Predicting Optimal and Unique Egg Sizes in Free-Spawning Marine Invertebrates

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PREDICTING OPTIMAL AND UNIQUE EGG SIZES IN FREE-SPAWNING MARINE INVERTEBRATES

Free-spawning marine invertebrates release eggs into the environment, where they are fertilized, develop, and grow without further parental investment. This trait provides a unique opportunity to investigate offspring provisioning and the evolutionary pressures on gamete evolution without the added complications of parental care. The optimal egg size, which maximizes parental fitness, has previously been thought to be a function of postzygotic influences on the survivorship and reproductive potential of offspring (e.g., Smith and Fretwell 1974). In an earlier article (Levitan 1993), I developed the hypothesis that prezygotic factors—fertilization success—can also influence selection on egg size; larger eggs are fertilized at a higher rate than are smaller eggs, which alters the relationship between offspring size and offspring fitness. The influence of fertilization on egg size evolution will be most apparent in situations when other selective agents are held constant or at least have reduced variance. The larvae of three congeneric sea urchins (*Strongylocentrotus* spp.) develop in the same planktonic environment, and size at metamorphosis after this phase is similar in all three (Emlet et al. 1987; Sinervo and McEdward 1988), which suggests that selection for the fivefold variation in egg size among these closely related species probably operates before the offspring enter the larval phase.

Podolsky and Strathmann (1996; hereafter abbreviated P&S) address several issues raised in my original article (Levitan 1993) and provide an analysis of the trade-off between fertilization and fecundity. We agree on some issues and disagree on others. For the most part, our differences lie in points of perspective and emphasis rather than contradiction.

One issue that requires substantial attention is the appropriate strategy for analyzing selection on egg size. Podolsky and Strathmann use an approach first developed by Vance (1973*a*) and choose parameter values that predict extremes in egg size. This prediction has a long history in marine larval ecology (Vance 1973*a*, 1973*b*; Christiansen and Fenchel 1979; Roughgarden 1989; Havenhand 1995), but it contradicts the empirical observation that nonextreme egg sizes are ubiquitous among marine invertebrate species (Emlet et al. 1987; Kohn and Perron 1994). Strathmann (1985) notes that many taxa have intermediate egg sizes and mixed developmental modes, and he offers a number of mechanisms that might produce intermediate optima but concludes that "no model has been offered to explore this possibility in detail" (pp. 346–347). This fundamental conflict between theory and data needs to be addressed.

In response to P&S's comments and the need to address the conflict between

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theory and evidence, this note will be in two parts. The first will be a discussion of why previous life-history models have failed to explain the patterns of egg size noted in marine invertebrates and of how examining the empirical data with a different theoretical framework, one that includes variation in female fertilization success, provides a potential solution to the apparent contradiction between theory and data. The second will be a point-by-point reply to the issues raised by P&S that are not covered by this first section.

PREDICTING OPTIMAL EGG SIZES

Vance's (1973*a*) original model and subsequent theoretical treatments attempting to explain patterns of egg size in marine invertebrates (Vance 1973*b;* Christiansen and Fenchel 1979; Roughgarden 1989; Havenhand 1995) have focused on a bimodal distribution of egg sizes. This bimodal distribution reflects the existence of two distinct feeding modes or developmental pathways among marine invertebrates: feeding (planktotrophic) and nonfeeding (lecithotrophic) larval forms. In response to this pattern, Vance suggests the fecundity–development time trade-off, in which the energy content of eggs is measured on a scale between zero and one unit of energy. An egg with zero energy must gather all energy to fuel development through larval feeding. An egg with one unit of energy has all the energy needed to fuel development in the yolk and does not need to feed as a larva. If the energy invested in reproduction remains constant, then egg number will vary inversely with egg energy content (or, as a surrogate, egg volume). If the relationship between egg size and development time is linear, and if the instantaneous mortality rate remains constant, then selection would favor extremes in egg volume (or energy content), such that eggs should have either zero or one unit of energy and never an intermediate value.

Herrara et al. (in press), on the other hand, suggest that Vance's model should not be applied to both planktotrophs and lecithotrophs, because the range in egg provisioning represented by Vance's 0–1 scale is contained within the planktotrophs; the largest planktotrophs, facultative planktotrophs, can develop through metamorphosis without feeding. Vance's model should therefore be applied only to planktotrophs and a different set of considerations used to evaluate nonfeeding forms.

However, when we apply Vance's model to planktotrophs, there is complete disagreement of the prediction of selection for extremes in egg size with empirical data. Among planktotrophic species, nonextreme egg sizes are the rule rather than the exception (e.g., annelids: Hermans 1979; arthropods: Reaka 1979; mollusks: Kohn and Perron 1994); in some groups (e.g., planktotrophic echinoids: Emlet et al. 1987), the distribution is near normal and dominated by species with intermediate egg sizes. Models using assumptions that predict extremes in egg size are not useful in explaining patterns of egg size in these groups.

