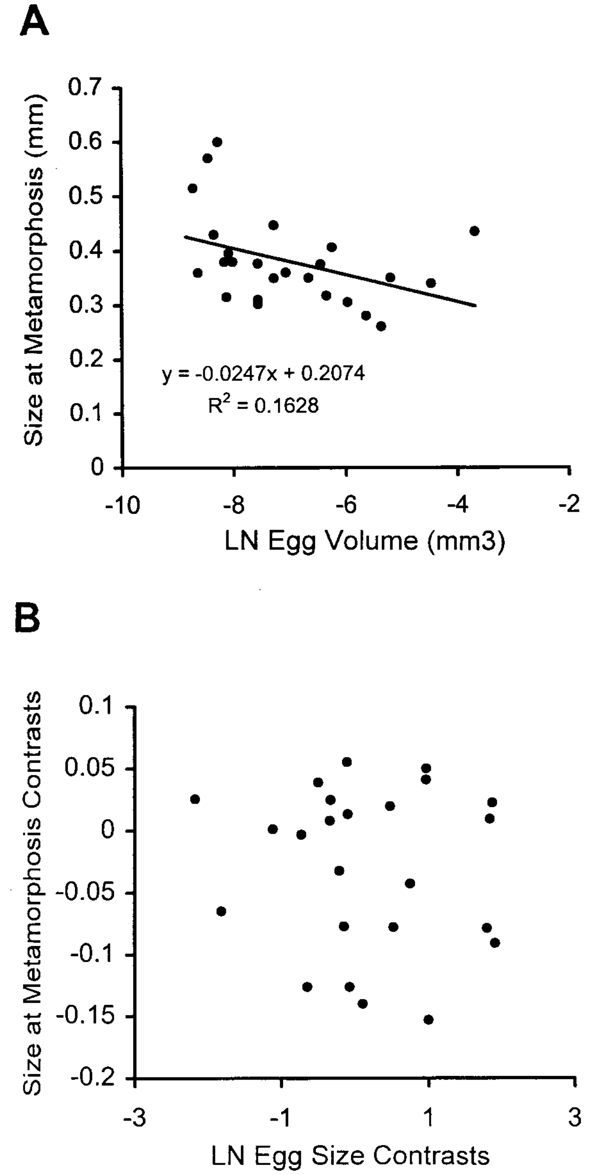

**Figure 7:** Relationship between egg size and size at metamorphosis in planktotrophic echinoids (see appendix for data). *A*, In the analysis of the extant species, there appears to be a slight negative relationship between egg and metamorph size; larger eggs produce smaller juveniles. *B*, Independent contrasts, however, indicate there is no evolutionary relationship between egg and metamorph size. Egg size evolved independently of metamorph size, and the apparent relationship noted in *A* is a result of species sharing traits by descent.

*bachiensis* (Sinervo and McEdward 1988; Hart 1996). In Sinervo and McEdward's study, a 50% reduction in egg size resulted in a 29% increase in development time (estimated from their fig. 3*a*). In Hart's study, a similar reduction in egg size resulted in a nonsignificant 7% increase in development time. *Strongylocentrotus droebachiensis* has large planktotrophic eggs (155 $\mu$), a size at which the relationship between egg size and development time is relatively flat (fig. 4). The present model predicts a 28% increase in development time for halved eggs of this size. It is therefore not surprising that these experimental studies noted only small increases in development time after egg size was halved.

The additional assumption that egg size is independent of size at metamorphosis is also confirmed by independent contrasts (fig. 7*B*), a result highlighted by comparisons within genera. For example, *Strongylocentrotus purpuratus* and *S. droebachiensis* differ sixfold in egg volume, yet both settle at 400 $\mu$ (Sinervo and McEdward 1988). *Clypeaster subdepressus* and *Clypeaster rosaceus* differ sevenfold in egg volume, yet both settle at 340 $\mu$ (Herrera et al. 1996). In both cases, the species with smaller eggs requires a longer developmental period to reach the conserved size at metamorphosis. One interpretation of these results is that egg size and development time trade off to produce a similar size at metamorphosis, which represents the threshold size at which the benefits of a benthic lifestyle outweigh the costs of a planktonic lifestyle. One set of selective factors may therefore influence size at metamorphosis (the relative costs of planktonic and benthic lifestyles) and another may determine the trade-off of egg size and development time (planktonic success) given a specific size at metamorphosis. If size at metamorphosis depends on egg size in other taxa, then both pre- and postmetamorphic factors would influence selection on egg size.

The verification of the extant-species relationship between egg size and development time and the rejection of the extant-species relationship between egg size and size at metamorphosis underscore the usefulness of phylogenies in estimating the evolutionary relationships between these critical life-history traits.

