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THE IMPORTANCE OF SPERM LIMITATION TO THE EVOLUTION OF EGG SIZE IN MARINE INVERTEBRATES

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Abstract.—Interspecific variation in egg size of marine invertebrates has been previously explained by a trade-off between gamete quality and quantity: the production of many small eggs with high mortality or fewer large eggs that develop quickly and experience reduced planktonic mortality. This theory assumes 100% fertilization of eggs and predicts that either strategy results in a similar number of settling offspring per unit of energy invested in reproduction. Empirical support for the theory has been equivocal. Here I offer an alternative hypothesis: larger eggs present a larger target for sperm and thus are fertilized at a higher rate. This theory suggests a trade-off between the production of many small eggs with a low probability of fertilization or fewer large eggs with a higher probability of fertilization. This hypothesis is tested with three congeneric sea urchins, *Strongylocentrotus purpuratus, Strongylocentrotus franciscanus,* and *Strongylocentrotus droebachiensis,* with a fivefold difference in egg volume. Species with larger eggs are fertilized at a higher rate and, if one assumes an equal allocation of resources, produce at least as many zygotes as species with smaller, more numerous eggs. This alternate hypothesis can explain continuous variation in egg size between species and provides a strong link between larval and adult life histories.

The degree to which individuals provision offspring with resources is a fundamental concern in life-history theory (Vance 1973*a*, 1973*b*; Smith and Fretwell 1974; Wilbur 1977; McGinley et al. 1987). In the absence of parental care, offspring provisioning can be measured as a function of propagule size. The optimal offspring size for maximal parental fitness is dependent on the relationship between offspring size and offspring fitness (Smith and Fretwell 1974; Wilbur 1977). Under most conditions, parental fitness is maximized when all offspring in a clutch have an equal allocation of resources (Smith and Fretwell 1974; McGinley et al. 1987). Thus, life-history theory dictates that organisms should produce many small offspring or fewer but larger offspring, dependent on the fitness of the offspring produced.

Generally, offspring fitness has been viewed as a function of offspring survival. However, fertilization success can also be a major factor determining offspring fitness. Increasing the likelihood of fertilization can be energetically costly to both adults and gametes, which would influence the energy available for offspring provisioning. Incorporating fertilization success into life-history theory would be

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particularly important if gamete provisioning directly influenced gamete fertilization. If so, then egg size would influence not only offspring number and survival but also the probability of fertilization. This study addresses how egg size and sperm swimming ability influence fertilization success and offspring production in free-spawning marine invertebrates.

One of the major questions concerning life-history evolution of marine invertebrates is an explanation for the diversity of egg size between closely related species (see, e.g., Thorson 1936, 1950; Hendler 1975; Rice 1975; Chia 1976; Hermans 1979; Reaka 1979; Sastry 1979; R. Strathmann 1985; Emlet et al. 1987; Sinervo and McEdward 1988). Given a constant allocation of energy to reproduction, any increase in egg size results in a decrease in egg number. Thus, the question, Why are eggs not as small as possible?

For close to 20 yr (Vance 1973*a;* reviews in R. Strathmann 1985 and Emlet et al. 1987) the answer has been the fecundity-time hypothesis. This hypothesis suggests that offspring from smaller eggs spend a longer time developing in the plankton and therefore suffer higher mortality. If the losses due to extra time in the water column equal the losses of egg number due to increases in egg size, a variety of egg sizes could result in a similar number of settling offspring.

Although the fecundity-time hypothesis is attractive, there are at least four problems in validating this theory. First, there is equivocal evidence that smaller eggs result in longer developmental times (see, e.g., Underwood 1974; Hendler 1975; Rice 1975; Emlet et al. 1987). Second, simply finding a significant relation between size and developmental time is not sufficient evidence to accept the fecundity-time hypothesis as the sole or even primary reason for large eggs. In order to test this hypothesis rigorously, accurate estimates of planktonic mortality are needed. Although progress has been made toward this end (R. Strathmann 1985; Rumrill 1990), the critical data for feeding (planktotrophic) and long-lived nonfeeding larvae are lacking. Third, theoretical treatments (Vance 1973*a,* 1973*b;* Christiansen and Fenchel 1979) predict extremes in egg size—either very small planktotrophic eggs or very large eggs with enough yolk to completely nourish nonfeeding larvae. Yet, experiments have documented that planktotrophic eggs are larger and energetically more expensive than necessary for development (Harvey 1949; Okazaki and Dan 1954; Dan-Sohkawa and Satoh 1978; Marcus 1979; Sinervo and McEdward 1988). These models cannot explain the variation in egg size present within a feeding mode (Emlet et al. 1987). Fourth, models of the fecundity-time hypothesis have assumed 100% fertilization of eggs (Vance 1973*b*), an assumption that appears to be false. The growing consensus from field studies is that female fertilization success, within a species, can be less than 1% and is highly variable (table 1 and references therein).

Here I offer an alternative, but not mutually exclusive, hypothesis: larger eggs present a larger target for sperm and are fertilized at a higher rate compared to smaller eggs. Mechanistically this is not a new concept. Models of fertilization kinetics incorporate egg size as the target area for sperm (Vogel et al. 1982; Denny and Shibata 1989). However, this notion has not been tested empirically, and the life-history implications of this idea have not been explored.

In this article, I first introduce the study organisms: three congeneric sea ur-

TABLE 1

VARIATION IN FERTILIZATION SUCCESS FROM FIELD EXPERIMENTS AND SURVEYS

Taxa	Mean (Range) (%)	Reference
Echinodermata:		
Asteroidea:		
Asterias forbesi	52 (2–99)	D. R. Levitan and S. S. Rumrill, unpublished data*
Echinoidea:		
Clypeaster rosaceus	30 (2–72)	D. R. Levitan and C. M. Young, unpublished manuscript*
Diadema antillarum	23 (0–99)	Levitan (1991)*
Strongylocentrotus droebachiensis	30 (1–95)	Pennington (1985)*
Strongylocentrotus franciscanus	18 (0–82)	Levitan et al. (1992)*
Holothuroidea:		
Cucumaria miniata	92 (1–100)	Sewell and Levitan (1992)†
Cnidaria:		
Hydractinia echinata	41 (0–91)	Yund (1990)*
Chordata:		
Teleostei:		
Halichoeres bivattatus	88 (20–100)	Petersen (1991)†
Thalassoma bifasciatum	76 (0–100)	Petersen et al. 1992†

NOTE.—Since experimental treatments and environmental conditions varied between studies, direct comparisons between means would not be appropriate.