An alternate approach is the Smith-Fretwell model (Smith and Fretwell 1974), which I advocated in my original article (Levitan 1993). This approach plots offspring fitness as a function of offspring size (or provisioning). If the relationship shows some diminishing influence of egg volume on offspring fitness, and if some

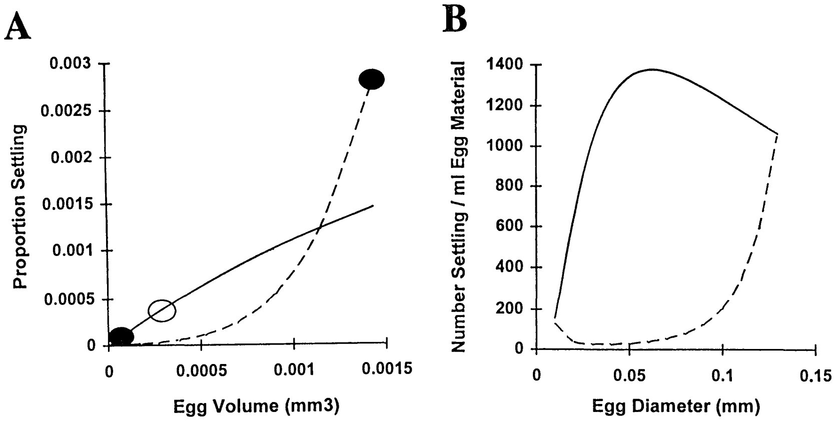

FIG. 1.—Selecting for intermediate rather than extremes of egg size using equation (1). *A*, Plot of proportion of released eggs settling (N_s/N_e) as a function of egg volume, assuming all eggs are fertilized. The solid line is based on a curvilinear relationship between egg volume and development time (from fig. 2*A*); the dashed line is from a linear relationship between egg diameter and development time (t [d] = -504.6 diameter [mm] + 107.2, from P&S). For both lines, the instantaneous mortality rate is 0.1615/d. The tangents of the curves through the origin represent optimal egg sizes. The solid line has an intermediate optimum (*open symbol*); the dashed line has optima at extremes of egg size (*solid symbols*). *B*, Plot of number of individuals settling per milliliter of egg material as a function of egg diameter based on *A*.

finite amount of provisioning is needed for development, then the tangent of the curve through the origin predicts an intermediate, optimal size. If the relationship is linear or exponential, then intermediate egg sizes will not be selected, and the empirical observation of intermediate egg sizes cannot be explained in a selective framework (fig. 1).

The difficult task in using the Smith-Fretwell model, or any model that attempts to predict optimal egg size, is finding a proxy for offspring fitness. This problem is particularly difficult for marine invertebrate species with multiphasic life cycles and small, highly dispersive propagules. However, if the size at metamorphosis is constant, then factors leading to selection on propagule size should be evident before settlement (Emlet et al. 1987). Additionally, if planktonic mortality is constant over time, then survivorship will be a function of the instantaneous mortality rate and the length of time spent in the plankton (Vance 1973*a*).

Rather than assuming a linear relationship between egg size and development time (as is done, e.g., in Vance 1973*a* and P&S), I have plotted the relationships for both the common echinoids at my study sites (Barkley Sound, British Columbia) and a group of echinoids off the subtropical coast of Florida (fig. 2), in which development times of species with a wide range of egg sizes were investigated by a single laboratory, eliminating protocol differences (Herrara et al., in press). The size distributions of both plots represent the full size range of planktotrophic echinoids and extend from obligate to facultative planktotrophs. In both plots, a diminishing relationship between egg size and development time is noted (plotted as either egg diameter or egg volume as in fig. 2). This interspecific relationship

