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NOTES AND COMMENTS

EVOLUTION OF EGG SIZE IN FREE-SPAWNERS: CONSEQUENCES OF THE FERTILIZATION-FECUNDITY TRADE-OFF

The role of fertilization ecology in the life-history evolution of marine organisms has received growing attention in the last decade (Pennington 1985; Denny and Shibata 1989; Levitan 1991; Petersen 1991; Oliver and Babcock 1992; reviewed in Levitan 1995). Recently, Levitan (1993) has proposed a hypothesis to explain the evolution of egg size in marine invertebrates in terms of the probability of egg fertilization. Using a model of fertilization kinetics developed by Vogel et al. (1982), Levitan predicts that larger eggs will be fertilized at a greater rate because they provide a larger target for sperm. He concludes that conditions of sperm limitation can select for larger eggs and that variation in such conditions can contribute to observed patterns of interspecific variation in egg size. Recognizing this advantage of large egg size makes an important contribution to evaluating the fitness consequences of how resources are divided among gametes. When included in life-history models that incorporate effects of size on development time and larval mortality (e.g., Vance 1973*b;* Christiansen and Fenchel 1979), the fertilization advantage could shift optimal egg size in a way that depends on sperm limitation (Levitan 1993).

To test the hypothesis that zygote production is enhanced by large egg size, however, Levitan uses an interspecific comparison in which other gamete attributes co-vary with egg size. He derives parameters for three species of the sea urchin *Strongylocentrotus*—including egg size, egg fertilizability, sperm speed, and sperm half-life—and uses them in the fertilization kinetics model to predict zygote production by each species under varying sperm concentrations. Because egg size is confounded with other species-specific characters, this comparison leads to the incorrect inference that rank order of zygote production among species is due, in part, to differences in egg size. As will be shown here, greater zygote production by *Strongylocentrotus droebachiensis* relative to its congeners results from interspecific differences in egg fertilizability and sperm half-life, not from larger egg size.

Furthermore, as Levitan points out, the fitness consequences of egg size must be evaluated within the framework of a life-history trade-off that limits egg size. For zygote production, the relevant trade-off is between the size and number of

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eggs produced from a given reproductive allocation. Thus, larger eggs are fertilized at a greater rate but are less numerous. Within this simple framework, the trade-off between fertilization and fecundity considered by Levitan would actually select for decreases in egg size under all sperm conditions. This is because the increase in fertilization alone cannot compensate for the decrease in fecundity that results from producing larger eggs.

Here we demonstrate these results formally through a simple dimensional analysis of how zygote number varies with egg diameter (d). We then explore further consequences of the fertilization-fecundity trade-off. Although this analysis is based on Levitan's model, he never explicitly examined the relationship between egg size and zygote production except in the empirical, interspecific comparison. Let the number of zygotes produced (N_z) equal the number of eggs produced (N_e) times the proportion fertilized (φ_∞),

$$N_z = N_e \varphi_\infty . \tag{1}$$

As a first approximation, assume that organic content is proportional to egg volume (Emlet et al. 1987; McEdward and Chia 1991) and that egg concentration is independent of egg volume. (Deviation from these assumptions will be considered below.) The number of eggs (N_e) produced from a given reproductive volume (V) is then inversely related to egg volume. Thus, for spherical eggs

$$N_e = \frac{V}{\frac{\pi}{6} d^3}$$

or

$$N_e = k_1 d^{-3} . \tag{2}$$

For further illustration throughout the text, when $V = 1$ mL, $k_1 = 1{,}910$ mm^3.

The proportion of eggs fertilized can be modeled by the fertilization kinetics equation of Vogel et al. (1982),

$$\varphi_\infty = 1 - \exp\left\{ -\frac{\beta}{\beta_0} \frac{S_0}{E_0} [1 - \exp(-\beta_0 E_0 \tau)] \right\}, \tag{3}$$

where S_0 is sperm concentration (per microliter), E_0 is egg concentration (per microliter), and τ is sperm half-life (or substitute sperm-egg contact time t, when $t < \tau$; in seconds). The parameters β and β_0(mm^3/s), the rate constants of fertilization and sperm-egg collision, respectively, are the only parameters that include egg size. Because both depend on area, their ratio is independent of egg size; this ratio measures the conditional probability of fertilization assuming contact between sperm and egg (or egg "fertilizability"). The term β_0, the rate constant of sperm-egg collision, is estimated as sperm speed (u_s) times the cross-sectional area of the egg ($\beta_0 = u_s[\pi/4]d^2$). Thus,