* Field experiment.

† Survey.

chins with a fivefold difference in egg volume. Second, I describe a theoretical model of fertilization kinetics (Vogel et al. 1982). Third, I collect relevant data on sperm and egg characteristics and rates of fertilization to estimate parameters of the model. Fourth, I use the model to test the hypothesis that increases in fertilization success, due to increases in egg size, can be large enough to compensate for decreases in egg number. Finally, I use a graphic model (Smith and Fretwell 1974) to predict optimal egg size based on both fertilization and mortality. The results indicate that fertilization success is sensitive to egg size; the cost of reduced egg number, due to producing large eggs, can be offset by an increase in fertilization success; and by incorporating fertilization success into life-history theory, a mechanism can be developed to explain the variation in egg size found within a developmental mode.

STUDY ORGANISMS

Much of the work on larval life history of marine invertebrates has been on echinoderms, particularly the echinoids or sea urchins. Yet, in this group the evidence for a relationship between egg size and developmental time is weak. For example, Emlet et al. (1987) found no significant relationship between egg size and developmental time in 29 species of echinoids with a feeding larval stage. When the nonfeeding larvae, which have large yolk-filled eggs, were added into

the regression, the results were significant but with an R^2 of only 0.007. It is unclear from these results whether this relationship is because of egg size per se or differences in developmental mode.

Here I explore patterns of fertilization in three species of co-occurring sea urchins with a feeding larval stage: *Strongylocentrotus purpuratus, Strongylocentrotus franciscanus,* and *Strongylocentrotus droebachiensis.* Egg sizes tend to vary within and between individuals but not to overlap between species; *S. purpuratus* eggs are 70–85 μm, *S. franciscanus* eggs are 120–140 μm, and *S. droebachiensis* eggs are 136–160 μm (Emlet et al. 1987; M. Strathmann 1987).

Adult body size is not correlated with egg size in *Strongylocentrotus. Strongylocentrotus purpuratus* and *S. droebachiensis* have similar body sizes (30–50 mm test diameter), while the species with intermediate egg size, *S. franciscanus,* has a much larger body size (140–160 mm test diameter).

Spermatozoan shape but not volume (of head and middle piece) is correlated with egg size between species. *Strongylocentrotus purpuratus* sperm are 5.0 × 2.0 (length × width) μm, *S. franciscanus* sperm are 6.0 × 1.6 μm, and *S. droebachiensis* sperm are 7.0 × 1.5 μm (Chia et al. 1975). Sperm are more elongate in species with larger eggs. Sperm volumes, measured as cones, are 5.24 μm^3, 4.02 μm^3, and 4.12 μm^3 for these three species, respectively.

Development times vary greatly depending on temperature (M. Strathmann 1987); however, all three species have been raised in the laboratory at the same temperature. No relationship was found between egg size and developmental rate from fertilization through the prism stage (Dickie et al. 1989). R. Strathmann (1978) found minimum time to metamorphosis to be 63, 62, and 51 d and maximum time to metamorphosis to be 86, 131, and 152 d for *S. purpuratus, S. franciscanus,* and *S. droebachiensis,* respectively. R. Strathmann's (1978) data suggest that larvae from larger eggs have the potential to spend more, rather than less, time in the water. McEdward (1986) did find a slower developmental time for *S. purpuratus* compared to the other larger congeners (65 vs. 30 d). The difference between the latter two studies is that the former reflects time to metamorphosis and includes any delay of "competent" larvae, whereas the latter reflects the developmental time until competence. Since planktonic mortality is dependent on the total planktonic period, it should include any delay of settlement by competent larvae (Underwood 1974). For these three congeners, there is mixed evidence of reduced planktonic period (and mortality) for species with larger eggs.

THE FERTILIZATION KINETICS MODEL

Vogel et al. (1982) developed a model to describe rates of fertilization based on the assumption that sperm attach to the first egg they contact, regardless of whether fertilization occurs. This model incorporates concentration of virgin sperm (S_0, sperm/μL) and concentration of eggs (E_0, eggs/μL), sperm swimming velocity (υ, mm/s) and half-life (τ, s), and egg cross-sectional area (σ_0, mm^2). It also incorporates two rate constants, β_0 and β. The first, β_0 (mm^3/s), is the rate constant of sperm and egg collision; it is estimated from the sperm swimming

velocity and the cross-sectional area of the egg:

$$\beta_0 = \upsilon \times \sigma_0 . \tag{1}$$

The second, β (mm^3/s), is the rate constant of fertilization. The ratio of β/β_0 is the average proportion of sperm contacts necessary for fertilization to occur. Vogel et al. (1982) derived their model by calculating the average number of potential fertilizers per egg and then used the Poisson distribution to estimate the probability of an egg's not being fertilized. The proportion of eggs fertilized is then

$$\varphi_\infty = 1 - \exp\left(-\frac{\beta S_0}{\beta_0 E_0}(1 - e^{-\beta_0 E_0 \tau}) \right). \tag{2}$$

The time of sperm-egg contact (the time an egg spends in a sperm solution), t, can be substituted for τ when t is less than τ (Vogel et al. 1982; Levitan et al. 1991). This model does not include sperm chemotaxis, which might increase the effective diameter of the egg by attracting sperm that might otherwise miss eggs. However, despite numerous attempts, sperm chemotaxis has not been documented in echinoids (Epel 1978), and sperm chemotaxis to intact eggs has not been demonstrated in any echinoderm (Miller 1985).