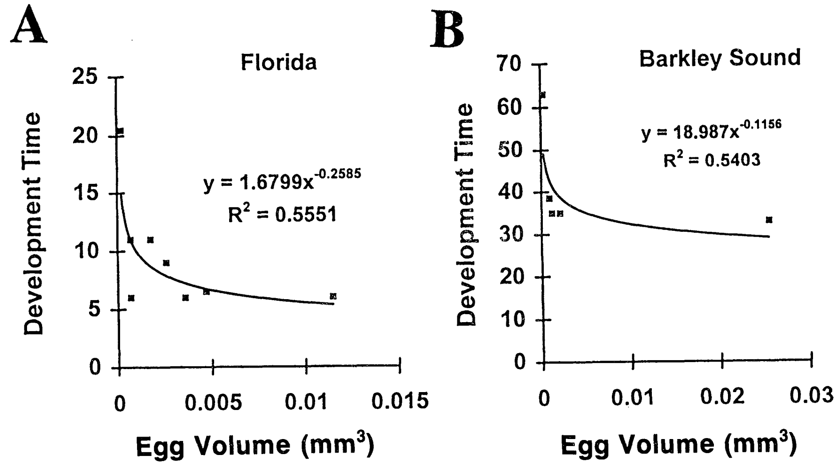

FIG. 2.—Development time as a function of egg volume for (*A*) subtropical species of Florida (Herrara et al., in press) and (*B*) the common echinoids of Barkley Sound. The species in *B* (in order of increasing size) are *Strongylocentrotus purpuratus* (Strathmann 1978, 1987; McEdward 1986), *Dendraster excentricus* (Emlet 1986; Strathmann 1987), *Strongylocentrotus franciscanus* (Emlet et al. 1987), *Strongylocentrotus droebachiensis* (Emlet et al. 1987), and *Brisaster latifrons* (Hart 1996). Reported temperatures for development in these temperate species are between 10° and 14°C.

is also supported by intraspecific experiments in which halving the relatively large eggs of *Strongylocentrotus droebachiensis* results in only a 6% (2.4-d) increase in development time (Hart 1995).

From these empirical data on development time and egg size, and with Vance's equation, the number of settling offspring (N_s) can be calculated as a function of the number of eggs (N_e), the development time (t), and instantaneous mortality rate (m):

$$N_s = N_e e^{(-tm)} \tag{1}$$

This value of N_s can be divided by N_e and plotted as a function of egg size to produce a Smith-Fretwell plot that uses the proportion of settling offspring as a measure of offspring fitness. These simulations, based on empirical data of developmental time and over a range of mortality rates consistent with estimates from field populations (Rumrill 1990), result in a curve of diminishing return on offspring size and therefore in intermediate optimal egg sizes (fig. 3).

A plot of optimal egg size as a function of mortality rate indicates that different mortality regimes can select for different intermediate egg sizes (fig. 4). This result provides a mechanism for selecting intermediate egg sizes but still does not explain the existence of unique egg sizes in the same planktonic environment or selective regime. The three congeners I studied have similar larval design (McEdward 1986) and overlapping spawning periods (Strathmann 1987). They also develop in the same water mass and metamorphose at a similar size (Emlet et al. 1987; Strathmann 1987). What selective mechanism could explain a fivefold difference in egg size among these species?

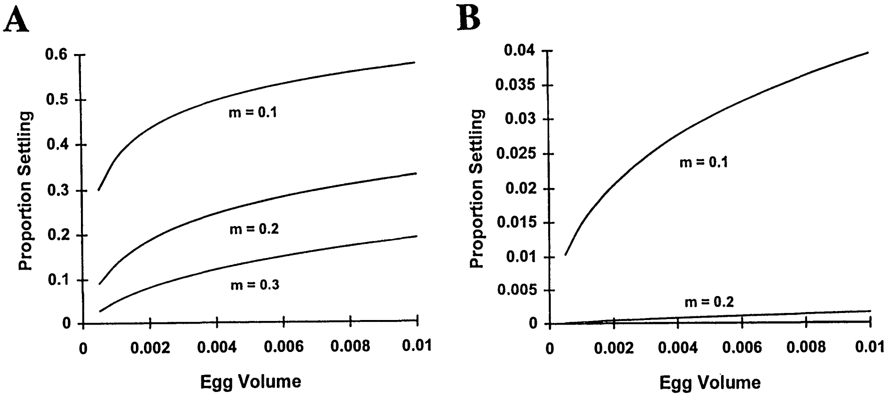

FIG. 3.—Proportion of settling offspring as a function of egg size, using equation (1) and assuming equal investment in egg material (1 mL). These graphs assume 100% fertilization and vary the mortality rate (*m*). *A*, Based on the Florida echinoid relationship between egg size and development time. *B*, Based on the Barkley Sound echinoid relationship between egg size and developmental time. The optimal egg size that maximizes parental fitness is the tangent to the curve through the origin.

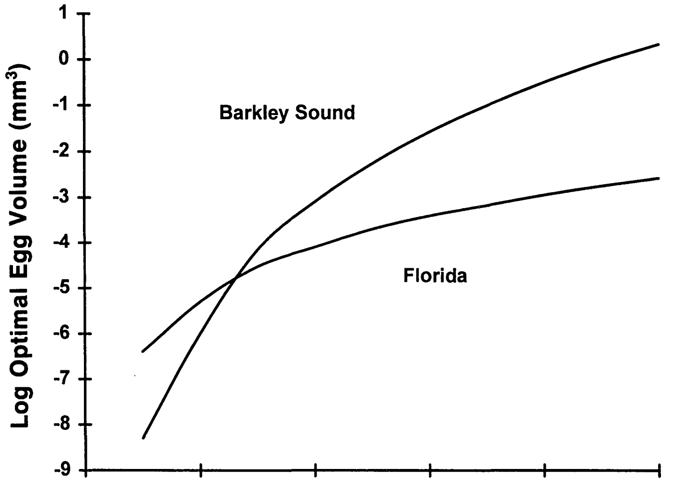

FIG. 4.—Log optimal egg size as a function of mortality rate based on the Florida and Barkley Sound relationships between egg size and development time. This graph assumes 100% fertilization.