$$\varphi_\infty = 1 - \exp\{-k_2[1 - \exp(-k_3 d^2)]\}, \tag{4}$$

TABLE 1

PARAMETER VALUES FOR THREE *STRONGYLOCENTROTUS* SPECIES USED IN GRAPHICAL PRESENTATION OF MODELS

PARAMETER	SPECIES		
	S. droebachiensis	*S. franciscanus*	*S. purpuratus*
Egg diameter (mm)	.145	.135	.084
Sperm speed (mm/s)	.088	.130	.145
Sperm half-life(s) = $10^{(a\log[\text{sperm}]+b)}$:			
a	.308	.391	.457
b	3.216	2.818	2.798
β (rate constant of fertilization, mm^3/s)	.000241	.0000952	.0000459
β_0 (rate constant of collision, mm^3/s)	.00145	.00186	.00082
β/β_0 (egg "fertilizability")	.1666	.05117	.0559

NOTE.—All values are from Levitan (1993).

where

$$k_2 = \frac{\beta S_0}{\beta_0 E_0}; \quad k_3 = \frac{\pi}{4} E_0 u_s \tau .$$

Multiplying the number of eggs produced (eq. [2]) by the proportion fertilized (eq. [4]) gives the relationship between zygote production and egg size:

$$N_z = k_1 \left(\frac{1 - \exp\{-k_2[1 - \exp(-k_3 d^2)]\}}{d^3} \right). \tag{5}$$

It can be shown for relevant values of d that N_z decreases monotonically with d (i.e., $\partial N_z/\partial d < 0$ for all $k_1, k_2, k_3 > 0$). Using parameter values given by Levitan (1993) for *S. droebachiensis* (table 1), we also demonstrate graphically how the number of zygotes produced declines with increasing egg size (fig. 1). Patterns for the other two species are similar, with steepest declines in zygote production occurring at smaller egg sizes and higher sperm concentrations. Thus, although conditions of sperm limitation reduce the relative advantage of small egg size, larger eggs produce fewer zygotes at all sperm concentrations.

The reason for this decline is stated by Levitan (1993): "Egg volume increases as a cubic function . . . while egg fertilization increases as a square function of egg diameter" (p. 529). He uses this scaling argument to explain why *Strongylocentrotus purpuratus,* which has smaller eggs, should theoretically produce more zygotes than *Strongylocentrotus franciscanus*. Clearly, this advantage to the species with smaller eggs applies to any species pair that differ in egg size. Contrary to Levitan's claim, greater zygote production under sperm limitation by *S. droebachiensis* relative to the other two species (fig. 2*A*) does not result from larger egg size; as demonstrated in figure 1, *S. droebachiensis* would produce even more zygotes from eggs that were as small as or smaller than those of its two congeners. Rather, the advantage to *S. droebachiensis* results entirely from a greater frequency with which sperm-egg collision results in fertilization ("fertilizability,"