This model was tested by Vogel et al. (1982) by varying both egg and sperm concentration with the sea urchin *Paracentrotus lividus*, and they found a good fit of predicted and empirical results. My colleagues and I (Levitan et al. 1991) also tested this model by varying egg and sperm concentration as well as sperm-egg contact time with *Strongylocentrotus franciscanus;* we also found a good fit of empirical data to the model. In this latter study, the two rate constants (β and β_0) were first predicted as the best fit to the data and then compared to empirical observations of β_0 by measuring egg size and sperm swimming velocity. The predicted and observed values were not significantly different from one another, which suggests the accuracy of the model and the importance of egg size and sperm velocity in influencing rates of fertilization.

METHODS

The sea urchins *Strongylocentrotus purpuratus, Strongylocentrotus franciscanus,* and *Strongylocentrotus droebachiensis* were collected from Barkley Sound on the west coast of Vancouver Island, British Columbia, Canada. Gametes were obtained by injecting urchins with 0.55 M KCl. Males were placed aboral side down into an empty glass bowl, and females were placed in a similar manner over a glass bowl filled with 1 μm filtered seawater. Eggs were diluted to a concentration of approximately 1.5/μL, and a 1-mL aliquot of this egg solution was placed into each of 18 vials containing 8 mL of filtered seawater (per replicate). An additional sample of eggs was kept to determine egg concentration (three counts per replicate) and egg diameter (20 eggs per replicate).

A 0.1-mL aliquot of "dry" sperm was added to a separate vial containing 9.9

mL of filtered seawater. The sperm solution was then run through a series of six 10-fold dilutions. One milliliter of each sperm dilution was added to one of six vials containing eggs (final serial sperm dilutions of 10^4 [1 part sperm to 9,999 parts seawater], 10^5, 10^6, 10^7, 10^8, and 10^9). The additional 12 vials containing eggs were used in a gamete age experiment (sperm are much more sensitive to age than eggs) (Pennington 1985). At intervals of 10, 50, and 250 min, a 1-mL aliquot from one of four sperm dilutions was added to a vial containing eggs (final serial sperm dilutions of 10^5, 10^6, 10^7, and 10^8). A sample from the 10^3 sperm dilution was fixed in Formalin for later sperm counts (eight counts per replicate).

Three hours after the introduction of sperm, 100 eggs from each treatment were scored for the presence of a raised fertilization membrane or later developmental stage. All experiments were run at 9°C. Each replicate series consisted of a unique male and female urchin, and five replicates of one species were conducted at a time.

To estimate sperm swimming velocity, 1 min after dilution, I placed a drop of the sperm suspension from the 10^3 dilution onto a depression slide and put it under a cooled stage (9°C) of a compound microscope. Swimming sperm were videotaped at 400 power. The plane of focus was set midway through the depression slide to diminish the influence of the glass sides on measurements of swimming velocity (walls several body lengths away from a swimming cell have a negligible influence on movement) (Winet 1973). Time was monitored on the videotape with an internal stopwatch. Sperm were later traced on acetate sheets and distances measured using a graphics tablet. Velocity was estimated for 20 sperm in each replicate.

RESULTS

Egg Size

There were significant differences in egg size between all three species (table 2). The mean egg diameters were 0.084, 0.135, and 0.145 mm for *Strongylocentrotus purpuratus, Strongylocentrotus franciscanus,* and *Strongylocentrotus droebachiensis,* respectively (fig. 1).

Sperm Velocity

For these three species, sperm swimming velocity was inversely related to egg diameter. There were significant differences in sperm swimming velocity between all three species (table 2). The mean swimming velocities were 0.145, 0.130, and 0.088 mm/s for *S. purpuratus, S. franciscanus,* and *S. droebachiensis,* respectively (fig. 2).

Sperm Longevity

Sperm half-life was calculated by fitting the results of the sperm-age experiment at each dilution and replicate to an exponential regression equation. For each equation, the half-life was calculated from the predicted time when fertilization was half the initial value at t_0. These half-life values (s; log transformed) then

TABLE 2

NESTED ANOVA TESTING DIFFERENCES IN EGG DIAMETER AND SPERM VELOCITY IN *STRONGYLOCENTROTUS PURPURATUS*, *STRONGYLOCENTROTUS FRANCISCANUS*, AND *STRONGYLOCENTROTUS DROEBACHIENSIS*

	df	SS	MS	*F*
Egg diameter:				
Species	2	.213897	.106949	321.218***
Individual	12	.003995	.000333	27.292***
Error	285	.003477	.000012	
Total	299	.221369		
Sperm velocity:				
Species	2	.203074	.101537	34.439***
Individual	12	.035380	.002948	5.634***
Error	285	.149153	.000523	
Total	299	.387606		

NOTE.—Twenty egg diameters or sperm velocities were measured for each of five individuals nested within a species. For both egg diameter and sperm velocity, all pairwise comparisons were significantly different (Duncan's critical value = 0.001 and 0.007 for eggs and sperm, respectively; see text for means). SS, Sum of squares; MS, mean squares.

*** $P < .001$.

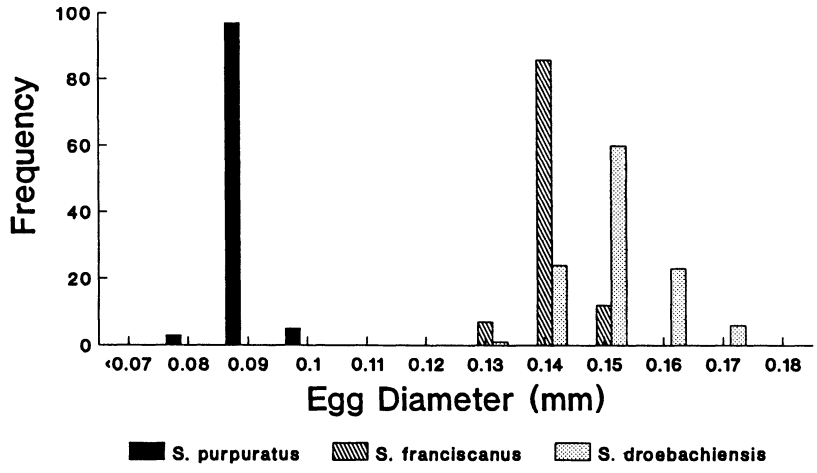

FIG. 1.—Frequency distribution of egg diameters for *Strongylocentrotus purpuratus*, *Strongylocentrotus franciscanus*, and *Strongylocentrotus droebachiensis*. For each species, 20 eggs from each of five individuals were measured (100 eggs per species).

were plotted as a function of sperm concentration (sperm/μL; log transformed) (fig. 3), and a linear regression was performed to predict τ values for the range of sperm concentrations used in the fertilization kinetics model. The slopes of the regression lines are directly related to sperm swimming velocity, whereas the intercepts are inversely related to sperm swimming velocity. Both relationships indicate that higher swimming velocities are associated with lower stamina.