The answer—assuming that selection is important to the evolution of egg size and that egg size is at some evolutionary equilibrium—is that, at some point during the life cycle of these species, the selective regimes must differ. The three general phases in which they might are before the embryos and larvae enter into the planktonic environment, the planktonic period, and after the newly metamorphosed individuals leave the planktonic environment. Postsettlement selective factors are both critically important and poorly understood. Much work is needed in this area, and, more important, the results must be incorporated into the general framework of offspring provisioning and life-history evolution in marine invertebrates (Roughgarden 1989; Grosberg and Levitan 1993). At least for echinoids, however, postsettlement factors are less likely to be important because size at metamorphosis is a conserved trait among species with a wide range of egg sizes (Emlet et al. 1987; Sinervo and McEdward 1988). Different egg sizes could be selected during the planktonic period if the planktonic environment differs among species or if differences in larval design exist (e.g., in morphology, physiology, or behavior) that do not co-vary with egg size. These circumstances seem less likely for these co-occurring congeners, although the geographical range of *S. droebachiensis* is different from (though it overlaps) those of the other two species; the former extends across the Arctic from New Jersey to Washington, whereas the latter two co-occur along the west coast of North America (McConnaughey and McConnaughey 1985). Here and previously (Levitan 1993), I address the third possibility: that the selective differences occur prezygotically, during spawning and fertilization. The fertilization hypothesis can explain the variation in egg size noted among these species.

I offer a hypothesis that, because these strongylocentrotid species differ in body size, population density, microhabitat distribution, and fertilization kinetics—all of which influence fertilization (Levitan 1995*a*)—the degree of sperm limitation and patterns of fertilization will differ among these species. Below, I demonstrate how this hypothesis can explain variation in egg size using the empirical relationship between development time and egg size and in situ measures of planktonic mortality. For simplicity, I assume that the planktonic and postsettlement environments do not vary among species. Relaxing this simplification would add to the complexity of factors influencing optimal egg size differences rather than invalidate the notion that variation in sperm limitation can influence optimal egg size.

Using an instantaneous larval mortality rate calculated from empirical measures of the *Strongylocentrotus* species in Barkley Sound (0.1615/d; Rumrill 1990), the relationship between egg size and development time calculated from the echinoid species assemblage in Barkley Sound at the water temperature appropriate to the time of spawning and larval development (fig. 2*B*), and a sperm-egg contact time appropriate for field conditions (10 min; D. R. Levitan, personal observation), I demonstrate through simulations how selection would favor an optimal egg size dependent on the degree of sperm availability and species-specific gamete attributes. Within a species, the optimal egg size (fig. 5*A*) that maximizes the number of settling offspring (fig. 5*B*) theoretically increases as the local sperm concentration decreases. Considering all three strongylocentrotid species examined indi-

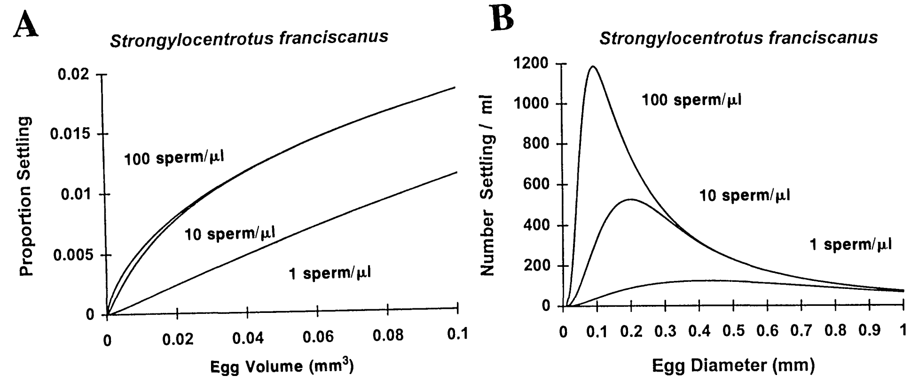

FIG. 5.—Influence of sperm concentration on settlement success based on gamete attributes of *Strongylocentrotus franciscanus*. Egg quantity is based on 1 mL of egg material divided by the variable egg volume. The proportion of eggs fertilized is determined by the fertilization-kinetics model (eq. [2] in Levitan 1993, same as eq. [3] in P&S) with a constant egg concentration of 0.01/μL and a sperm-egg contact time of 10 min. Planktonic survivorship is based on an instantaneous mortality rate of 0.1615/d (Rumrill 1990) and the relationship between egg volume and development time (time = 18.987 [egg volume(mm)]$^{-0.1156}$) from figure 2. *A*, Proportion settling as a function of egg volume. *B*, Number settling as a function of egg diameter. Egg diameter is used as the independent variable because this is the parameter most often reported in the literature. The tangent of each curve through the origin in *A* represents the optimal egg size, which maximizes parental fitness and coincides with the peak in *B*.

cates that optimal egg size varies as a function of both sperm abundance and species-specific gamete attributes (fig. 6). The species in figure 6 have a consistent rank order at any one sperm concentration (because of species-specific gamete attributes), but as they encounter different sperm concentrations, selection will favor an increase or decrease in egg size. This finding is in contrast to P&S's conclusion that "advantages maintaining larger egg sizes are postzygotic" (p. 168).

