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Life-History Consequences of Investment in Free-Spawned Eggs and Their Accessory Coats

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ABSTRACT: The optimal trade-off between offspring size and number can depend on details of the mode of reproduction or development. In marine organisms, broadcast spawning is widespread, and external coats are a common feature of spawned eggs. Egg jelly coats are thought to influence several aspects of fertilization and early development, including the size of the target for sperm, fertilization efficiency, egg suspension time, polyspermy, embryo survival, and fecundity. These costs and benefits of investment in jelly result in trade-offs that can influence optimal reproductive allocation and the evolution of egg size. I develop an optimization model that sequentially incorporates assumptions about the function of egg coats in fertilization. The model predicts large variation in coat size and limited variation in ovum size under a broad range of conditions. Heterogeneity among spawning events further limits the range of ovum sizes predicted to evolve under sperm limitation. In contrast, variation in larval mortality predicts a broad range of optimal ovum sizes that more closely reflects natural variation among broadcast-spawning invertebrates. By decoupling physical and energetic size, egg coats can enhance fertilization, maintain high fecundity, and buffer the evolution of ovum size from variation in spawning conditions.

Keywords: egg size, fertilization efficiency, jelly coat, polyspermy, broadcast spawning, life-history evolution.

A major goal of life-history theory is to identify forces that shape the optimal trade-off between offspring size and number (Roff 1992; Stearns 1992). While striving to be broadly applicable, life-history models are often built around biological details that can help to reveal the evolutionary significance of variation in important characters (Parker and Begon 1986; Stearns and Koella 1986; Congdon and Gibbons 1987; Sargent et al. 1987; Winkler and Wallin 1987; Sinervo and Licht 1991; Winemiller and Rose 1993; Carlon and Ebersole 1995; Strathmann 1995; Hendry et al. 2001). In marine invertebrates, for example, reproduction often involves copious egg production, external fertilization, and pelagic larval development. Life-history models for these taxa have therefore focused traditionally on risks of planktonic development (Vance 1973; Christiansen and Fenchel 1979; Strathmann 1985) and more recently on the risk of incomplete fertilization (Levitan 1993, 2000*a*). Because both types of risk depend on egg size and are traded off against fecundity, a central focus of theory has been to understand how these processes can account for the large variation in egg size among broadcast-spawning taxa (Strathmann 1978; Emlet et al. 1987; Sinervo and McEdward 1988; Havenhand 1993; Hart 1995; Hoegh-Guldberg and Pearse 1995; Robertson 1996; Sewell and Young 1997; Levitan 2000*a*).

Although egg size factors into both prezygotic (fertilization) and postzygotic (larval and juvenile) risks, these two consequences of size are distinguished by the difference between physical and energetic size. Physical size, or the "target" presented to sperm, affects the probability of gamete collision (Rothschild and Swann 1951; Vogel et al. 1982; Cox and Sethian 1985; Levitan 1993). Energetic size, in contrast, influences developmental processes (Wray 1992; McEdward and Morgan 2001) and dictates the number of eggs produced per unit investment (Jaeckle 1995). This distinction is critical for understanding how pre- and postzygotic processes contribute to optimal egg size (Podolsky and Strathmann 1996; Randerson and Hurst 2000; Jantzen et al. 2001). For example, postzygotic (energetic) benefits can be sufficient to offset fecundity costs (Strathmann 1985; Levitan 1996*b*; Podolsky and Strathmann 1996), whereas prezygotic (target size) benefits cannot (Podolsky and Strathmann 1996).

Target size and energetic size are often related, but they can also be decoupled by several mechanisms. First, simple hydration could enlarge target size with minimal energetic

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cost (Craik and Harvey 1987; Thorsen et al. 1996). Second, energetic and physical size could be adjusted independently through changes in the relative proportions of carbohydrates, protein, and lipids (Turner and Lawrence 1979; Crisp 1984; Jaeckle 1995). Scaling relationships, however, generally do not support changes in hydration or composition as mechanisms to adjust egg size (Jaeckle 1995) or to compensate for the loss in fecundity associated with larger eggs (Podolsky and Strathmann 1996). Third, eggs of some species release sperm attractants that can enlarge the egg target (Miller and King 1983; Maier and Muller 1986; Jantzen et al. 2001). Attractant production could be costly and may be effective only under certain hydrodynamic conditions, although such costs and limits are not well established (Dusenbery 2000; Jantzen et al. 2001).

Fourth, eggs can be enclosed within accessory structures, which can increase target size at low cost and independently of hydrodynamic conditions (Rothschild and Swann 1951; Farley and Levitan 2001; Podolsky 2001, 2002). These structures—including jelly coats and thickened envelopes (cnidarians, ctenophores, nemerteans, annelids, sipunculans, prosobranch and bivalve molluscs, echinoderms), test and follicle cells (ascidians), and egg hulls (polyplacophoran molluscs)—are a common and prominent feature of eggs free spawned in marine environments. Unfortunately, this view derives more from passing descriptions than from quantitative data. For example, jelly coats are typical of the eggs of echinoid echinoderms (Pearse and Cameron 1991), yet the original sources for only three of 53 broadcast-spawning species with feeding larvae described by Emlet et al. (1987) that I could access reported jelly coat size. Similarly, the presence of an external coat is noted for all major groups of broadcast spawners by Strathmann (1987), yet size is reported for only 24 of 168 such species. Among such reports (see appendix in the online edition of the *American Naturalist*), target size (cross-sectional area) is increased by external coats on average 4.3-fold (max = 11.9, $N = 32$) and by jelly coats in particular on average fivefold (max = 11.9, $N = 19$). These figures illustrate the substantial contribution that external coats can make to target size.

In addition to increasing target size, however, egg coats may have other consequences for offspring production. First, coats use resources that could be invested into larger or additional ova. Although the organic density of jelly is relatively slight, the large volume of jelly can constitute 10%–20% of the material cost of an egg (Bolton et al. 2000; Marsh and Manahan 2000; Podolsky 2002). Second, jelly coats, follicle cells, and egg hulls are low-density and high–surface area structures that can slow the sinking of a suspended egg (Buckland-Nicks 1993; Podolsky 2001). Settling time can alter fertilization probability when sperm are limiting and eggs are suspended by water motion or adult behaviors (Podolsky 2002). Third, an external covering could alter fertilization efficiency or the probability of fertilization per sperm contacted (Rothschild and Swann 1951; Vogel et al. 1982). In echinoids, jelly improves efficiency by inducing the acrosome reaction (SeGall and Lennarz 1981; Vacquier and Moy 1997) but could also lower efficiency by acting as a physical barrier to sperm (Hagström 1956*b*; Farley and Levitan 2001). Finally, external coats could alter the probability of polyspermy (McLaughlin and Humphries 1978; Lambert and Lambert 1981; Schuel 1984; Mozingo and Hedrick 1996), one potential cost of large target size (Styan 1998). These costs and benefits define a set of trade-offs that could limit or favor investment in external coats as a way to increase target size.