### *Predictions and Patterns of Egg Size*

All environmental factors I modeled resulted in continuous shifts in optimal egg size. The rank order of the sensitivity of optimal egg size to a 400% change in the parameter value was fertilization (163%), size-dependent mortality (178%), food availability (406%), size-independent mortality (420%), and water temperature (788%). The effects of the parameter values were not linear, however, and often optimal egg size was particularly sensitive to extreme parameter values (fig. 3).

Higher sensitivity to a factor does not necessarily imply greater importance of that factor to the evolution of egg size; influence on evolution should be conferred by a combination of sensitivity to that factor and the factor's variability in nature. The effect of temperature may provide insight into large biogeographical, or perhaps seasonal, patterns of egg size and development mode but may be less helpful in explaining why species with similar ranges and spawning seasons have dissimilar egg sizes. Within a region and season, temperature may not vary nearly as much as mortality, food availability, and fertilization, which all depend to some degree on fluctuations in populations (predators, prey, and mates) and the patchy, turbulent nature of planktonic systems. For example, *S. franciscanus* and *S. purpuratus* have completely overlapping species ranges from Baja California to Alaska on the west coast of North America, yet their egg sizes differ fourfold. They spawn during the same season (Rumrill 1987; Levitan 1993, 1996*b*, 1998) and often simultaneously (D. R. Levitan, unpublished data), larvae are found in the water column at the same time (Rumrill 1987), and size at metamorphosis is similar (McEdward 1986). They differ, however, in estimated fertilization rates, which are high in *S. purpuratus* and lower and more variable in *S. franciscanus* (Levitan 1996*c*, 1996*b*, 1998) and which, models suggest, can explain the egg-size differences (Levitan 1996*b*, 1996*c*). Optimality models and field data also predict the even larger egg sizes observed in a third co-occurring congener, *S. droebachiensis*, because of fertilization differences (Levitan 1993, 1996*c*, 1998), but this study suggests that the overlapping but higher-latitude distribution of this species may also contribute to its larger egg size through the effect of temperature on development time.

Lessios (1990) examined the degree to which adaptation and phylogeny influenced egg size in echinoderms across the Isthmus of Panama. He noted that six of seven geminate species pairs, isolated from one another for approximately 3 million years, showed significantly smaller egg size in the Pacific than in the Caribbean (mean 26% difference in volume). Differences among genera are larger than differences between members of geminate pairs and persist across the isthmus. Lessios proposed that environmental differences, such as the higher planktonic food availability in the Pacific, may have caused a general shift in egg size but that genus-specific constraints may prevent all species in each ocean from converging to a common size. This analysis supports Lessios's idea that higher food availability in the Pacific (D'Croz and Robertson 1997) could result in decreased egg size, but the lower temperature there (Glynn 1972; D'Croz and Robertson, 1997) would tend to select for larger egg sizes. The counteracting forces of higher food availability and lower temperature could lead to the small but consistent differences noted among geminate species pairs. If the other taxon-specific differences in life history remain constant over the isthmus (e.g., fertilization or mortality rates), then there is no reason to expect egg sizes to converge in either ocean.

The potential for temperature to affect egg size directly or indirectly has been recognized (Thorson 1946; Emlet et al. 1987) and has been noted with respect to seasons (Patel and Crisp 1960; Emlet et al. 1987) but might be more obvious across latitudinal gradients. Within species, *S. droebachiensis* and *Strongylocentrotus pallidus* demonstrate 40%–50% increases in egg volume with increasing latitude along the coast of Norway (Hagström and Lönning 1967). More data on intraspecific trends in egg size along latitudinal gradients would be useful, particularly studies that separate genetic from environmental influences and temperature effects from other correlated traits associated with latitude, such as day or season length.

Among species, a long-established biogeographic pattern of egg size and development mode is Thorson's rule (Thorson 1950; Mileikovsky 1971): lower-latitude and shallow-water taxa have small eggs and feeding larvae, whereas higher-latitude and deeper-water taxa have larger eggs and nonfeeding larvae. Thorson suggested that low availability of food at depth in higher latitudes has selected for nonfeeding larvae, and Highsmith (1985) suggested that shifts in mortality could also cause this pattern. Neither author, however, provides an explicit mechanism or model for how food or mortality could cause this shift, and the evidence for increasing food limitation or mortality at higher latitudes or in deeper water remains equivocal (reviewed in Havenhand 1995). The model presented here indicates that a simple drop in temperature to 5°C is enough to cause optimal egg volume to increase to a size at which feeding is not required for development. If fertilization or food availability is $<100\%$ or daily mortality is $>0.15$, then this egg-size threshold is predicted to be reached at warmer temperatures. Egg-size shifts may precede the morphological shift to nonfeeding larvae (Hart 1996). If so, then the temperature differences found at higher latitudes or greater depths are enough to cause the observed biogeographical differences in development mode. That biogeographic transitions in egg size and developmental mode are not abrupt and have exceptions probably results from the dependence of factors such as mortality, resource availability, and fertilization rates on taxon, habitat, and spawning season.