In figure 6, I also decouple the two effects of varying egg size: changing the rate at which sperm encounter eggs (egg target size) and changing the relationship between egg size and number given a specific allocation of material to reproduction (fecundity). If egg target size is held constant for each species (as egg size varies in the model), the optimal egg size remains constant at all sperm concentrations and across all three species; because there is no differential fertilization as a function of egg size, variation in fertilization cannot influence optimal egg size. In simulations, the sensitivity of optimal egg size to changes in sperm concentration is due entirely to the effects of egg target size.

Increasing the larval mortality rate or decreasing the sperm-egg contact time results in larger optimal egg sizes, but neither alters the conclusion that optimal egg size varies as a function of ambient sperm concentration. Figure 6 indicates that, for these empirical measures of development time and planktonic mortality, when all eggs are fertilized, optimal egg diameter is 0.06 mm. This egg size coin-

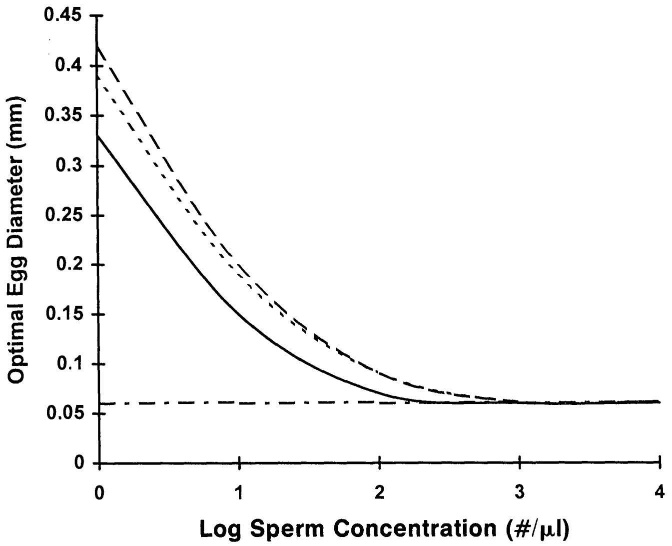

FIG. 6.—Optimal egg diameter as a function of sperm concentration. Egg number is based on 1 mL of egg material. Proportion of eggs fertilized is based on the fertilization-kinetics model (eq. [2] in Levitan 1993, same as eq. [3] in P&S) with a sperm-egg contact time of 10 min, egg concentration of 0.01/μL, and species-specific gamete attributes (see Levitan 1993 or P&S's table 1). Zygote survivorship is based on equation (1), the Barkley Sound echinoid relationship between egg size and developmental time (fig. 2*B*), an instantaneous mortality rate of 0.1615/d (*solid line, Strongylocentrotus droebachiensis; dashed line, Strongylocentrotus franciscanus; dotted line, Strongylocentrotus purpuratus*). The dot-dashed line is the case in which egg target size remains constant and true to each species (all species have a constant value of 0.06 mm across all sperm concentrations).

cides with the minimum noted among echinoids (Emlet et al. 1987). As sperm availability decreases, the optimal egg size increases. The steepness of the curve at the egg sizes noted among planktotrophic species (between 0.06 and 0.35 mm; fig. 6) suggests that selection for egg size will be very sensitive to fertilization dynamics. The rank order of ambient sperm concentration estimated in my original article (*Strongylocentrotus purpuratus* > *Strongylocentrotus franciscanus* > *S. droebachiensis*) once again suggests that egg size in these species should increase in the same order, as it is seen empirically to do.

The observed egg sizes of *S. purpuratus* (0.84 mm), *S. franciscanus* (0.135 mm), and *S. droebachiensis* (0.145 mm) are predicted by this model when female fertilization successes are 97%, 80%, and 82%, respectively. These values are reasonable, on the basis of natural observations and experiments on fertilization success of these species and given the distribution and abundance of these species (Levitan et al. 1992; Levitan and Young 1995; D. R. Levitan, unpublished data). These values also indicate that fertilization rates need not be low in order for sperm concentration to influence selection on egg size.