Constituents of egg jelly have well-documented effects on sperm physiology, sperm-egg interaction, and egg protection (Kopf et al. 1979; Garbers et al. 1983; Suzuki 1989; Vacquier and Moy 1997; Thomas et al. 1999; Vilela-Silva et al. 2002). Recent work has also shown that jelly coats enhance rates of sperm-egg collision (Farley and Levitan 2001) and fertilization (Podolsky 2001) and that changes in target size and density can account for most of the change in fertilization rate when jelly coats are removed (Podolsky 2002). These results provide evidence for the importance of coat size in a sperm-egg encounter, a function that may also apply to follicle cells of ascidian eggs (Havenhand 1995) and hulls of chiton eggs (Buckland-Nicks 1993). By weakening the association between physical size and energetic size, external coats may play an important role in life-history evolution by altering size-specific trade-offs that govern resource allocation to individual offspring. The goal of this study is to evaluate the extent to which this common form of extraembryonic investment influences the evolution of egg size under different pre- and postzygotic risks to reproduction.

I use an optimization model to integrate consequences for fertilization and development that have been suggested to result from investment in accessory coats. To ground the analysis, I start with character values for gametes of the sand dollar *Dendraster excentricus*, and I explore parameter ranges drawn from published literature. By sequentially introducing effects to the model, I ask how optimal egg traits would shift under particular conditions and assumptions. *Dendraster excentricus* is near the midrange of egg sizes reported for planktotrophic echinoids (Emlet et al. 1987), and the jelly coat increases target size 5.9-fold, close to the average reported for jelly coats (see appendix). The goal of this optimization approach, combined with several conservative assumptions about the role of jelly, is not to discount phylogenetic (Lessios 1990) or

genetic (Charlesworth 1990) constraints on egg size evolution but rather to estimate the maximum scope for changes in ovum size that could result from particular selection pressures. I use the resulting egg size ranges to address statements in the literature concerning evolutionary responses of ova and jelly coats to environmental variation. Specifically, I address the following questions: How do optimal size, fecundity, fertilization percentage, and selection strength depend on the presence or absence of a jelly coat? What magnitude and pattern of change in relative investment are predicted under different assumptions about fertilization efficiency, polyspermy, and egg suspension? What are the relative strengths of pre- and postzygotic selection? How do predicted ranges of optimal egg size compare with those among broadcast-spawning species? How does violation of the assumption of constant sperm conditions affect evolutionary predictions of optimal size? How do accessory structures bear on arguments about the evolution of anisogamy?

Model

The model uses iteration to find the combination of ovum volume (V_o) and jelly volume (V_j) that maximizes propagule number—zygotes (N_z) or metamorphs (N_m)—per unit energy invested. Calculating N_z or N_m requires estimating three relationships that depend on V_o and V_j: fecundity effects (the number of eggs produced; N_e), prezygotic effects (the proportion of eggs that fertilize successfully into zygotes), and postzygotic effects (the proportion of zygotes that reach metamorphosis) of relative investment. Each section describes the general model and modifications to consider how different assumptions about the function of jelly would alter selection on relative investment. The model was created in MS Visual Basic using the Solver algorithm, with starting conditions varied to check for multiple peaks. Throughout this article, I use the term "egg" to refer to the reproductive cell with or without a jelly coat and "ovum" to refer to the reproductive cell only.

Conclusions from the model are based on metamorph number but not size. In species with planktotrophic (feeding) larvae, initial investment is correlated with time to but not size at metamorphosis (Emlet et al. 1987; Levitan 2000*a*). Egg size plays a fundamentally different role in nonfeeding (lecithotrophic) development, affecting energy content at metamorphosis and juvenile risks (Emlet and Hoegh-Guldberg 1997; Villinski et al. 2002). Confining the analysis to planktotrophs, a group with a developmental end point (metamorph size) that is independent of the starting point (ovum size), allowed me to relate more clearly the relative investment to risks during the delimited period of larval development.

The model also assumes that the optimal egg size–number trade-off is independent of the total reproductive allocation. Functional analyses suggest that this assumption can be violated for eggs held in clutches (Winkler and Wallin 1987; Strathmann 1995; Caley et al. 2001). In broadcast spawners, variation in egg size between or within populations (e.g., George 1996; Honkoop and Van Der Meer 1998; Marshall et al. 2000) could also be evidence of an adaptive allocation strategy or could result from environmentally induced maternal effects, but mechanisms have not been identified to link optimal egg size to reproductive effort.

In addition to asymmetries in organic cost, specific gravity, and effects on larval survival, jelly and ovum have a structural asymmetry that affects the model predictions; jelly forms a shell around the ovum, so the effect on target size of a unit change in jelly volume depends on ovum volume but not vice versa. To aid visualization, I report results in terms of the contributions of ovum and jelly to total egg radius (ovum radius and jelly coat thickness).

Standard parameter values used throughout the article (table 1) are actual measurements, or values calculated from measurements, for eggs and sperm of *Dendraster excentricus* (Podolsky 2002). The standard values (denoted

Table 1: Standard parameter values used as starting conditions in the model

Parameter	Symbol	Value
Ovum radius (μm)[a]	R_o'	64.4
Jelly coat thickness (μm)[a]	T_j'	91.6
Ovum volume (μL)[a]	V_o'	.00112
Jelly volume (μL)[a]	V_j'	.0148
Ovum organic density (μg μL^{-1})[a]	δ_o'	193.96
Jelly organic density (μg μL^{-1})[a]	δ_j'	2.91
Ovum dry organic weight (DOW; μg)[a]	M_o'	.217
Total dry organic weight (μg)[a]	M_t'	.26
Egg target area (mm^2)[a]	A_e'	.0764
Sperm swimming speed (mm s^{-1})[a]	u_s'	.195
Egg sinking speed (mm s^{-1})[a]	u_e'	.104
Fertilization efficiency[b]	F_e'	.0382
Initial sperm concentration (μL^{-1})[b]	S_0'	.8364
Instantaneous larval mortality (d^{-1})[b]	M'	.1281
Initial egg concentration (μL^{-1})[c]	E_0'	.05
Sperm-egg contact time (s)[c]	t'	600

Note: Values are from Podolsky (2002) except for S_0' and M', which are derived in this article.