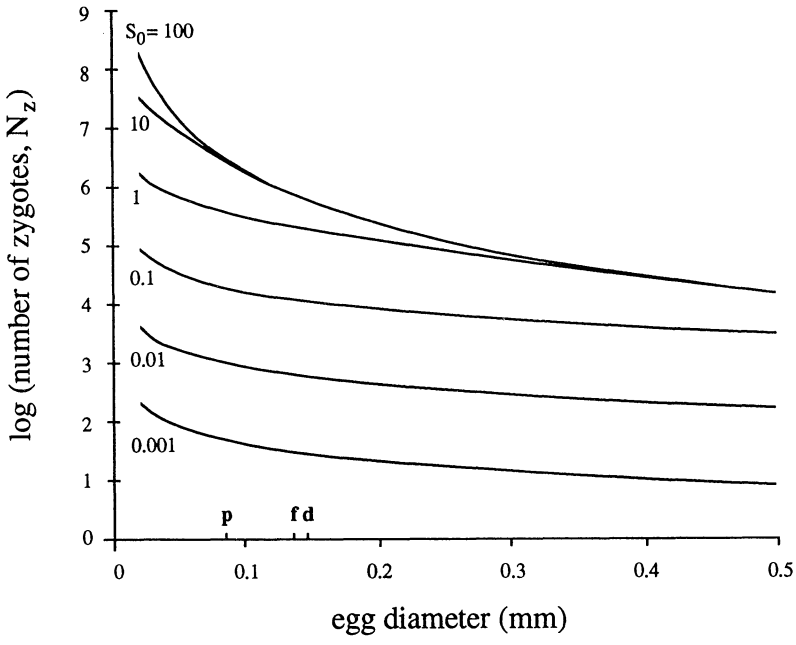

FIG. 1.—Number of zygotes produced per milliliter of egg material as a function of egg size. Curves depict different sperm concentrations, which decrease at each step by an order of magnitude. The top curve represents complete fertilization at all egg sizes. Parameters used in the model (table 1) are for *Strongylocentrotus droebachiensis* from Levitan (1993). Egg concentration is 0.01/μL. Mean egg sizes are indicated for *Strongylocentrotus purpuratus* (*p*), *Strongylocentrotus franciscanus* (*f*), and *Strongylocentrotus droebachiensis* (*d*) (Levitan 1993).

β/β_0) and greater sperm longevity (fig. 3). Unless physiological properties of the egg depend indirectly on size, neither of these characteristics is causally related to egg size.

When the effects of egg fertilizability and sperm longevity are removed by holding them equal across all three species (e.g., using parameter values for *S. droebachiensis*), zygote production becomes inversely related to egg size (fig. 2*B*). At limiting sperm concentrations, the threefold greater fertilizability shown by *S. droebachiensis* elevates its zygote production relative to that of its congeners (fig. 2*C*), and greater sperm longevity alone has a similar effect, especially at low sperm concentrations (fig. 2*D*). Thus, although larger eggs may be fertilized at a greater rate, total zygote production declines under all sperm conditions because of the loss in fecundity. For *S. droebachiensis,* this loss is compensated by the combined effects of gamete qualities other than egg size.

In theory, large egg size could have a previously unexplored, indirect benefit: the production of fewer, larger eggs could result in a lower egg concentration, which, according to the model, should increase fertilization rate (eq. [3]). It is difficult to predict exactly how egg concentration would vary with egg number under natural free-spawning conditions; rate of egg release, viscosity of spawn,