Recent empirical findings support the notion that sperm limitation can influence the evolution of egg size. Laboratory studies indicate that, both among and within females of the same species, larger eggs are preferentially fertilized (Levitan 1994). Field studies indicate that differences in gamete performance both within (Levitan 1994) and among (Levitan 1995*b*) species are reflected in levels of fertilization in the sea. These studies provide evidence that subtle differences in gamete attributes can influence rates of fertilization and that these differences are not overwhelmed by environmental conditions. Sperm limitation is therefore likely to exert a strong selective pressure on egg size.

Considering other aspects of the life cycle, such as fertilization, reveals how intermediate and unique egg sizes can be selected. The challenge facing biologists interested in the evolution of marine life-history traits will be to incorporate other aspects of the life cycle in addition to the planktonic period.

RESPONSES TO SPECIFIC CRITICISMS

Podolsky and Strathmann examine the net effect of varying egg size on zygote production through a series of simulations and show that increasing egg size, while increasing the probability of fertilization, results in a net decrease in zygote production. This finding agrees with my earlier conclusion based on a comparison of two species with similar gamete attributes (*Strongylocentrotus purpuratus* and *Strongylocentrotus franciscanus*); the former species, with smaller eggs, produced more zygotes per unit energy invested in reproduction under all sperm concentrations (Levitan 1993). The rationale for this conclusion, as I have noted (Levitan 1993) and P&S have stated more formally, is that, with increases in egg size, the probability of fertilization increases as a square function, while the material cost of increasing volume increases as a cubic function of egg diameter. Therefore, when sperm are limiting, the cost of producing larger eggs is reduced but cannot totally compensate for the fecundity advantage of individuals producing smaller eggs.

When zygote production in a third species (*Strongylocentrotus droebachiensis*) is compared to those of *S. purpuratus* and *S. franciscanus,* the results differ. *Strongylocentrotus droebachiensis* has larger eggs, slower but longer-lived sperm, and a higher susceptibility to fertilization for a given sperm-egg collision frequency than do the other two species (Levitan 1993). Laboratory experiments demonstrate that, at low sperm concentrations, *S. droebachiensis* produces more zygotes per unit egg material invested in reproduction than either of the other two species, even though it produces the largest and thus fewest eggs per unit investment (Levitan 1993). This empirical finding highlights how, under conditions of sperm limitation, interspecific comparisons of zygote production per unit investment in reproduction are largely independent of egg production per unit investment in reproduction.

Podolsky and Strathmann point out that interspecific comparisons of fertilization may be confounded by other factors and lead to a misidentification of the causal trait(s) responsible for differences in zygote production among species. We agree on the net effect of varying egg size on zygote production, but it is also important to recognize how various fertilization attributes contribute to species differences in zygote production. Given that a reduction in egg production is