[a] Averages of direct measurements for eggs of *Dendraster excentricus*.

[b] Fitted estimates that explain maximum variance in empirical fertilization rates (F_e') or that make other standard values optimal as measured by metamorph production (S_0', M').

[c] Typical values that were assumed for the estimation of other standard values.

by a prime) give starting conditions from which changes in V_o and V_j are predicted. To track changes from an adaptive peak, the model is first used to solve for values of two ecological parameters—initial sperm concentration and larval mortality rate—at which standard eggs maximize metamorph production and are therefore optimal. Exploring the parameter space is equivalent to asking how this peak on an adaptive landscape shifts in response to changes in parameter values. This approach assumes that average values for the study population have been optimized by selection on model parameters or that constraints or unknown parameters that maintain current values away from an optimum continue to operate under conditions imposed in the model.

Fecundity

General Model. Egg number (N_e) is the total reproductive allocation divided by the energy content per egg. Energy contents of the ovum and jelly coat (M_o, M_j) are the products of volume (V_o, V_j) and organic density (δ_o, δ_j) measured as dry organic weights (DOW):

$$N_e = \frac{M_t'}{\left(M_o + M_j\right)}, \tag{1}$$

where $M_o = V_o\delta_o$ and $M_j = V_j\delta_j$. Total reproductive allocation (M_t') was fixed arbitrarily as the organic content of a single standard egg ($M_o' + M_j'$) so that N_e, N_z, and N_m always scale as a proportion of the number of standard eggs. The enormous ratio of ovum to jelly organic densities in *D. excentricus* (67 : 1) is nearly identical to the same ratio in *Arbacia punctulata* (71 : 1), calculated using wet oxidation instead of DOW (Bolton et al. 2000). Using either measure to estimate total organic cost assumes that synthesis costs are small relative to material costs and ignores the different energetic values of lipids, carbohydrates, and proteins (Crisp 1984). These simplifications produce a conservative estimate of the cost of investment in ovum relative to jelly (Podolsky 2002) and therefore liberal predictions of changes in ovum size relative to jelly coat size.

Organic Density. The general model assumes that ovum organic density scales isometrically with volume. Allometric change in organic density could alter the relationship between physical and energetic size as well as the strength of selection on relative investment in ova and jelly (Podolsky and Strathmann 1996). As one variation of the model, I allow organic density to change as a function of ovum size by substituting the following equation for M_o in equation (1):

$$M_o = M_o'\left(\frac{V_o}{V_o'}\right)^c. \tag{2}$$

This equation is scaled relative to standard values for DOW and volume so that curves for all c pass through the actual organic density for eggs of *D. excentricus*. Values of c in the range $0 < c < 1$ represent decreasing organic density with increasing ovum size. I use this equation to find the critical value c where increased investment results in fertilization benefits that balance the fecundity costs of producing larger eggs.

Prezygotic Effects

General Model. I use the equation of Vogel et al. (1982) to model fertilization as a function of sperm concentration. Although other nonlinear equations can be fit to fertilization data, this equation is convenient because it is based on a physical model of sperm-egg collision with measurable parameters; it provides a good fit to data (Vogel et al. 1982; Levitan et al. 1991; Levitan 1993) and has been used previously to model gamete evolution, providing a basis for comparison (Levitan 1993, 2000*b*, 2002; Podolsky and Strathmann 1996; Styan 1998; Styan and Butler 2000; Farley 2002; Podolsky 2002); and it has already been modified to incorporate two processes—egg suspension (Podolsky 2002) and polyspermy (Styan 1998)—that can be influenced by external coats.

The model by Vogel et al. (1982) predicts the proportion of eggs ultimately fertilized (φ_∞),

$$\varphi_\infty = 1 - e^{-x}, \tag{3}$$

where

$$x = F_e\frac{S_0}{E_0}(1 - e^{-\beta_0 E_0 t}),$$

given the following starting conditions: initial sperm concentration (S_0, μL^{-1}); initial egg concentration (E_0, μL^{-1}); the shorter of sperm-egg contact time or sperm half-life (t, s); the collision constant (β_0, $mm^3\ s^{-1}$), estimated as average speed of a sperm swimming along its helical path (u_s, $mm\ s^{-1}$) times the average projected area of the egg ($A_e = \pi r^2$, mm^2); and egg fertilizability (β/β_0, $= F_e$ in Styan 1998), estimated by adjusting β to fit the model to data. The dimensionless ratio F_e, the proportion of sperm contacts resulting in fertilization, is a size-independent measure of fertilization efficiency. The sperm-egg contact time assumed in the model ($t' = 600$ s) is shorter than the half-life for sperm of *D. excentricus* (Podolsky 2002) but is a realistic field interval for sperm-egg interaction

(Levitan 1996*b*) and is the contact time at which F_e' was estimated (Podolsky 2002). Longer contact times in the model behave like higher sperm concentrations; sperm become increasingly saturating and target size increasingly irrelevant to fertilization rate. Use of an intermediate contact time provided conditions where sperm would be limiting and favored more liberal estimates of evolutionary change in ovum size. Because the analysis starts by solving for the sperm concentration at which standard eggs are optimal, use of shorter contact times would shift the estimate of the standard sperm concentration (see "Results").

Fertilization Efficiency. The general model assumes that jelly and ovum material are equally effective in converting sperm collisions into fertilizations. In support, Farley and Levitan (2001) found no significant difference between intact and jelly-stripped eggs in the probability of sperm collision or the probability of fertilization per collision (i.e., the parameter F_e). From a separate assay, however, they estimated that F_e for intact eggs was only 0.42 times that of stripped eggs. It should be noted that the latter assay may have been biased against eggs with jelly coats and thereby created or inflated relative differences in efficiency (see also Hagström 1956*b*; Podolsky 2002).

To examine the effect of jelly inefficiency on relative investment, I make the efficiency coefficient F_e a declining function of two parameters: jelly coat thickness (T_j) and the efficiency of an egg with a standard jelly coat relative to one with no jelly coat ($E_{j'}$):

$$F_e = F_e' e^{\ln(E_{j'})(T_j/T_j')}. \tag{4}$$

This equation gives a family of curves with intercepts at F_e' that pass through the point (T_j', $E_{j'}F_e'$). The exponential decline is consistent with a proportional loss of efficiency per unit jelly thickness. Using the model, I explore effects on optimal investment in jelly and ovum for declining values of $E_{j'}$ from 1 to 0.4 (Farley and Levitan 2001).