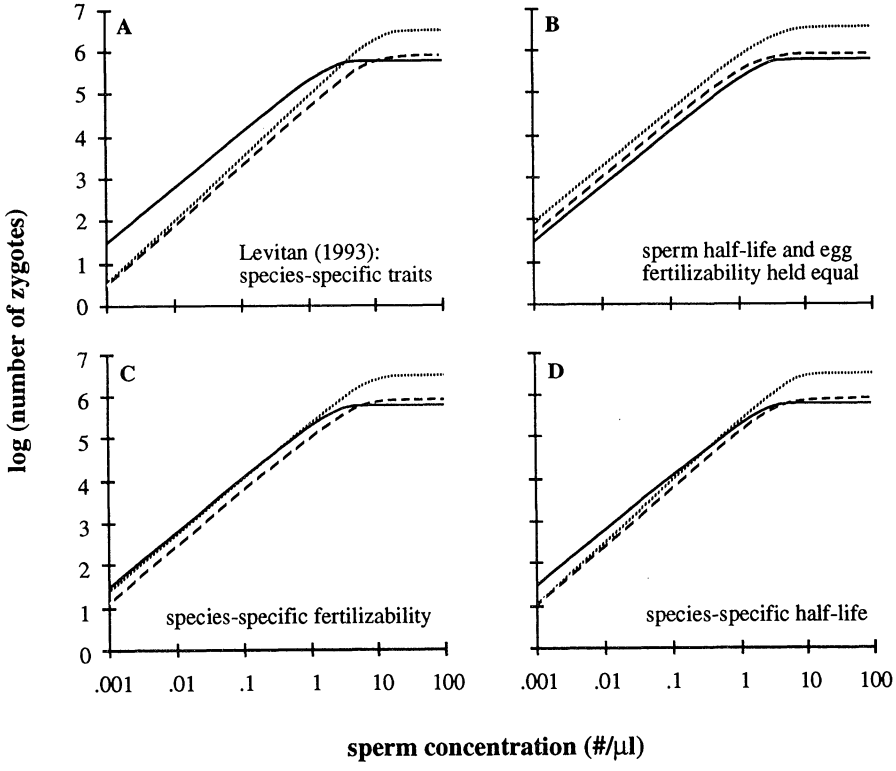

FIG. 2.—Theoretical zygote production per milliliter of egg material as a function of sperm concentration for *Strongylocentrotus purpuratus* (*dotted line*), *Strongylocentrotus franciscanus* (*dashed line*), and *Strongylocentrotus droebachiensis* (*solid line*). *A*, Reproduction of Levitan's figure (1993, p. 528, fig. 6*A*) in which all parameters are species specific (table 1). *B*, As in *A*, except that fertilizability and half-life are equal across species (using values for *S. droebachiensis*). With effects of these variables removed, zygote production is inversely related to egg size. *C*, Effect of egg fertilizability, with sperm half-life equal across species; as in *B*, except that fertilizability takes on species-specific values. Greater egg fertilizability for *S. droebachiensis* shifts its curve relatively higher. *D*, Effect of sperm half-life, with fertilizability equal across species; as in *B*, except that half-life takes on species-specific values. Greater sperm longevity for *S. droebachiensis* results in greater zygote production. The longevity effect intensifies at lower sperm concentrations (see fig. 3*B*) because the slope of the relationship between sperm concentration and longevity is shallowest for *S. droebachiensis* (Levitan 1993, p. 524).

and ambient currents can affect the strength of this relationship in a complex fashion (Thomas 1994). Nevertheless, a simple example can illustrate the point. Consider a female spawning eggs into a tide pool; egg number and concentration will then vary inversely with egg volume. Figure 4 plots zygote production according to the original model, with fixed egg concentrations (*solid lines*), and a model with size-dependent concentrations (*dashed lines*). We considered the range of egg sizes exhibited by the three *Strongylocentrotus* species (0.08–0.17 mm; Levitan 1993). (Egg concentrations for the smallest egg size are set equal in

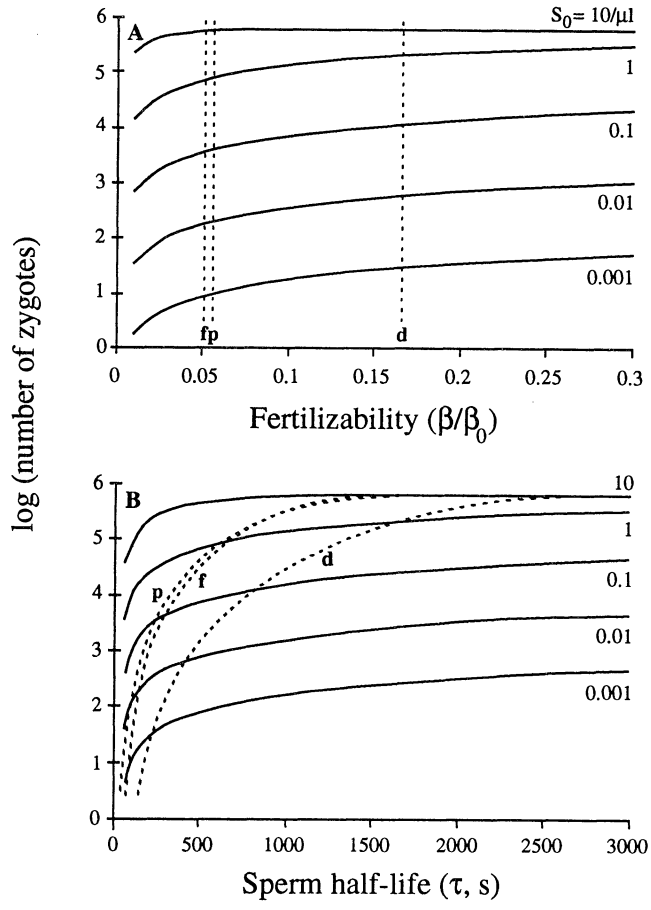

FIG. 3.—Effects of (*A*) egg fertilizability (proportion of sperm contacts that result in fertilization) and (*B*) sperm half-life on zygote production per milliliter of egg material. Solid curves depict different sperm concentrations, which decrease at each step by an order of magnitude from top to bottom. Species-specific values for egg fertilizability and sperm half-life are indicated by points of intersection between dashed and solid lines for *Strongylocentrotus purpuratus* (*p*), *Strongylocentrotus franciscanus* (*f*), and *Strongylocentrotus droebachiensis* (*d*) (Levitan 1993); in *B*, dashed lines curve because half-life depends on sperm concentration. All other parameters are as in figure 1 and table 1 for *S. droebachiensis*.

the two models; concentration then decreases according to model 2 by an order of magnitude.) The discrepancy between models 1 and 2 depends on where egg concentration starts at the smallest egg size (fig. 4). The absolute difference in zygote production is greatest around 1/μL, while the relative increase is greatest at 10/μL and higher concentrations. In this example, the effect of size-dependent concentration is to reduce the relative advantage of small eggs, but only at relatively high egg concentrations. In no case do larger eggs produce more zygotes than smaller eggs.