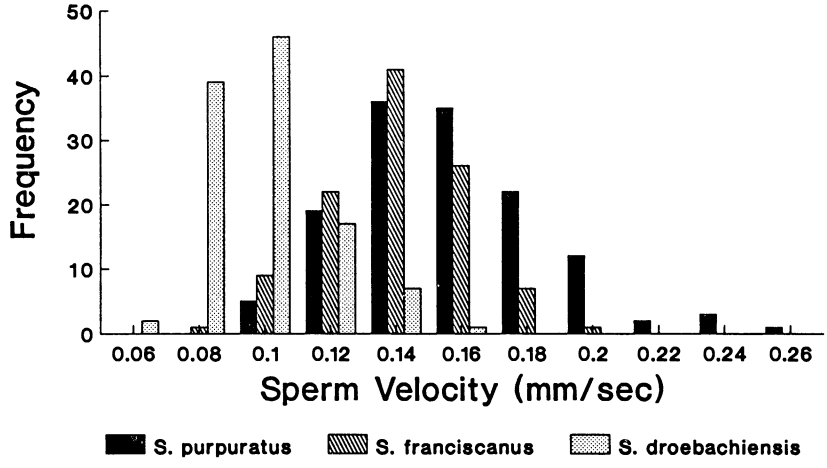

FIG. 2.—Frequency distribution of sperm swimming speed for *Strongylocentrotus purpuratus, Strongylocentrotus franciscanus,* and *Strongylocentrotus droebachiensis*. For each species, 20 sperm from each of five individuals were measured (100 sperm per species).

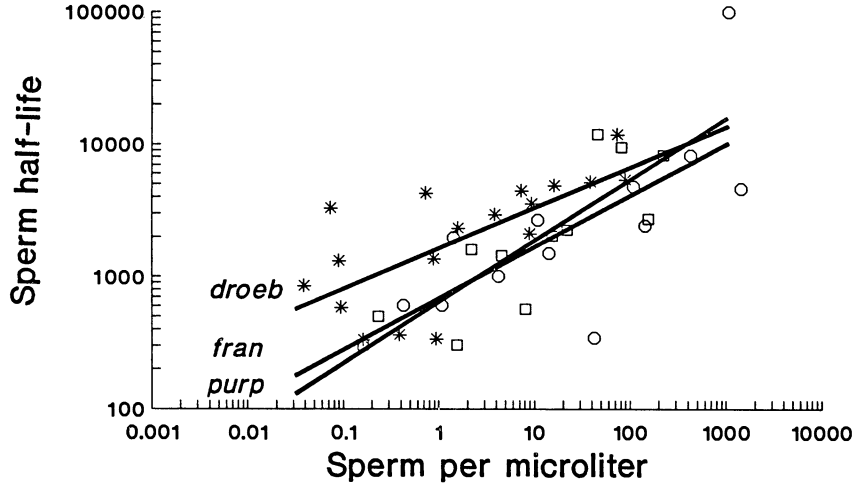

FIG. 3.—Sperm half-life (τ, s) as a function of sperm concentration (μL). *Strongylocentrotus purpuratus* (*squares*): $\log \tau$ = (log sperm concentration $\times$ 0.457) + 2.798, $R^2 = 0.715$, $P < .001$, $N = 12$. *Strongylocentrotus franciscanus* (*circles*): $\log \tau$ = (log sperm concentration $\times$ 0.391) + 2.818, $R^2 = 0.509$, $P < .01$, $N = 12$. *Strongylocentrotus droebachiensis* (*asterisks*): $\log \tau$ = (log sperm concentration $\times$ 0.308) + 3.216, $R^2 = 0.503$, $P < .001$, $N = 18$.

Fertilization Assays

The fertilization assays demonstrate a direct relationship between the probability of fertilization and egg diameter for the three species of *Strongylocentrotus* (fig. 4). The lines fitted to the fertilization data are the results of the fertilization kinetics model (table 3). The model was calculated by including the appropriate values for each treatment (sperm and egg concentration, sperm half-life and velocity, and egg size) with the exception of the constant β. This constant was estimated by iterating the Marquart method of nonlinear regression (SAS 1988). For all species, the fitted regression line explained over 95% of the variation in fertilization. The estimated values of β were 4.59×10^{-5}, 9.52×10^{-5}, and 2.42×10^{-4} mm^3/s. These rate constants of fertilization increase with increases in egg diameter. The 95% confidence intervals for the regression equations (fig. 4*D*) indicate the distinct fertilization distributions of the three species.

Importance of Egg Size

To evaluate the sensitivity of fertilization success to egg size, I used the fertilization kinetics model to predict fertilization success using the species values of β, β_0, and sperm half-life, and egg concentrations of 0.01/μL. The sperm concentration chosen was the amount of sperm necessary to provide 50% fertilization (F_{50}) for each species (F_{50} = 8.92/μL, 5.68/μL, and 1.55/μL for *S. purpuratus, S. franciscanus,* and *S. droebachiensis,* respectively). Egg diameter then was increased in the model from 0.01 mm to 0.5 mm.

Fertilization success is very sensitive to changes in egg size for all three species (fig. 5). The convergence of 100% fertilization at egg sizes of 0.4 mm is only a reflection of the sperm concentration chosen; slightly higher sperm concentrations would result in convergence at a smaller egg diameter, and slightly lower concentrations would result in convergence at a larger egg diameter.