A change in a simple assumption, confirmed by empirical data, results in prediction of intermediate rather than extreme egg sizes. As we learn more about larval biology and incorporate these findings into more complex models, the quantitative predictions presented here will probably change, but the task of explaining both variation in egg size and intermediate egg size, at least among echinoid species, is no longer a mathematical paradox and has instead become a process of testing a series of alternative hypotheses that could independently or in concert produce the patterns of egg sizes observed in nature.

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## APPENDIX

**Table A1:** Echinoid taxonomy, egg size (mm diameter), development time (d), culture temperature (°C), metamorph size (mm diameter), and reference

| Taxa | Egg size | Time | Temperature | Metamorph size | Reference |
|---|---|---|---|---|---|
| Subclass Cidaroidea: | | | | | |
| Order Cidaroidea: | | | | | |
| Family Cidaridae: | | | | | |
| *Eucidaris tribuloides* | .086 | 25 | 25 | .380 | Emlet et al. 1987 |
| *Eucidaris thouarsi* | .089 | 30 | 28 | … | Emlet 1988, 1995[a] |
| *Prionocidaris bispinosa* | .150 | 28 | 28 | … | Mortensen 1938 ; Emlet 1995[a] |
| Subclass Euechinoidea: | | | | | |
| Order Diadematoida: | | | | | |
| Family Diadematidae: | | | | | |
| *Diadema antillarum* | .068 | 34 | 23 | .515 | Eckert 1998 |
| | .068 | 60 | 23 | … | T. Capo, unpublished data |
| *Diadema mexicanum* | .067 | 42 | 28 | … | Emlet 1995 |
| Cohort Echinacea: | | | | | |
| Order Arbacioida: | | | | | |
| Family Arbaciidae: | | | | | |
| *Arbacia lixula* | .077 | 26 | 22 | .430 | George et al. 1990; Emlet 1995[a] |
| *Arbacia punctulata* | .074 | 60 | 23 | .460 | Harvey 1956; Emlet et al. 1987[a] |
| | .075 | 20.5 | 27 | .680 | Herrera et al. 1996 |
| *Arbacia stellata* | .065 | 22 | 28 | … | Emlet 1995 |
| Order Temnopleuroida: | | | | | |
| Family Temnopleuridae: | | | | | |
| *Mespilia globulus* | .120 | 25 | 25 | … | Emlet 1995 |
| | .080 | 35 | 26 | .377 | Onoda 1936; Emlet et al. 1987[a] |
| *Salmacis bicolor* | .100 | 23 | 25 | … | Aiyar 1935; Emlet 1995[a] |
| *Temnotrema sculptum* | .097 | 26 | 20 | … | Emlet 1995 |
| Order Echinoida: | | | | | |
| Family Echinidae: | | | | | |
| *Paracentrotus lividus* | .083 | 18 | 21 | .315 | Cellario and George 1990; Emlet 1995[a] |
| *Psammechinus miliaris* | .097 | 58 | 13 | … | Shearer et al. 1913; Emlet 1995[a] |
| Family Echinometridae: | | | | | |
| Subfamily Strongylocentrotidae: | | | | | |
| *Strongylocentrotus droebachiensis* | … | … | … | .406 | Sinvervo and McEdward 1988 |
| | .158 | 35 | 10 | … | Emlet 1995 |
| | .155 | 28 | 11 | … | Strathmann 1987 *a* |
| | .155 | 98 | 10 | … | Strathmann 1987 *a* |
| | .155 | 36.5 | 10.5 | … | Hart 1995 |
| *Strongylocentrotus franciscanus* | … | … | … | .350 | Strathmann 1987*a* |
| | .130 | 40 | 12 | … | Cameron and Schroeter 1980; Strathmann 1987*a*[a]; Emlet 1995[a] |