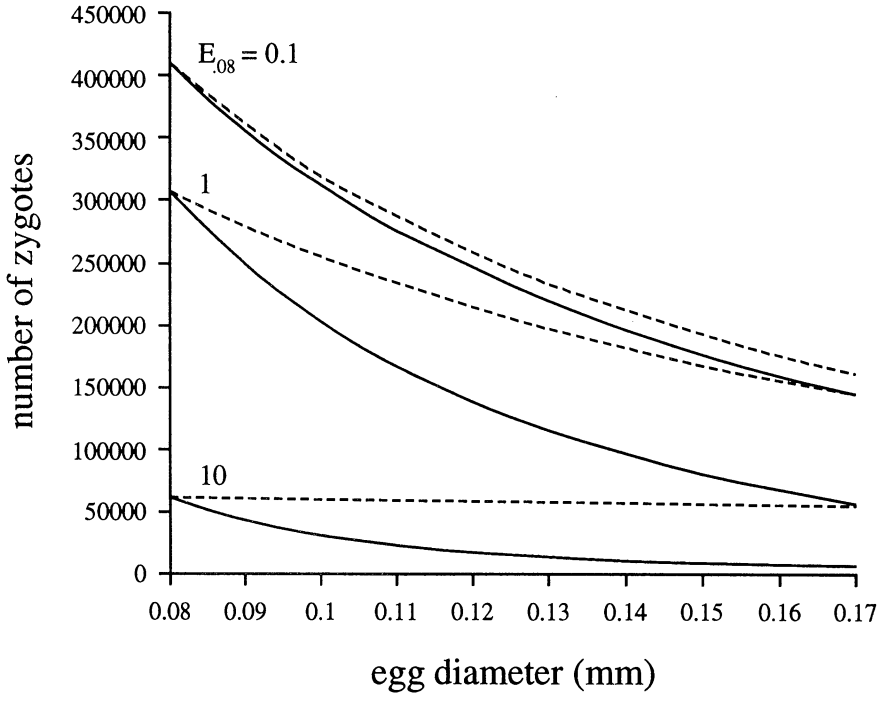

FIG. 4.—Relative zygote production per milliliter of egg material under two different models: fixed egg concentration (*solid lines*) and egg concentration that depends on egg size (*dashed lines*). The starting egg concentration ($E_{0.08}$) for each pair of lines is the concentration of 0.08-mm-diameter eggs; in model 2, concentration then declines as a linear function of egg volume. Pairs of curves illustrate three different starting egg concentrations ($E_{0.08}$ = 0.1, 1, 10/μL), which were chosen in order to bracket the largest observed effect of including size-dependent egg concentration. For reference, the concentration of packed eggs of 0.08-mm-diameter is on the order of 1,000/μL. Sperm is at a limiting concentration (1/μL).

As noted by Levitan, a second factor that could theoretically alter the relationship between zygote production and egg size is the scaling of egg organic content. All previous calculations have assumed that organic density (e.g., g C/μL) is independent of egg volume—that is, that larger eggs are simply bigger carvings from a standard pie. If eggs were instead enlarged partly through hydration, for example, then gains in fertilization could more equally balance fecundity losses. Allometric change in organic density can be modeled as a power function that relates organic content to egg volume:

$$\text{organic content} = a(\text{volume})^b. \tag{6}$$

Values of b less than one indicate decreasing organic density with increasing egg size; hence, more large eggs can be produced from a fixed amount of organic material than when $b = 1$. The effect of allometric changes in organic density