Estimates of Zygote Production

The increase in fertilization success with increases in egg diameter suggests that selection should favor increases in egg size. However, increases in egg size result in decreases in egg number if the energy available for reproduction remains constant. Thus, there is a potential trade-off between the quantity of eggs produced and the probability of fertilization. To estimate this trade-off, I calculated the volume of a sphere for the egg sizes of the three *Strongylocentrotus* species: 3.103×10^{-4}, 1.288×10^{-3}, and 1.596×10^{-3} mm^3 for *S. purpuratus, S. franciscanus,* and *S. droebachiensis,* respectively. I then calculated the number of eggs for a constant volume of egg material as 3.223×10^6, 7.764×10^5, and 6.266×10^5 eggs per 1 cm^3 of egg material. Zygote production then was calculated as the number of eggs produced times the proportion fertilized. Fertilization success was predicted from the fertilization kinetics model using sperm-egg contact times of 3 h, 3 min, and 3 s (fig. 6).

These calculations demonstrate that with 100% fertilization, the sea urchin with the smallest eggs, *S. purpuratus,* produces over 2.5 million more zygotes than the sea urchin with the largest eggs, *S. droebachiensis,* per 1 cm^3 of egg material.

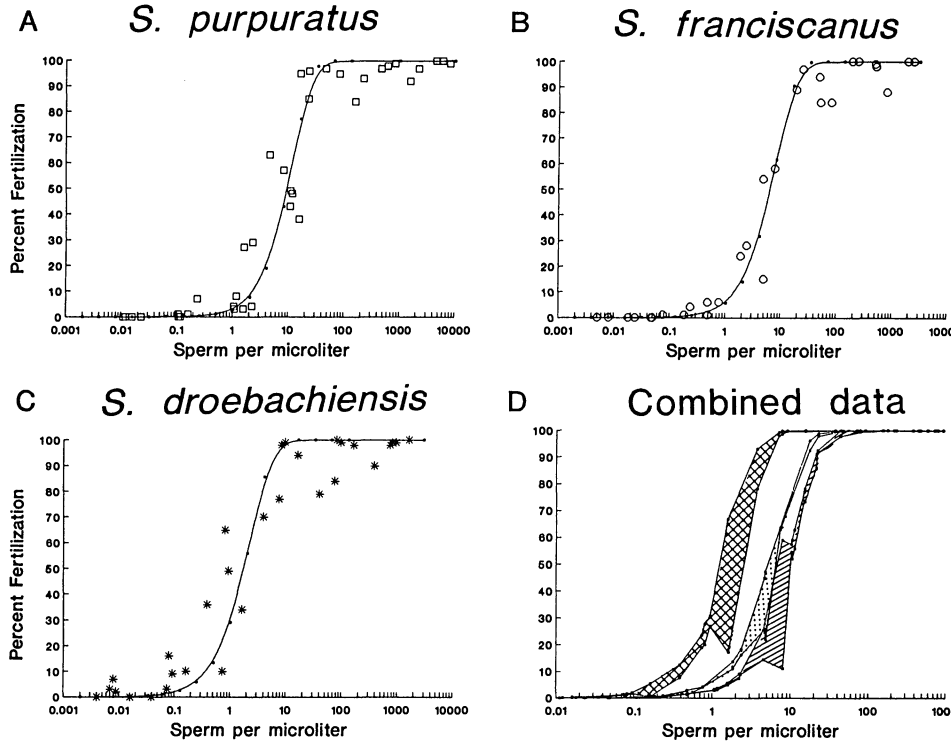

FIG. 4.—Fertilization assays of *Strongylocentrotus* spp., showing percentage fertilization as a function of sperm concentration (μL). Regression lines are calculated from Vogel et al.'s (1982) model; see text and table 2 for details. *A*, *S. purpuratus;* egg diameter 0.084 mm, $R^2 = 0.962$. *B*, *S. franciscanus;* egg diameter 0.135 mm, $R^2 = 0.985$. *C*, *S. droebachiensis;* egg diameter 0.145 mm, $R^2 = 0.965$. *D*, The 95% confidence interval on the mean for the predicted value of each observation: *single hatched, dotted,* and *double hatched patterns* indicate *S. purpuratus*, *S. franciscanus*, and *S. droebachiensis*, respectively (the range of sperm concentration is reduced compared to *A*, *B*, and *C* for clarity). Much of the apparent variation around the regression lines in these two-dimensional plots is explained by within-species differences in egg concentration, sperm swimming speed, and egg diameter. These factors are all incorporated into the regression model.

However, when fertilization success is less than 100%, this relationship changes. In fact, when sperm are limiting, the species with the largest (and fewest) eggs produces the most zygotes per unit of egg material (fig. 6).

As the time of sperm-egg contact diminishes from 3 h to 3 s, the three species converge in zygote production. When sperm and eggs are in contact for 3 h, at sperm concentrations of 1 per μL, *S. droebachiensis* produces 332% more zygotes than *S. franciscanus* and 121% more than *S. purpuratus*. When sperm and eggs are in contact for only 3 s, these figures drop to 105% and 3%, respectively. The reason for the convergence is that, at shorter sperm-egg contact times, sperm swimming velocity becomes more important than sperm longevity. *Strongylocen-*

TABLE 3

NONLINEAR REGRESSION OF FERTILIZATION DATA USING VOGEL ET AL.'S (1982) FERTILIZATION KINETICS MODEL (β ESTIMATED BY ITERATION)

	df	SS	MS	F	R^2	β_0 (mm^3/s)	β (mm^3/s)	β/β_0
Strongylocentrotus purpuratus						.00082	.0000459	.0559
Regression	1	14.720	14.720	920.000	.962			
Residual	37	.585	.016	. . .	. . .			
Total	38	15.304						
Strongylocentrotus franciscanus						.00186	.0000952	.05117
Regression	1	11.361	11.361	1862.459	.985			
Residual	29	.177	.006	. . .	. . .			
Total	30	11.538						
Strongylocentrotus droebachiensis						.00145	.000241	.1666
Regression	1	13.385	13.385	789.676	.965			
Residual	29	.491	.017	. . .	. . .			
Total	30	13.876						

NOTE.—SS, Sum of squares; MS, mean squares.