**Table A1:** (*Continued*)

| Taxa | Egg size | Time | Temperature | Metamorph size | Reference |
|---|---|---|---|---|---|
| | .130 | 50 | 12 | … | Cameron and Schroeter 1980; Strathmann 1987*a*[a] |
| | .130 | 37 | 16.5 | … | Strathmann 1987*a* |
| | .130 | 70 | 9.5 | … | Strathmann 1971, 1987*a*[a] |
| | .130 | 100 | 10 | … | Strathmann 1978 *a*, 1987*b*[a] |
| *Strongylocentrotus pallidus* | .165 | 35 | 10 | … | Emlet et al. 1987 |
| *Strongylocentrotus purpuratus* | … | … | … | .391 | Rowley in Strathmann 1987*a* |
| | | | | .400 | Sinervo and McEdward 1988 |
| | .080 | 30 | 15 | … | Cameron and Schroeter 1980; Emlet 1995 [a] |
| | .084 | 75 | 10 | … | Strathmann 1978 *a*, 1987*b*[a] |
| | .084 | 38 | 15 | … | Strathmann 1987 *a* |
| | .084 | 36 | 16.5 | … | Strathman 1987*a* |
| *Allocentrotus fragilis* | .110 | 141 | 10 | … | Strathmann 1979; Emlet et al. 1987[a] |
| *Hemicentrotus pulcherrimus* | .099 | 33 | 16 | … | Emlet 1995 |
| Subfamily Echinometridae: | | | | | |
| *Anthocidaris crassispina* | .090 | 37 | 23 | … | Onoda 1931; Emlet 1995[a] |
| *Echinometra lucunter* | .082 | 14 | 24 | … | Cameron 1986; Emlet 1995[a] |
| | .082 | 23 | 27 | .380 | Emlet et al. 1987 |
| *Echinometra vanbrunti* | .070 | 18 | 27 | .360 | Emlet 1995 |
| *Echinometra viridis* | .091 | 14 | 24 | … | Cameron 1986; Emlet 1995[a] |
| *Heterocentrotus mamillatus* | .100 | 42 | 28 | .302 | Mortensen 1937; Emlet 1995[a] |
| Subfamily Toxopneustidae: | | | | | |
| *Tripneustes ventricosus* | .079 | 28 | 24 | .600 | Cameron 1986; Emlet 1995[a] |
| *Lytechinus variegatus* | .110 | 14 | 24 | … | Cameron 1986 Emlet 1995[a] |
| | .110 | 11 | 27 | .485 | Herrera et al. 1996 |
| | .110 | 33 | 23 | .410 | Mazur and Miller 1971 ; Emlet et al. 1987 [a] |
| Cohort Irregulata: | | | | | |
| Order Cassiduloida: | | | | | |
| Family Cassididae: | | | | | |
| Family Echinolampadidae: | | | | | |
| *Echinolampas crassa* | .220 | 41 | 15 | .320–.380 | Clark 1923; Emlet et al. 1987 |
| Order Clypeasteroida: | | | | | |
| Family Clypeasteridae: | | | | | |
| *Clypeaster rosaceus* | .280 | 6 | 27 | .340 | Herrera et al. 1996 |
| | .280 | 7 | 27 | … | Emlet et al. 1987 |
| *Clypeaster subdepressus* | .150 | 11 | 27 | .340 | Herrera et al. 1996 |
| | .150 | 16 | 27 | … | Emlet et al. 1987 |
| Family Laganidae: | | | | | |
| *Laganum depressum* | .100 | 14 | 28 | .310 | Mortensen 1938; Emlet et al. 1987[a] |
| Family Dendrasteridae: | | | | | |
| *Dendraster excentricus* | .118 | 38 | 12.5 | .360 | Highsmith 1982; Strathmann 1987*a*[a] |
| | .118 | 21 | 15 | … | Emlet et al. 1987 |
| | .118 | 115 | 10 | … | Strathmann 1978*a*, 1987*b*[a] |

**Table A1:** (*Continued*)

| Taxa | Egg size | Time | Temperature | Metamorph size | Reference |
|---|---|---|---|---|---|
| Family Echinarachniidae: | | | | | |
| *Echinarachnius parma* | .145 | 31.5 | 10 | .375 | Harvey 1956; Emlet et al. 1987[a] |
| Family Mellitidae: | | | | | |
| *Encope aberans* | .190 | 6 | 27 | .280 | Herrera et al. 1996 |
| *Encope michelini* | .170 | 9 | 27 | .305 | Herrera et al. 1996 |
| *Leodia sexiesperforata* | .208 | 6.5 | 27 | .260 | Herrera et al. 1996 |
| *Mellita quinquiesperforata* | .110 | 6 | 27 | .350 | Herrera et al. 1996 |
| | .110 | 7 | 27 | … | Caldwell 1972; Emlet et al. 1987[a] |
| Order Holasteroida: | | | | | |
| Family Schizasteridae: | | | | | |
| *Brisaster latifrons* | .365 | 33 | 10 | .420 | Hart 1996 |

[a] Review article that compiled various data.

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