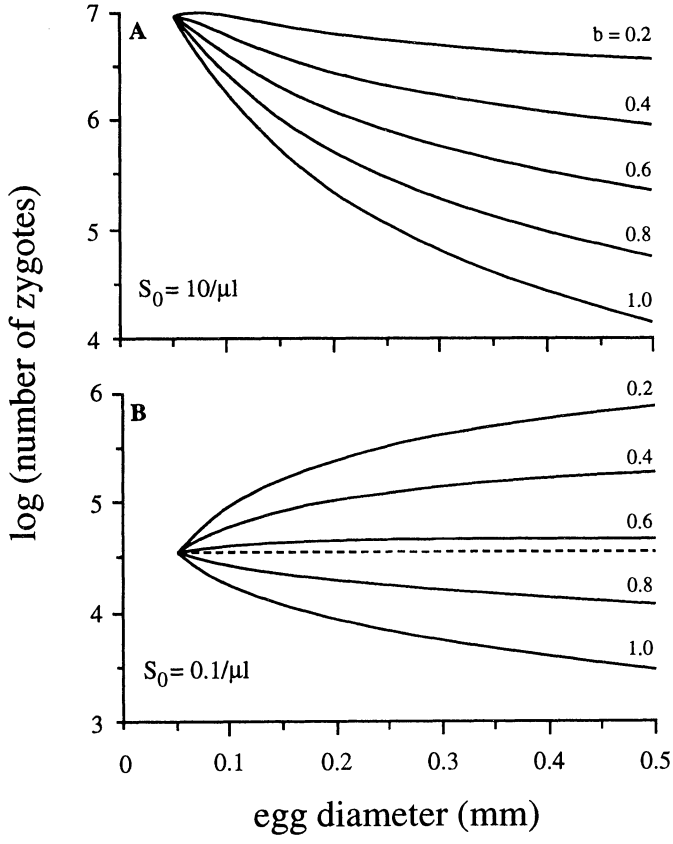

FIG. 5.—Number of zygotes produced per milliliter of egg organic material as a function of egg size. Curves were generated by using organic content (eq. [6]) as the currency for egg volume in equation (1), with varying allometric exponents (*b*). All other parameters are as in figure 1. To standardize curves, the intercept (*a*) for each scaling function was chosen to hold constant the organic content of 0.05-mm-diameter eggs. *A*, Saturating sperm concentration, where fertilization is 100% within the plotted range of egg sizes. All exponent values result in greater zygote production by smaller eggs. *B*, Limiting sperm concentration, at which fertilization never reaches 100%. The dashed line indicates the exponent value (≈0.65) at which zygote production is independent of egg size, owing to the balance between fertilization gains and fecundity costs. This exponent is relatively insensitive to further decreases in sperm concentration (e.g., $\beta \approx 0.66$ when $S_0 = 0.001$).

for *S. droebachiensis* depends on sperm concentration (fig. 5). At high concentration (fig. 5*A*), zygote production decreases regularly with increasing egg size for all exponent values. At a limiting sperm concentration (fig. 5*B*), zygote production can increase or decrease with egg size depending on the value of *b*. In this example, increased fertilization balances reduced fecundity, making zygote production independent of egg size, at an exponent around 0.65 (fig. 5*B*).

Values from the echinoderm literature suggest that the scaling exponent of organic content with egg size rarely goes this low. Data for eight species with

feeding larvae produced an exponent of 0.77 (RMA slope of log-log data), which was significantly different from 0.67 (Strathmann and Vedder 1977). Analysis of two data sets for nonfeeding larvae generated exponents of 1.02 (McEdward and Chia 1991) and 1.04 (Lawrence et al. 1984). Furthermore, the smaller eggs of feeding larvae generally have lower organic density than the larger eggs of nonfeeding larvae (Emlet et al. 1987). In these interspecific comparisons, organic density does not change with egg size or does so by an amount that is insufficient to reverse the inequality between fertilization costs and fecundity benefits of larger eggs.

Given the potential for increasing egg size nonorganically, why do many free-spawners maintain small eggs? One hypothesis is that physical constraints could set a lower limit on organic density. Such constraints could be related to structural properties of the egg, the mechanics of cell division, the effect of enzyme concentration on reaction kinetics, or the capacity of females to store eggs before spawning. Alternatively, fertilization could be exerting relatively weak selection on egg size because behaviors that ensure successful fertilization may account for a larger portion of variance in fertilization success. For example, high fertilization rates measured for many natural spawnings (Petersen 1991; Babcock et al. 1992, 1994; Petersen et al. 1992; Sewell and Levitan 1992; Benzie et al. 1994), as compared with experimentally induced spawnings (Pennington 1985; Yund 1990; Levitan 1991; Levitan et al. 1992), indicate the critical role that adult behaviors, such as aggregation and synchronous spawning (Babcock et al. 1992), play in fertilization success. Similarly, despite the presence of a micropyle that limits fertilizable surface area to a single spot in many fish eggs (Ginzburg 1968), high fertilization rates are achieved, presumably through coordinated adult behaviors (e.g., Petersen 1991; Petersen et al. 1992). Attributing selection pressure to fertilization success further prompts the more fanciful question of why egg shape, rather than size, is not more often molded by selection; nonspherical shapes (e.g., Meijer 1979) can increase average projected area, enlarging the size of the target.