Egg Suspension. The general model calculates sperm-egg collision on the basis of sperm movement, but egg sinking can also contribute to relative gamete motion and alter contact time (Podolsky 2001, 2002). Investment in ovum and jelly determines egg size and specific gravity, both of which factor into sinking speed as calculated by Stokes's equation (Podolsky 2002). Podolsky (2002) modified Vogel et al.'s (1982) model to include effects of egg sinking on the collision parameter (β_0) and on time of suspension in a sperm cloud (t). The two modified parameters—here denoted by an asterisk and substituted into equation (3) for unmodified parameters—are

$$\beta_0^* = \pi R_{oj}^2 \left(\frac{u_{sl}^2 + 3u_{fa}^2}{3u_{fa}} \right),$$

$$t^* = t' \frac{u_e'}{u_e}, \tag{5}$$

where R_{oj} = egg radius; u_{sl} and u_{fa} refer to the speeds of the slower and faster gamete type, respectively; u_e is egg-sinking speed; and u_e' is the sinking speed of a standard egg (table 1). Although egg buoyancy may be important whenever eggs are suspended, the use of such equations is most appropriate for stationary or laminar flow conditions where suspended eggs would sink relative to a sperm cloud or plume.

Polyspermy. Polyspermy, or multiple fertilization, disrupts zygote development. (Although technically postzygotic, polyspermy is described here because the processes are related more to fertilization than to larval risks.) The general model was modified by Styan (1998) to include polyspermy risk given the increased rate of sperm collision with larger eggs. Styan's (1998) model predicts the proportion of eggs fertilized by only one sperm (φ_{mono}) by discounting multiple fertilizations on the basis of the probability of a second fertilizing sperm contacting the egg within the time period (t_b) before a polyspermy block is erected:

$$\varphi_{mono} = 1 - e^{-x} - (1 - e^{-x} - xe^{-x})(1 - e^{-b}), \tag{6}$$

where

$$b = F_e \frac{S_0}{E_0}(1 - e^{-\beta_0 E_0 t_b})$$

and x is defined in equation (3).

Although it takes account of target size, this model does not distinguish effects of investment in ovum versus jelly as means of increasing target size. Polyspermy can increase after removal of accessory coats (Hagström 1956*a*; Lambert and Lambert 1981; Farley and Levitan 2001), indicating that target size and polyspermy risk can be decoupled and that accessory structures play a direct role in reducing polyspermy. Polyspermy risk is typically low for intact echinoid eggs, even at exceptionally high sperm concentrations (Schuel and Schuel 1981; Nuccitelli and Grey 1984; Dale 1985; but see Franke et al. 2002). Although the mechanism of increased risk on coat removal can differ among species (Lambert and Lambert 1981; Schuel 1984; Jaffe and Gould 1985; Mozingo and Hedrick 1996), the process must involve an increase in either the interval t_b

or the number of fertilizing sperm reaching the ovum within the interval t_b.

Here I further modify the model to include the potential contribution of polyspermy to selection on relative investment in jelly and ovum. To control the interval t_b, I make t_b a function of jelly coat thickness (T_j) in a form similar to equation (4), with two parameters: the time for a polyspermy block in the absence of jelly, assumed to be a maximum (t_b^{max}, s), and the proportion that t_b^{max} is reduced by the jelly coat thickness of a standard egg ($B_{j'}$):

$$t_b = t_b^{max} e^{\ln(B_{j'})(T_j/T_j')}. \quad (7)$$

This equation describes a proportional reduction in t_b as a function of jelly coat thickness; the actual form of this relationship is unknown. Farley and Levitan (2001) provide the only joint estimates of t_b^{max} (0.709 s) and $B_{j'}$ (0.69) for eggs of the sea urchin *Lytechinus variegatus*. To evaluate effects of a change in sperm number, I simply use fertilization efficiency (eq. [4]) to control changes in the number of fertilizing sperm contacted within the interval t_b.

Postzygotic Effects

General Model. I use a standard rate equation ($N_m = N_z e^{-MT_m}$; Vance 1973; Rumrill 1990) to estimate metamorph number (N_m), assuming a constant per diem mortality rate (M, d^{-1}) and a developmental period that depends on ovum size (T_m, d). Investment in jelly is presumably lost from development (but see Marsh and Manahan 2000), so T_m depends on ovum volume only. For the function T_m, I use Levitan's (2000*a*) temperature-corrected regression estimate for extant echinoids with planktotrophic larvae, which defines an inverse proportional relationship between ovum size and development time: $T_m = (0.0135 \ln V_o + 0.1376)^{-1}$. Although interspecific data show scatter around this regression ($R^2 = 0.51$), my goal is to predict within-species shifts in investment under selection on development time, and I use this regression as the best available approximation to the underlying functional relationship.

After solving for M' using standard parameter values, I varied M over the range $M' \pm 1$ SD on the basis of published estimates of planktonic larval mortality. Using data from Rumrill (1990), I calculated a mean and standard deviation for M among 24 species ($M = 0.124 \pm 0.088$ d^{-1}) and applied the same coefficient of variation to M'. I excluded estimates for seven species based on unknown or short sampling intervals (<10 d), and for a given species, I used the estimate based on the longest sampling interval because short intervals are biased toward higher estimates of M (Rumrill 1990). This procedure eliminated higher values and gave a more conservative estimate of mean and variance for M.

Size and Protection. The general model assumes that per diem mortality M is independent of investment in jelly or ova. I acknowledge but exclude four potential violations of this assumption because there is no basis to relate the effect to coat size or because the scale of the effect is beyond the scope of this model. First, jelly could deter predation (Chia and Atwood 1982), as seen with eggs of *D. excentricus* and predation by conspecific adults (Timko 1979), though not by crab larvae (Rumrill et al. 1985). Second, jelly could protect eggs or embryos from shear during spawning or water turbulence (Thomas and Bolton 1999; Thomas et al. 1999). Third, jelly could slow deposition into benthic habitats, where predation risk for solitary offspring may be greater (Highsmith 1982; Strathmann et al. 2002). Fourth, predation could be size specific (but see Rumrill et al. 1985). Most of these effects would favor additional investment in jelly beyond the model predictions.