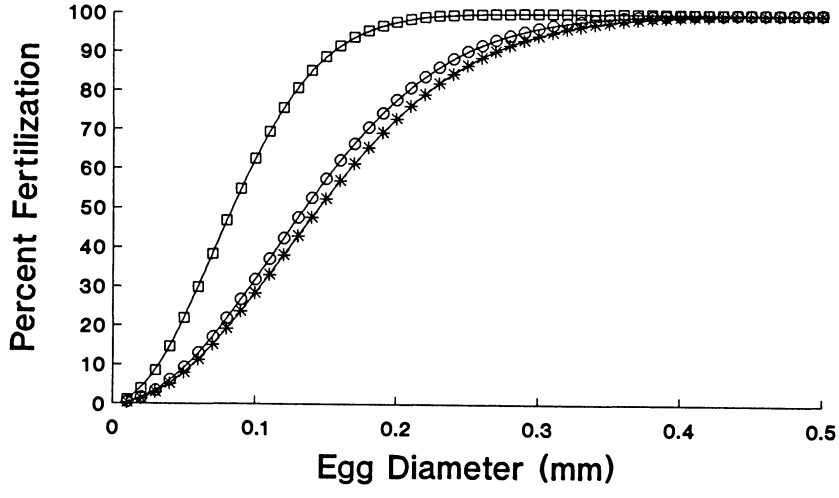

FIG. 5.—Relationship between egg diameter and the percentage of eggs fertilized. Sperm concentration is the concentration required to fertilize 50% of eggs when egg diameter is as measured empirically (see text for details). *Squares*, *circles*, and *asterisks* represent predictions based on fertilization kinetics of *Strongylocentrotus purpuratus*, *Strongylocentrotus franciscanus*, and *Strongylocentrotus droebachiensis*, respectively. Egg concentration is 0.01 per μL.

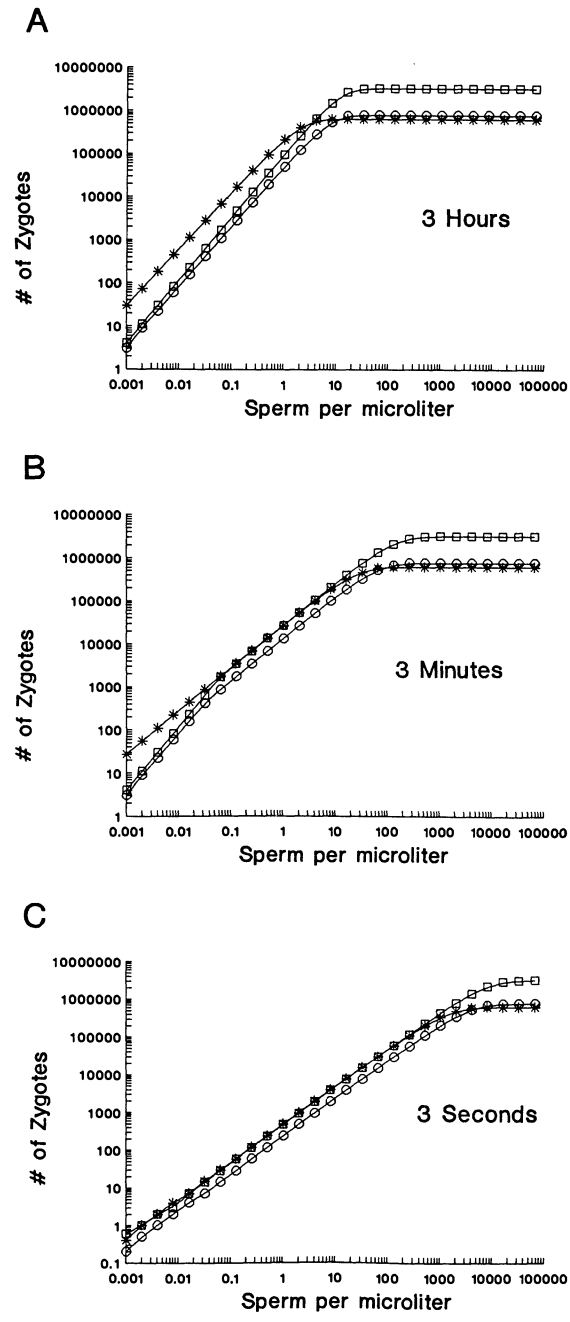

FIG. 6.—Total number of zygotes produced when the total reproductive output is equivalent to 1 mL of egg material. *Squares*, *circles*, and *asterisks* represent *Strongylocentrotus purpuratus*, *Strongylocentrotus franciscanus*, and *Strongylocentrotus droebachiensis*, respectively. *A*, Based on sperm-egg contact time of 3 h; *B*, 3 min; and *C*, 3 s. Egg concentration is 0.01 per μL.

trotus droebachiensis, with the slowest but longest-lived sperm, exhibits the greatest decline in fertilization.

The success of *S. droebachiensis* at low sperm concentrations is primarily because of increased egg size but also the relatively high fertilizability of the egg (β/β_0) (table 3). *Strongylocentrotus franciscanus,* the species with intermediate egg size and a similar ratio of β/β_0, always produces slightly fewer zygotes compared to *S. purpuratus,* the species with the smallest eggs (fig. 6). This result occurs because egg volume increases as a cubic function of egg diameter, while egg fertilization increases as a square function of egg diameter. Thus, individual egg fertilization increases greatly with egg size, but total zygote production decreases slightly with egg size, assuming that other gamete characteristics are constant (although sperm swimming ability and egg fertilizability vary between species) and that egg volume is directly related to energetic content (see below).

There is much variability in energetic content of eggs between and within species (Turner and Lawrence 1979; McEdward and Carson 1987; McEdward and Coulter 1987). Among *Strongylocentrotus* spp. larger eggs are calorically less dense than smaller eggs (Strathmann and Vedder 1977) but not necessarily for other species (Turner and Lawrence 1979). Organic matter scales as a 0.75 exponent of egg volume (Strathmann and Vedder 1977), which is closer to a function of egg surface area than egg volume. This suggests that zygote production per unit of energy would be greater for species with larger eggs than predicted by figure 6.