An alternative path to increasing effective target size is to endow eggs with chemical attractants or accessory structures such as jelly coats, hulls, or follicle cells (Buckland-Nicks 1993; J. Havenhand and T. Bolton, personal communication). Levitan points out that chemotaxis has not been demonstrated for echinoids, but its potential importance in other free-spawners (Miller 1985) might limit the generality of a hypothesis based strictly on egg size. Furthermore, eggs of the three *Strongylocentrotus* species include jelly coats that increase the effective diameter of the egg beyond those in Levitan's calculations. In the sand dollar *Dendraster excentricus,* the egg jelly coat doubles egg diameter and quadruples cross-sectional area; experiments suggest that the presence of the jelly coat increases fertilization rate and does not substantially increase organic investment per egg (R. Podolsky and O. Iribarne, unpublished data). By remaining outside the cell membrane, the jelly coat does not compromise structural or physiological properties of the egg, and it avoids any potential limitation on storage within the female by swelling only after exposure to seawater.

Because the trade-off between fertilization and fecundity favors dividing resources into smaller eggs, the burden remains with explaining why species invest

in eggs that are larger than the minimum size required for development. Results presented here (e.g., fig. 1) indicate that advantages maintaining larger egg sizes are postzygotic. A simple model in which to combine effects of egg size on fertilization and on the period of larval development was presented with Vance's (1973*b*) fecundity-time hypothesis. The model predicts the number of larvae reaching competence to metamorphose (N_j) when fecundity (F) varies inversely with egg volume, larvae from smaller eggs have a longer development time (t, days), and larvae face a constant instantaneous mortality risk (m, per day) in the plankton (Emlet et al. 1987). In echinoderms, egg size has little or no effect on length of the prehatching period (Emlet et al. 1987; Dickie et al. 1989). To include fertilization kinetics, zygote number (N_z, eq. [5]) replaces egg number (F) in Vance's model to give

$$N_j = N_z e^{-tm}. \tag{7}$$

For illustration, data for three echinoid species (McEdward 1986) were used to calculate a linear relationship between egg diameter and development time (t [days] = -504.6 diameter [millimeters] + 107.2). As before, given the complex form of N_z, we illustrate graphically the effect of adding fertilization kinetics to the classic fecundity-time model for *S. droebachiensis* (fig. 6). In both graphs, small eggs result in more juveniles when larval mortality is low, whereas large eggs are favored under high mortality risk (i.e., when differences in development time translate into large differences in larval survivorship). These graphs illustrate three important points. First, the model predicts selection for either the extreme large or small egg size, not for intermediate sizes. Second, in this model, favored egg size depends on the degree of larval mortality. Adding fertilization kinetics to the model shifts the mortality value (m) at which the transition from small to large eggs occurs from about 0.05 (fig. 6*A*) to about 0.02 (fig. 6*B*). Third, adding fertilization to the model changes the linearity and steepness of slopes, which indicates weaker selection on egg size at low values of m but stronger selection at higher m than Vance's (1973*b*) model would predict.

Levitan (1993, p. 529) carried out a similar exercise, but with different results: the outcome of Levitan's model was independent of the degree of larval mortality, and it predicted the position of intermediate, optimal egg sizes. These differences between models result from the use of different larval mortality functions. Levitan used a linear curve to relate egg size to larval mortality, citing a commonly used linear relationship between egg size and development time. However, assuming constant mortality risk (Rumrill 1990), a linear relationship between egg size and development time translates not into a linear mortality curve but rather into an exponential curve, as used here. Obviously, a model's behavior is driven by its assumptions. However, the different outcomes of these models, which both include differential fertilization success, suggest that the ability of the model to predict intermediate egg size depends not on the inclusion of fertilization kinetics per se but rather on the shape of the larval mortality function. Life-history models with greater predictive power will need to incorporate factors like environmental heterogeneity; size-specific growth and mortality (Christiansen and Fenchel 1979; Winemiller and Rose 1993) resulting from differential predation (Pennington et