Sperm Concentration

General Model. After solving for the unique sperm concentration (S_0', μL^{-1}) and larval mortality rate (M', d^{-1}) that make standard volumes optimal, I ran the model at a series of initial sperm concentrations (S_0) to examine shifts in optimal volumes of jelly and ovum away from the standard volumes. The initial concentrations were varied over at least three orders of magnitude ($\log S_0 = -1$ to 2 μL^{-1}) around S_0' until optimized volumes reached low and high plateaus.

Sperm Heterogeneity. Fertilization models typically use fixed sperm concentrations to predict optimal egg sizes (Vogel et al. 1982; Levitan 1996*b*, 2000*a*; Podolsky and Strathmann 1996; Styan 1998; Podolsky 2002). Such optima would be relevant to egg size evolution if individuals experienced little variation in spawning conditions. In reality, eggs spawned by a given female can encounter different sperm concentrations within or between spawning events (Babcock et al. 1992; Oliver and Babcock 1992; Meidel and Scheibling 2001). Because fertilization kinetics are nonlinear (Vogel et al. 1982), the optimal egg across variant conditions may not be predictable from the average condition. Models have been used to estimate fertilization success by integrating the effects of gamete concentrations in space and time (Denny and Shibata 1989; Babcock et al. 1994; Benzie et al. 1994; Claereboudt 1999) but have not accounted for the effects on egg size evolution of heterogeneity over multiple spawning events.

To examine the effect of heterogeneity, I modeled op-

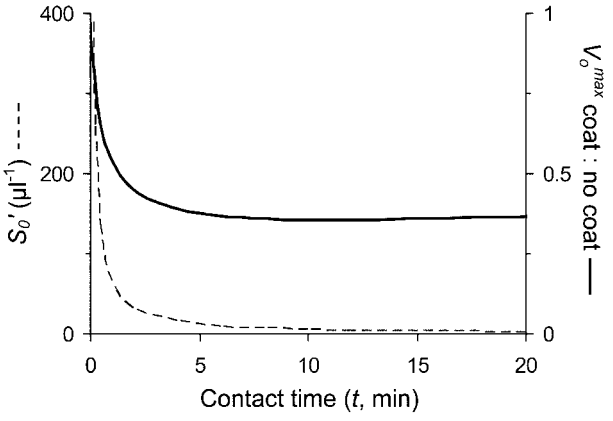

Figure 1: Relationships between assumed sperm-egg contact time (t', s^{-1}) and both the initial sperm concentration (S_0', μL^{-1}) at which standard eggs are optimal (*dashed line*) and the ratio of maximal ovum volumes (V_o^{max}) predicted by the general model relative to a model that excluded investment in jelly coats (*solid line*). Estimates for both measures become highly sensitive to contact time at $t < 2$ min.

timal egg volumes as a function of the mean (ranging from $\log S_0 = -1$ to 2 μL^{-1}) and variance (ranging from 0 to 2 μL^{-2}) of initial sperm concentrations. For each mean-variance combination, the model calculates total metamorph production for a given ovum-jelly volume combination integrated over a lognormal distribution of sperm concentrations. This process was iterated while successively narrowing the range of volumes examined to a final precision of four significant figures. (The algorithm used a discrete approximation by sampling at 21 sperm concentrations evenly spaced from −3 to +3 SD around the mean, weighted and normalized by the probabilities of each sperm concentration according to a Gaussian distribution.) In effect, I ask what single combination of ovum and jelly volume maximizes metamorph production for a female whose eggs encounter different initial sperm concentrations at different spawning events.

Results

Zygote production. For *Dendraster excentricus*, the critical scaling exponent where fertilization benefits balance fecundity costs—and zygote production becomes a positive function of ovum size—drops from $c = 0.65$ when jelly coats are excluded (Podolsky and Strathmann 1996) to around $c = 0.05$ when predicted by the general model. Of the three prezygotic modifications to the model, only fertilization efficiency is expected to favor greater investment in ova. Even when jelly makes fertilization highly inefficient ($E_{j'} = 0.4$), the critical value of c is only around 0.35. These critical values of c, calculated at a limiting sperm concentration ($S_0 = 0.1$ μL^{-1}), are unaffected by lower concentrations and decline further at higher concentrations (see Podolsky and Strathmann 1996).

Solving for standard environmental parameters. The standard ovum and jelly volumes maximize metamorph production (N_m) relative to all other combinations of V_o and V_j when initial sperm concentration (S_o') is 6.861 μL^{-1} and mortality rate (M') is 0.1281 d^{-1}. This estimate for M' is close to the average ($M = 0.124$) that I calculated for values by Rumrill (1990). Mortality rate does not depend on sperm-egg contact time (t). Estimates of S_o' increase slightly with decreasing t to about 2 min but then increase steeply (fig. 1).

General model. Ovum and jelly volumes that maximize

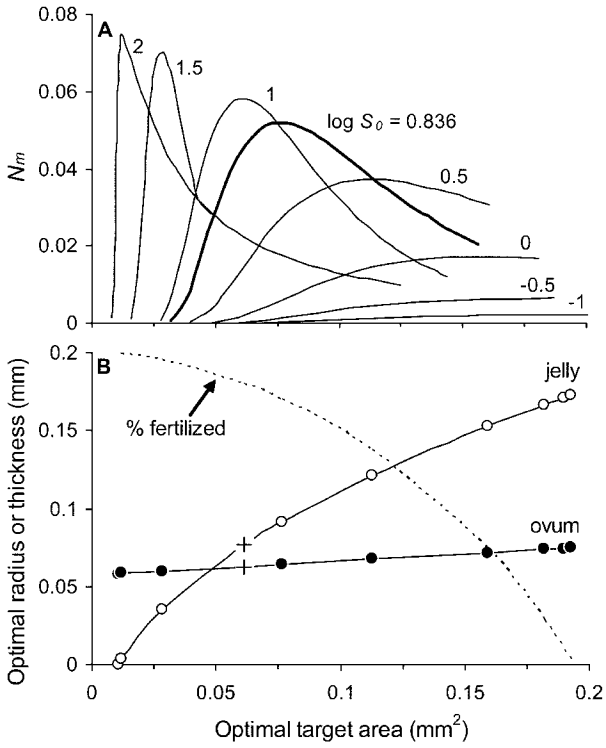

Figure 2: Changes in optimal egg size predicted by the general model. *A*, Metamorph production (N_m) as a function of egg target area (A_{oj}) and initial sperm concentration ($\log S_0$). The N_m along each curve was calculated by solving for the optimal proportion of ovum and jelly at each target size. Peaks occur at the optimal A_{oj} for each sperm concentration. The N_m for standard eggs is shown in the thick curve. *B*, Changes in optimum ovum radius and jelly coat thickness as a function of optimal egg target size. Points on the line correspond to peaks directly above them in *A* (except for the first and last points at $\log S_0 = 2.5$ and -1.5 μL^{-1}, which were omitted from *A* for clarity). Note that optimal sizes plateau and do not change beyond the sperm concentrations shown. Crosses mark the standard ovum and jelly sizes. The dashed curve shows how the fertilization rate of optimal eggs goes from 100% to 0% as sperm concentration declines.