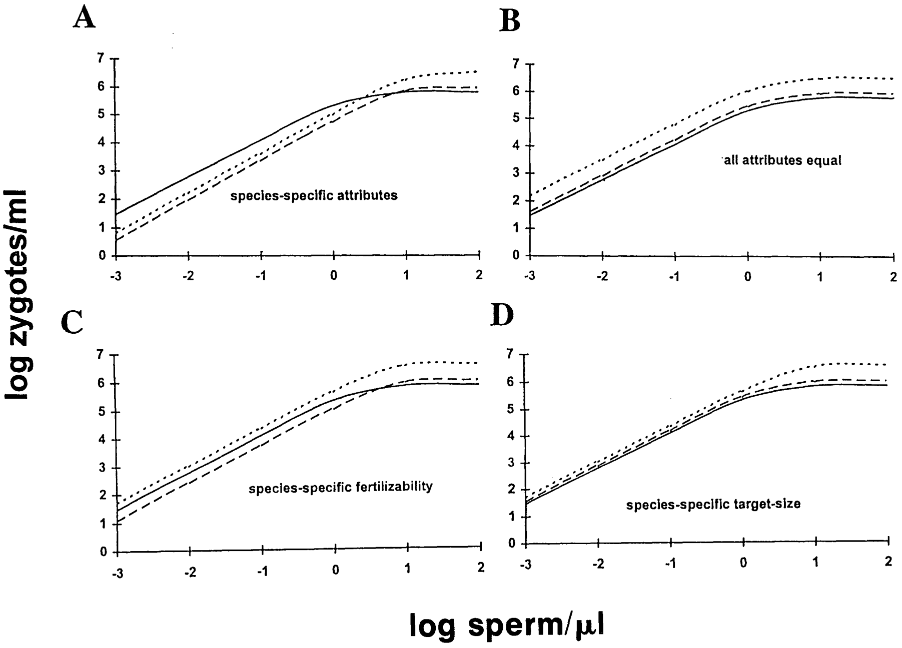

FIG. 7.—Theoretical zygote production per milliliter of egg material as a function of sperm concentration for *Strongylocentrotus purpuratus* (*dotted line*), *Strongylocentrotus franciscanus* (*dashed line*), and *Strongylocentrotus droebachiensis* (*solid line*). *A*, All gamete attributes are species specific (same as Levitan 1993, fig. 6*A*, and P&S, fig. 2*A*). *B*, All gamete attributes (egg target size, egg fertilizability, sperm swimming velocity, sperm longevity) are equal across species (using values for *S. droebachiensis*). *C*, As in *B* but with species-specific egg fertilizability. *D*, As in *B* but with species-specific egg target size. Podolsky and Strathmann ask what gamete attributes cause *S. purpuratus* to have lower zygote production than *S. droebachiensis* at low sperm concentrations (the change between the solid and dotted lines in *A* and *B*). Both egg fertilizability and egg target size (*C* and *D*) shift the position of *S. purpuratus* lower relative to *S. droebachiensis* at low sperm concentrations. Also note that only egg target size influences the shift of decreased zygote production in *S. purpuratus* compared to *S. franciscanus* (*dashed line*) at low sperm concentrations.

associated with increasing egg size, what can account for the increased zygote production of *S. droebachiensis* relative to the other two species? Possible factors include the fertilization benefit of larger eggs (egg target size, which is a function of egg cross-sectional area), egg fertilizability (the proportion of sperm collisions that result in fertilization), sperm velocity (affecting the rate at which sperm collide with eggs), and sperm longevity (affecting the interval during which sperm can find eggs). Podolsky and Strathmann suggest that the advantage of *S. droebachiensis* "does not result from larger egg size . . . [but] results entirely from a greater frequency with which sperm-egg collision results in fertilization . . . and greater sperm longevity" (pp. 162–163). To determine the relative importance of each factor I present simulations similar to those of P&S (their fig. 2), but instead of varying only fertilizability and sperm longevity, I additionally vary egg target size and sperm velocity (figs. 7, 8).

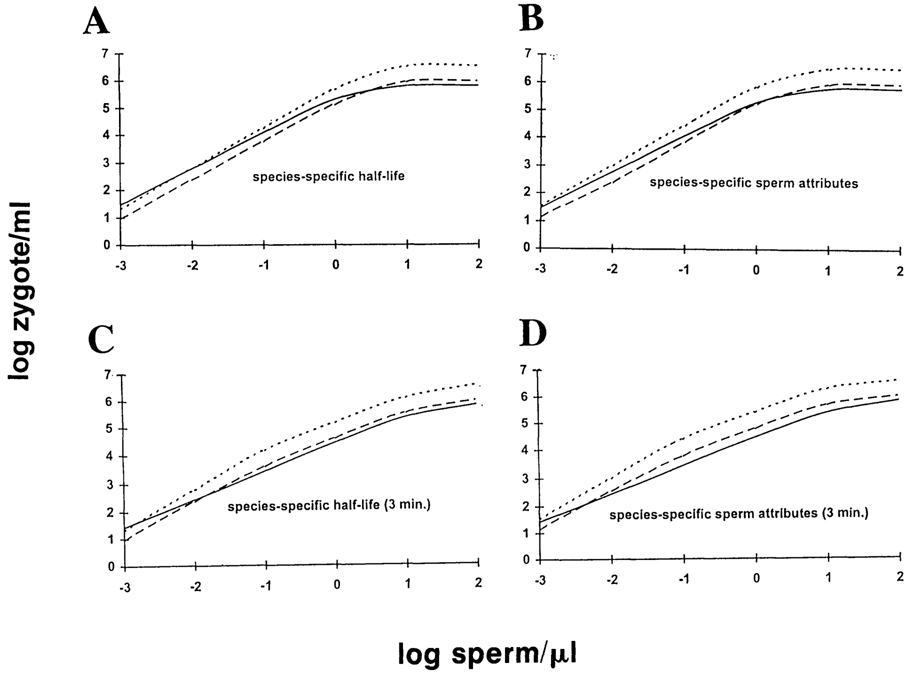

FIG. 8.—Influence of sperm swimming ability on per-milliliter zygote production as a function of sperm concentration. *A*, Species-specific sperm half-life. *B*, Species-specific sperm half-life and sperm swimming speed. *C*, Same as *A* but with a sperm-egg contact time of 3 min rather than 3 h. *D*, Same as *B* but with a sperm-egg contact time of 3 min rather than 3 h.

The results of these simulations indicate that egg target size and egg fertilizability can contribute equally to the relative advantage of *S. droebachiensis*. For example, at a sperm concentration of 0.1/μL, when all fertilization traits are held constant, zygote production for *S. droebachiensis* is 19% of that of *S. purpuratus*. When species-specific egg target size is considered, zygote production for *S. droebachiensis* is 58% of that of *S. purpuratus*. Similarly, when species-specific fertilizability is considered, zygote production for *S. droebachiensis* is also 58% of that of *S. purpuratus*. Neither factor alone can increase zygote production of *S. droebachiensis* above that of *S. purpuratus*. Sperm longevity, although important, has reduced consequences when sperm have only a brief opportunity to interact with eggs (e.g., zygote production for *S. droebachiensis* decreases from 70% to 19% of that of *S. purpuratus* when sperm-egg contact time decreases from 3 h to 3 min), which may be a more realistic natural condition.