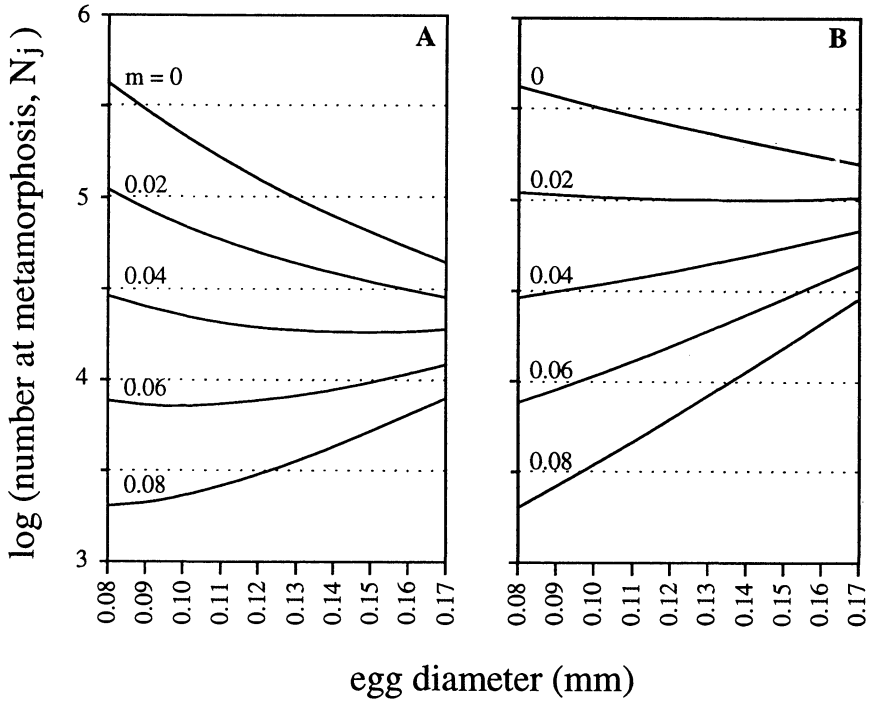

FIG. 6.—Number of juveniles at metamorphosis as a function of egg size. Curves depict different values of the instantaneous mortality coefficient (m). *A*, Vance's (1973*b*) model, with equal fertilization success at all egg sizes. *B*, The model including size-dependent fertilization. Large egg size is favored for values of m above 0.05 and 0.02, respectively. These critical values do not depend on the level of fertilization success used in *A*, which was chosen so as to standardize curves in the two graphs to the same starting values (percentage fertilization in *A* was set equal to percentage fertilization for 0.08-mm eggs in *B*). In *B*, sperm is at a limiting concentration (1/μL), and percentage fertilization increases from 11.4% to 41.6% over the range of egg sizes.

al. 1986), feeding ability (Strathmann 1987), or starvation resistance (Mashiko 1985); and the effect that egg size can have on postmetamorphic stages by influencing size at metamorphosis (Strathmann 1977) and generation time (Havenhand 1993).

Finally, some of Levitan's statements concerning the literature on life-history evolution could be misleading. First, life-history models that relate egg size to larval survivorship do not require that 100% of eggs be fertilized. This is a simplification, rather than an assumption, of such models (e.g., Vance 1973*a*). Instead, these models have assumed that the probability of fertilization is not biased by qualities of the egg, such as size, that depend on how resources are divided among eggs. Levitan has shown that such a bias exists and can have an important effect on predictions of life-history models. Second, the hypothesis that smaller eggs result in longer development times has stronger support from experiment and comparison than Levitan suggests. Interspecific comparisons (Sinervo and

McEdward 1988; Havenhand 1993; Kohn and Perron 1994) and experimental manipulation of egg size (Sinervo and McEdward 1988) both indicate longer periods of development for larvae from smaller eggs. Departures from this pattern occur when size at metamorphosis, rather than development time, is correlated with egg size, as has been shown in some comparative (Strathmann 1977) and experimental data (M. Hart, personal communication). In either case, a decrease in egg size results in postzygotic changes that are expected to increase larval or juvenile risks. Third, the kinetics of Levitan's model apply to freely spawned gametes that depend on encounter in the water column. The fact that species with internal fertilization—and presumably high fertilization rates—display similar patterns of egg size variation (Strathmann 1985; Clarke 1993; Kohn and Perron 1994) suggests that factors other than gamete encounter can be a sufficient explanation for egg size evolution across disparate modes of reproduction.

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