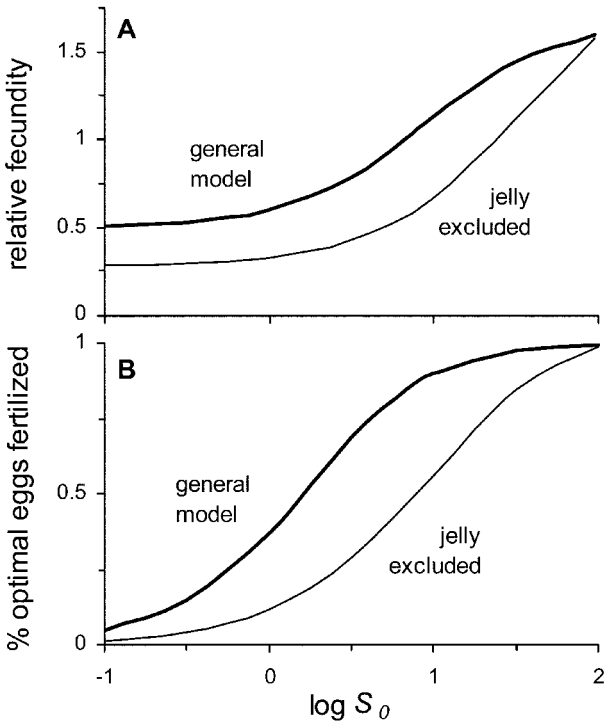

Figure 3: Changes in fecundity (*A*) and fertilization success (*B*) for optimal eggs as predicted by the general model (*thick curve*) and a model that excludes investment in jelly (*thin curve*). Fecundity is scaled as the number of eggs produced relative to the number of standard eggs that would be produced from the same total investment.

N_m involve trade-offs among costs of ovum and jelly, fertilization benefits of increased target size, and survival benefits of increased ovum size. As sperm concentration declines, the model predicts increases in optimal target size (fig. 2*A*), as shown previously (Levitan 2000*a*; Farley and Levitan 2001). Optimal ovum and jelly coat sizes, however, are influenced to different degrees (fig. 2*B*). Over three orders of magnitude change in sperm concentration, jelly coat thickness increases from 0 to 173 μm, while ovum radius increases from 58 to only 75 μm (16% above and 10% below the standard ovum). Jelly thickness is a decelerating function of ovum radius because the shell of jelly thins as ovum size increases.

Presence versus absence of jelly. The number of optimal eggs produced per unit investment was greater at all nonsaturating sperm concentrations—increasing up to 80%—in the general model as compared with a model where investment in jelly was excluded (i.e., V_j held at 0; fig. 3*A*). Fertilization success was also higher in the general model, with up to an additional 40% of optimal eggs fertilized when jelly coats were included (fig. 3*B*).

The maximum optimal ovum size, predicted to occur at low sperm concentrations, was only 35% as large in the general model as compared with the model that excluded jelly coats for most values of sperm-egg contact time, t (fig. 1). However, as was the case when estimating S_0', the difference between models became highly sensitive to t below about 2 min. As t goes to 0, the maximum volume predicted by the two models converges (fig. 1), indicating that jelly coats are unimportant to the evolution of large egg size only under an assumption of brief sperm-egg contact (see "Discussion").

Egg suspension. When egg sinking is allowed to vary as a function of size and density, the model favors greater relative investment in jelly at all sperm concentrations because the lower specific gravity of jelly improves suspension time. Optimal eggs have suspension times that are longer at low sperm concentrations and shorter at high concentrations than when contact time is fixed at 600 s (fig. 4*A*). Because relaxing the constraint on contact time generally benefits fertilization, absolute investment in both jelly and ovum declines relative to the general model (fig. 4*B*). The most important consequence of including these assumptions about egg sinking is that the range of optimal ovum sizes is reduced to only 2 μm across all sperm concentrations.

Fertilization efficiency. As expected, optimal investment

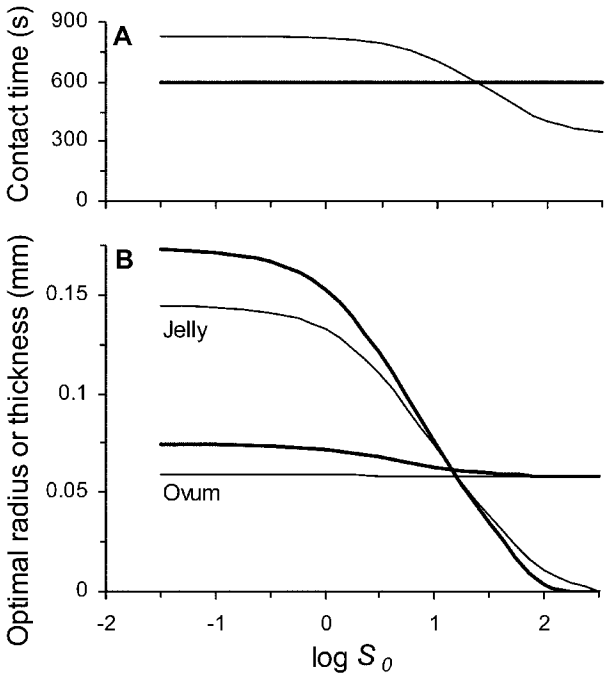

Figure 4: Effects of including egg sinking on suspension time (*A*) and ovum and jelly contributions to size (*B*) of optimal eggs. Results of the general model (contact time fixed at 10 min) are shown by bold curves, and results of the modified model are shown by thin curves.