Most important, regardless of the differences in gamete attributes among these three species, and regardless of the relative importance of different gamete attributes to zygote production, all three species demonstrated the same change in optimal egg size to variation in sperm limitation (fig. 6). Under realistic and empirically derived parameter values, optimal egg size varies as a function of sperm limitation, mediated by changes in egg target size.

The next issue is the influence of jelly coats and chemotaxis on fertilization and whether these alternate means of increasing sperm collisions are more efficient mechanisms for increasing the probability of fertilization than is increasing the size of the egg.

Jelly coats have been shown to increase the probability of fertilization in the laboratory (Rothschild and Swann 1951). For the three *Strongylocentrotus* species, jelly-coat thickness increases with egg size (D. R. Levitan, unpublished data). If a constraint on jelly-coat thickness depends on egg size, then it may not be possible or efficient for small eggs to produce relatively large jelly coats.

Sperm chemotaxis has been demonstrated in the laboratory for some taxa but not others and has yet to be demonstrated in echinoids (Miller 1985). More important, the influence of sperm chemotaxis on increasing fertilization success has not been demonstrated, nor has sperm chemotaxis been demonstrated under field conditions. If the rate of chemical released depends on the surface area of the egg, then increasing the effectiveness of chemotaxis may be linked with increases in egg size.

Podolsky and Strathmann also argue that natural levels of fertilization are higher than experimental levels, indicating that adult spawning behavior may explain most of the variation in fertilization success, which leaves little variation to be explained by gamete attributes.

Present empirical data do not support the idea that natural levels of fertilization are higher than experimental levels (reviewed in Levitan 1995*a*). Direct comparison of experimental and natural observations of mean levels of fertilization are not appropriate because experimental treatments do not always re-create the range of conditions noted in the limited number of quantitative assessments of natural spawning observations. The conclusions of both experiments and natural observations indicate that, when individuals spawn in close contact, at high density, or in large populations, fertilization success can be relatively high. Similarly, when individuals spawn alone, at great distances from each other, or at higher levels of water flow, fertilization success is low (Levitan 1995*a;* Levitan and Petersen 1995).

These studies, both experimental and observational, also indicate that the range in fertilization success among females can be extreme, from 0% to 100% of eggs fertilized, even when conditions for high levels of fertilization are ideal (e.g., Sewell and Levitan 1992). Female fertilization success is variable, so selection on characters that influence fertilization success will be important.

In addition, as noted above, the predicted levels of fertilization required to select for eggs of observed size ranged from 80% to 97% for the three congeners studied, so fertilization does not need to be near zero for sperm limitation to play a critical role in selecting for egg size.

Finally, recent experiments indicate that variation in gamete performance noted in the laboratory, both within and among species, influences rates of fertilization in the field (Levitan 1994, 1995*b*). Variance in gamete attributes, such as egg size, that influence rates of fertilization are not swamped by environmental factors and therefore are likely to be under intense selective pressure.

In another comment, P&S suggest that 100% fertilization is not an assumption of previous life-history models. However, Vance's (1973*b*) model, under the "Assumptions" heading, states "1. All eggs are fertilized" (p. 354). Podolsky and Strathmann imply that Vance is incorrect and that the statement is really a simplification rather than an assumption. Regardless, variation in fertilization has not been considered in previous models, and the consequence of incorporating fertilization is that predictions of optimal egg size can change drastically, dependent on the degree of sperm limitation.

Finally, P&S suggest that, because species with internal fertilization "display similar patterns of egg size variation, . . . factors other than gamete encounter can be a sufficient explanation for egg size evolution across disparate modes of reproduction" (p. 171).

Given a constant allocation to reproduction, egg size and fecundity must covary. A wide range of terrestrial and aquatic taxa including vertebrates, invertebrates, and plants (Roff 1992) demonstrates a relationship between propagule size and number. The important question is not whether this trade-off exists but the nature of the selective forces on investment per offspring and total investment in reproduction (Winkler and Wallin 1987; Venable 1992). We should not expect any one selective agent, such as fertilization or planktonic mortality, to explain patterns of investment across a wide range of taxa or environments.

Smith and Fretwell (1974) give the general solution to the problem of egg provisioning: optimal egg size will be determined by the relationship between offspring size and offspring fitness. Offspring (gamete) fitness can be influenced by many factors: fertilization, larval mortality, postsettlement survival, and reproduction. Species that brood or deposit eggs face ample opportunity for differential mortality in different microhabitats, but if eggs are cast into the same planktonic environment, and if the larval design is constant, then selection will favor a single optimal size. Incorporating fertilization success into this theoretical framework overcomes this problem and provides a mechanism for selection of unique egg sizes under sympatry.

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