Optimal Egg Size

In order to predict the optimal egg size for each species, it would be reasonable to incorporate both fertilization and larval survival. The relationship between egg size and fertilization would be different between species because of microhabitat differences in water flow, distribution and abundance of spawning conspecifics, and species-specific gamete characteristics. The relationship between egg size and larval mortality would be similar for co-occurring species with a similar larval design, since released eggs would quickly drift into the same planktonic environment. Egg size can influence larval survival, both through differences in development time (Vance 1973*a*) and size-dependent mortality (Christiansen and Fenchel 1979; Rumrill 1990). Unfortunately, the quantitative relationship between egg size and survival is poorly known for planktonic larvae (Rumrill 1990).

To illustrate how fertilization and survival can influence optimal egg size, I generated an arbitrary size-dependent survival rate curve as a linear relationship of egg diameter (linear relationships have been used to relate egg diameter to development time; see, e.g., Perron and Koehn 1985; Emlet et al. 1987). This survival rate curve set zero individuals surviving at an egg size smaller than 0.04 mm (smallest reported echinoid egg diameter approximately 0.05 mm; Emlet et al. 1987) and all eggs surviving at an egg size greater than 1 mm. This represents the proportion of released eggs settling assuming 100% fertilization (*upper curve* in fig. 7). Note that changing the degree of mortality without changing the shape of the survival rate curve would have no influence on optimum egg size. Incorporating the fertilization kinetics data appropriate for each species and multiplying the proportion fertilized by the proportion surviving provide the proportion of

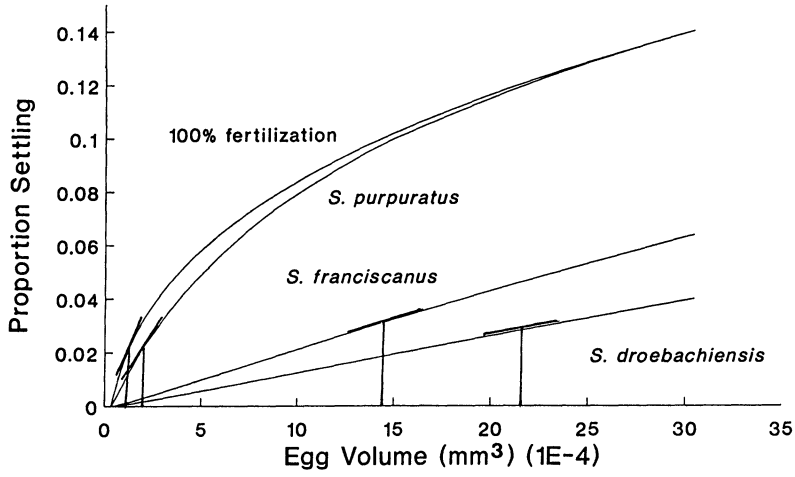

FIG. 7.—Optimal egg size for maximal parental fitness, shown by the proportion of larvae settling as a function of egg volume. *Top curve* assumes 100% fertilization; the three *lower curves* are based on the fertilization kinetics of *Strongylocentrotus purpuratus, Strongylocentrotus franciscanus,* and *Strongylocentrotus droebachiensis,* respectively (egg diameter is varied in the model). Egg concentration is 0.01 per μL. Sperm-egg contact time is 5 min. Sperm concentration for *S. purpuratus* is 100 per μL (based on concentration of 1 mL of sperm released into a 1-m^3 tide pool). Sperm concentration for *S. franciscanus* is 12 per μL (based on average fertilization for this subtidal species from Levitan et al. [1992]). Sperm concentration for *S. droebachiensis* is 3 per μL (based on reduced sperm production and lower population density for this subtidal species compared to *S. franciscanus;* D. R. Levitan, unpublished data and personal observation). Tangents of these curves through the origin are predictions of optimal egg volume. Uniformly changing the degree of mortality (i.e., the order of magnitude on the *Y*-axis) has no influence on the prediction of optimal egg size.

released eggs settling assuming variable fertilization (*lower curves* in fig. 7). The optimal egg size for maximal parental fitness is the tangent of these curves through the origin (Smith and Fretwell 1974). Assuming 100% fertilization, the optimal egg diameter is 0.059 mm. For typical sperm concentrations based on the spawning conditions of each species (see legend in fig. 7 and Discussion), the optimal egg diameters are 0.072 mm, 0.140 mm, and 0.163 mm for *S. purpuratus, S. franciscanus,* and *S. droebachiensis,* respectively. In this illustration, the predicted egg sizes fall within the natural range of egg sizes for each species.

DISCUSSION

Sperm limitation can lead to important variation in the rates at which eggs of different sizes are fertilized. Fertilization success increased with egg size, in spite of the associated decrease in sperm velocity in these three species. Even when sperm-egg contact time was reduced to 3 s (when sperm longevity becomes irrelevant), the model predicts greater fertilization success of larger eggs and similar zygote production compared to urchins with smaller, more numerous eggs (fig. 6). If zygote production is dependent on egg size and sperm concentration, the

evolutionarily optimized size of eggs may be a function of the average ambient sperm concentration.

Ambient sperm concentration is a function of the distribution and abundance of males releasing sperm and the rate of dilution. Increases in population density, population size, level of aggregation, body size, and spawning synchrony result in increased sperm concentration (Levitan 1991; Levitan et al. 1992; Sewell and Levitan 1992), while increases in current velocity, turbulence, and distance between spawning individuals result in increased dilution (Pennington 1985; Denny and Shibata 1989; Yund 1990; Grosberg 1991; Levitan 1991; Petersen 1991; Levitan et al. 1992; Petersen et al. 1992; D. R. Levitan and C. M. Young, unpublished manuscript).

When the above factors result in sperm limitation, gamete qualities such as egg size, sperm velocity and longevity, and the fertilizability of the egg determine fertilization success. For the three *Strongylocentrotus* species, egg diameter was inversely related to sperm velocity, sperm velocity was inversely related to sperm longevity, and there was no pattern detected with egg fertilizability (β/β_0). These correlations suggest that some gamete characteristics are coevolved. This is no surprise to biologists studying sperm-egg morphology and interactions (see, e.g., Chia et al. 1975; Eckelbarger et al. 1989*a;* Minor et al. 1991; Palumbi and Metz 1991). What is of concern here is whether environmental factors, mediated through fertilization success, can influence this coevolution.