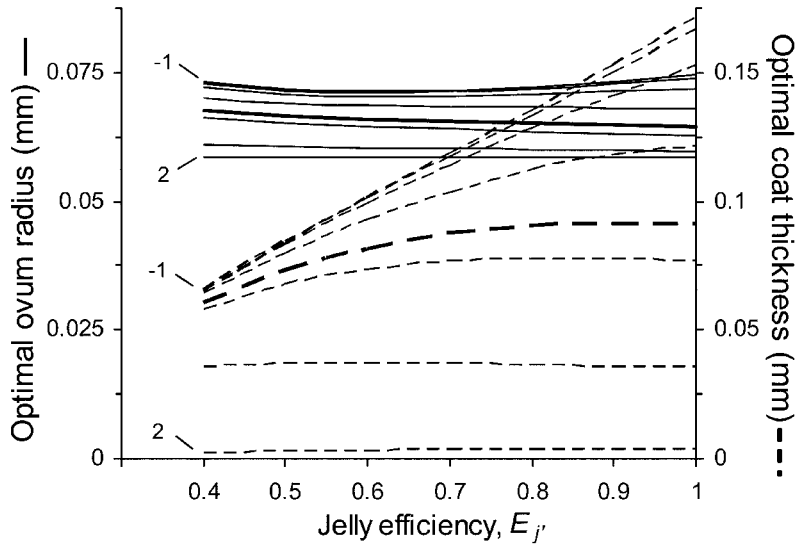

Figure 5: Changes in optimal egg radius (*solid curves*) and coat thickness (*dashed curves*) when fertilization efficiency depends on coat thickness. Thin curves are for sperm concentrations ($\log S_0$) in half–order of magnitude steps, with starting and ending concentrations indicated. For standard eggs (*thick curves*), ovum size increases and jelly coat thickness decreases as fertilization efficiency of jelly declines. Note that the jelly scale is double the ovum scale.

shifts from jelly toward ova as jelly becomes increasingly inefficient to fertilization (fig. 5). For standard eggs at the standard sperm concentration, however, ovum radius increases by only 5% as the jelly efficiency factor ($E_{j'}$) decreases from 1 to 0.4 (fig. 5, *thick solid curve*), whereas jelly coats increase by 50% with increasing values of $E_{j'}$ (fig. 5, *thick dashed curve*). At all sperm concentrations, jelly coat thickness declines monotonically with decreases in $E_{j'}$ (fig. 5, *dashed curves*). At the lowest sperm concentrations, changes in $E_{j'}$ favor the most rapid declines in jelly but also small initial declines in ovum size (fig. 5). Although slight, this decline is sufficient to maintain ovum size in a relatively narrow range as a function of sperm concentration for all values of $E_{j'}$.

Polyspermy. Including polyspermy risk drives down optimal ovum size at elevated sperm concentrations (fig. 6*A*), as noted previously (Styan 1998; Farley and Levitan 2001). The assumption that jelly reduces the time to a polyspermy block (t_b), however, has no effect on relative investment because polyspermy influences ovum size only beyond the sperm concentration where jelly is already eliminated (fig. 6*A*). This result holds even if t_b^{max} is increased to 30 s or more (not shown) or if jelly is instead assumed to reduce the number of fertilizing sperm contacting the ovum within the interval t_b ($E_{j'} = 0.4$; not shown).

Thus, at elevated sperm concentrations, the costs of large egg size (increases in collision rate and investment) outweigh a potential benefit of jelly in reducing polyspermy, at least when $B_{j'}$ (the standard reduction in t_b) is assumed to be 0.69. If, however, jelly is extremely effective in reducing the time to a polyspermy block (e.g., $B_{j'} = 0.02$), the model predicts that thick jelly coats can be optimal not only at low sperm concentrations, where they increase sperm-egg contact, but also at high concentrations, where they diminish polyspermy risk (fig. 6*B*).

Larval mortality. Changes in larval mortality strongly affect predictions of optimal ovum and jelly coat sizes. Under sperm limitation ($\log S_0 = -1$), optimal ovum radius varies from 45 to 100 μm given $M \pm 1$ SD. The range of ovum sizes resulting from variation in larval mortality is on average about three times greater than the range resulting from variation in sperm concentration (fig. 7). Coat thickness is an increasing function of M at most sperm concentrations but becomes a decreasing function of M at the highest sperm concentration.

Sperm variance. Heterogeneity in sperm concentrations among spawning events further restricts the range of optimal ovum sizes predicted by the model. Optimal ovum sizes contract to 55% of their original range when sperm concentrations around each mean are distributed with a variance of 1 log unit and to 35% when distributed with a variance of 2 log units (fig. 8). Because the greatest contraction occurs at the lowest sperm concentrations, sperm heterogeneity most strongly limits selection for large ova. Jelly coat thickness undergoes similar range contractions, to 55% and 40% of their original widths, respectively, although the magnitude of change is instead greatest at the highest sperm concentration (data not shown).

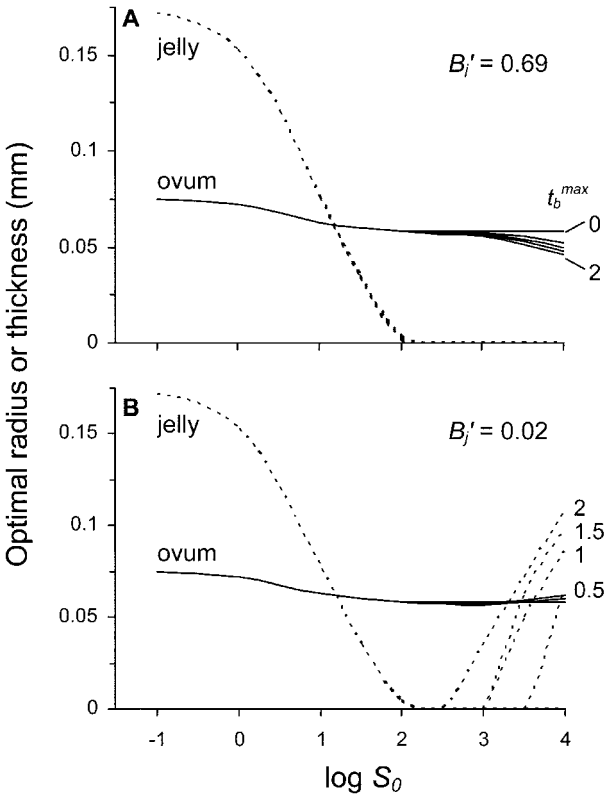

Figure 6: Changes in optimal egg size when polyspermy risk depends on jelly coat thickness. Time to a polyspermy block with no jelly coat (t_b^{max}), shown beside curves, changes in 0.5-s increments. *A*, When the reduction in time to a polyspermy block per unit thickness (B_j') is weak or moderate, optimal ovum sizes begin to diverge around 10^2 μL^{-1}, beyond where optimal jelly coat thickness goes to 0. *B*, If jelly is extremely effective at blocking polyspermy ($B_j' = 0.02$), thick jelly coats are also optimal at high sperm concentrations.