The relationship between sperm swimming velocity and stamina is probably an energetic trade-off; given a certain amount of energy, sperm can move quickly for a short duration or move more slowly for a longer duration. This relationship may be similar to the relationship between sperm concentration and sperm half-life; increased dilution leads to increased activity but shorter longevity (fig. 3; discussed in Chia and Bickell 1983; Levitan et al. 1991).

The relationship between increasing sperm velocity and decreasing egg size may reflect the more complex issues of how male and female reproductive strategies are influenced by gamete concentration. When gamete concentration is high, fertilization success should be high, and eggs should therefore be small and numerous. Simultaneously, sperm should be fast at the cost of being short-lived, in order to search a small volume of water vigorously for a rapidly diminishing pool of virgin eggs. When gamete concentration is low, larger eggs would increase target size and the chance of sperm collisions. Longer-lived but slower sperm might survive long enough for water movements to combine distantly spawned gamete plumes.

Off Vancouver Island, the species with the smallest eggs and fastest sperm, *S. purpuratus,* lives in shallow water and is often found in tide pools. Both factors would tend to concentrate sperm and result in high levels of fertilization. *Strongylocentrotus franciscanus,* with intermediate egg size and sperm velocity, is found subtidally, but it is often at very high population density and is much larger (and produces up to an order of magnitude more sperm; D. R. Levitan, unpublished data) than the subtidal species with the largest eggs and slowest sperm, *S. droebachiensis.* Thus, for these species egg size and sperm velocity are consistent with expectations based on probabilities of sperm-egg encounters.

Without incorporating fertilization, optimal egg size is predicted to be uniformly small for all three species. Previous life-history models of marine invertebrates have also predicted that species with feeding (planktotrophic) larvae should produce vanishingly small eggs (Vance 1973*a*) or eggs at the minimal size needed for development (Christiansen and Fenchel 1979). These former models do not provide a mechanism explaining the wide variety of egg sizes found in marine invertebrates (Underwood 1974; Emlet et al. 1987) and cannot explain why planktotrophic eggs are larger than needed for development (Sinervo and McEdward 1988). In contrast, the present model predicts larger and unique optimal egg sizes, dependent on the fertilization characteristics of each species and the environmental conditions during spawning.

Variation in sperm-egg encounter frequencies also could explain the pattern of increasing egg size (Emlet et al. 1987) and sperm head length (Eckelbarger et al. 1989*a*) with increasing depth distribution in echinoids. Experimental evidence suggests that fertilization success decreases with water depth from 0.5 to 8 m, because of increased dilution effects (D. R. Levitan and S. S. Rumrill, unpublished data). Over larger depth ranges, differences in abundance patterns (Pawson 1982) or lack of spawning cues (Rokop 1974) could lead to reduced sperm-egg encounters in deep water. Several modifications of usually conservative characteristics of echinoid sperm found in the deep sea, such as elongated sperm nuclei (Eckelbarger et al. 1989*a*), sperm containing lipid stores (Eckelbarger et al. 1989*b*), and the presence of paraspermatozoa used to deliver euspermazoa (Eckelbarger et al. 1989*c*), would increase sperm longevity and fertilization success. The increase in egg size would also improve fertilization and thus reproductive success of sparse deep-sea spawners.

Under some conditions, sperm concentration may be so low that increasing egg size would have a negligible influence on fertilization. Under these conditions, other modifications may be needed to ensure at least some degree of fertilization. It has been suggested that at least one deep-sea echinoderm has developed modified spines for transferring sperm directly to females (Eckelbarger et al. 1989*a*). Intense selective pressure to fertilize eggs may have led to patterns of sperm transfer, sperm storage, and internal fertilization in marine invertebrates and other groups. Additionally, hermaphroditism, selfing, and asexual reproduction would provide mechanisms for increased reproduction when fertilization becomes less likely (Levitan 1991).

Although the present treatment focuses on organisms that release both eggs and sperm, similar considerations should be made for organisms that release sperm (or pollen) and retain eggs. Since sperm and pollen limitation has been noted for both plants (Schemske et al. 1978; Willson et al. 1979; Schemske 1980; Weller 1980; Bierzychudek 1981) and brooding invertebrates (Brazeau and Lasker 1990; Grosberg 1991; D. A. Brazeau, personal communication), it would be worthwhile to incorporate sperm-egg encounter probability and fertilization into the life-history theory of these organisms.

Both egg and sperm characteristics influence fertilization success, zygote production, and ultimately fitness, which suggests that more attention should be focused on the male contribution to reproductive success. This consideration is

especially important since factors enhancing ambient sperm concentration can be detrimental to egg production (e.g., high population density) (Levitan 1991). Previous attention to male function has shed light on sex allocation in flowers (Bell 1985) and sperm-mediated gene flow in ascidians (Grosberg 1991).

The importance of adult characteristics to ambient gamete concentration, gamete characteristics to fertilization success, and egg characteristics to larval developmental mode suggests important links between these various phases of the life cycle. Environmental influences on adult life history (i.e., size, energy allocation, population distribution) could have cascading effects on fertilization and larval life history. Similarly, constraints or selective pressures on larval design could influence egg size, fertilization rates, and ultimately adult life history. Although other links of egg size to adult characteristics have been found, these have involved constraints on the upper limit to egg size (Luetenegger 1979; Reaka 1979; Strathmann et al. 1984; Congdon and Gibbons 1987; Sinervo and Licht 1991).

These results provide an alternate but not exclusive hypothesis to the fecundity-time hypothesis in explaining variation in egg size between species. The importance of the fecundity-time hypothesis depends on the relationship between egg size and planktonic mortality. The importance of the fertilization success hypothesis depends on the frequency of sperm limitation and patterns of gamete kinetics. Although there have been few studies, the available data indicate that sperm limitation may be common in nature. Hence, both fertilization and mortality may be potent selective agents in the evolution of marine invertebrate life histories.

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