Because increasing variance can push sperm concentrations to elevated levels, I also ran the model including polyspermy risk. Dashed curves in figure 8 show changes for the two highest sperm concentrations ($\log S_0 = 1.5$ and 2 μL^{-1}; other curves were weakly affected), with $t_b^{max} = 2$ s. Adding polyspermy risk flattens the curves and thus reduces the influence of sperm variance at high sperm concentrations.

Discussion

Variation in Prezygotic Risks

Trade-offs among energetic costs, fertilization rate, and larval survival lead to shifts in investment in jelly and ova that depend on the functions assumed of jelly. One way to summarize these effects is by the ranges of optimal ovum size generated by different models (see fig. 9). In the general model (*a*), variation in sperm concentration predicts an absolute range of ovum diameters (~33 μm) that is small relative to predictions with jelly coats excluded (*dotted line*) and to a range of egg sizes among planktotrophic echinoids (*histogram*). Including sperm variance (*b*) further reduces the range of predicted sizes, while assuming that contact time is inversely related to egg-sinking speed (*c*) virtually eliminates it (~2 μm). Including fertilization efficiency (*d*), in contrast, has little effect on the optimal size range. If assumptions about egg suspension or sperm variance are ecologically relevant for a given species, then fertilization effects would account for a decreasing fraction of interspecific variation in ovum sizes.

Incorporating a nonzero time to a polyspermy block (*e*) can expand the predicted size range to lower values, but including sperm variance (*f*) as well limits the expansion of this range (fig. 9). More important, including sperm variance makes the bounds on this range insensitive to further increases in the time to a polyspermy block. Thus, the evolution of small eggs under selection to avoid polyspermy would require sperm concentrations that were not only elevated but also highly consistent. As a result, even when the average polyspermy risk is high, sperm heterogeneity can maintain a size range that is no larger than predicted by the general model (though shifted toward smaller sizes, which dominate the distribution for planktotrophic echinoids). Given natural variability in spawning conditions (Levitan and Petersen 1995; Yund 2000), adjusting the sensitivity of a specific response, such as the timing of an activated block (Jaffe and Gould 1985), may be a more likely outcome of selection against polyspermy than would be a general response such as the evolution of small ovum size.

A second way to compare models is by the conditions needed for major shifts in optimal egg size. For example, the inflection point in the sigmoid curve relating optimal ovum size to sperm concentration occurs at $\log S_0 = 0.66$ μL^{-1} in the general model, 0.97 μL^{-1} in the model that excludes jelly coats, and 1.14 μL^{-1} in the model that includes fertilization efficiency. Thus, somewhat more severe sperm limitation is required to favor a shift to larger ovum sizes when jelly coats are present, and fertilization inefficiency of jelly relaxes this requirement.

A third way to characterize models is by the strength of stabilizing selection on ovum size. When fitness surfaces are shallow (Levitan 1993), the consequences of deviating from an optimum will be small, and selection will weakly oppose other evolutionary forces. Using N_m as a fitness measure, one index of stabilizing selection is the range of ovum sizes that produces a given percentage or more of the maximum N_m; this range will be narrow when stabilizing selection is strong. A comparison among models provides at least three important results (see fig. 10). First,

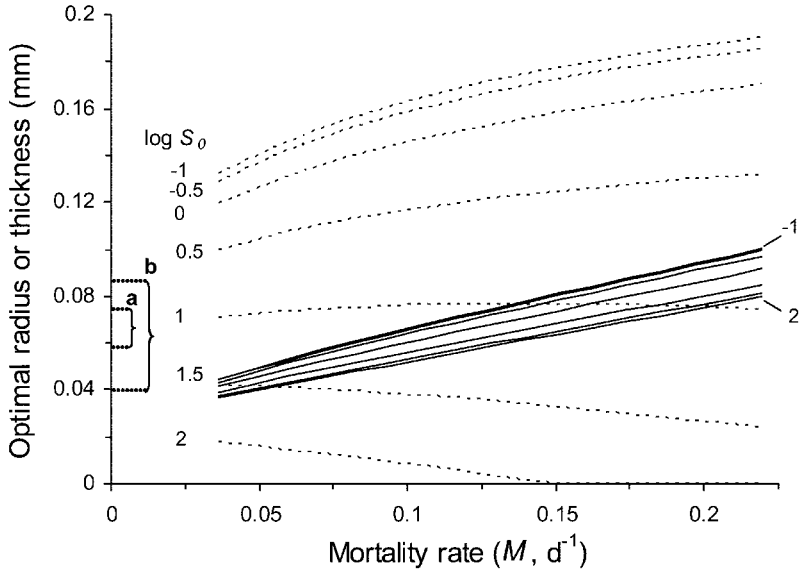

Figure 7: Effect of changes in larval mortality rate (M, d^{-1}) on optimal ovum radius (*solid lines*) and jelly coat thickness (*dashed lines*). Initial sperm concentrations ($\log S_0$) shown beside curves change in half–order of magnitude steps. The range of M used is $M' \pm 1$ SD, calculated from published values. The short bracket (*a*) shows the range of optimum ovum sizes when S_0 varies and $M = M'$, and the long bracket (*b*) shows the range when M varies and $S_0 = S_0'$.

stabilizing selection is weakest at low sperm concentrations, when large egg size is favored. Second, successively adding sperm variance (model *b*) and then polyspermy (model *f*) to the model increases the strength of stabilizing selection at low and high sperm concentrations, respectively. Third, stabilizing selection at low sperm concentrations is considerably weakened when jelly is excluded from the model (fig. 10, *inset*).

In light of these comparisons, it is worth reconsidering the suggestion that jelly coats do not weaken selection for large ovum sizes (Farley and Levitan 2001). This conclusion was based on a prediction that under increasing sperm limitation, ovum size would converge on the same maximum value with or without a jelly coat. Three results of the current study, however, weigh against this conclusion. First, convergence of maximum ovum sizes depended on assuming an extremely short (10 s) contact time (Farley and Levitan 2001) because optimal ovum sizes with and without a coat converge only as contact time approaches 0 (fig. 1; fig. 9, model *a*). Maximum ovum size under sperm limitation increases close to threefold when coats are excluded, indicating that jelly can significantly alter the outcome of selection for large ovum size. Second, even assuming a short contact time, the shift from small to large egg size occurred at a sperm concentration that was two orders of magnitude higher when jelly coats were excluded (Farley and Levitan 2001). The more extreme sperm limitation (stronger selection pressure) necessary to drive the shift to larger sizes is evidence that jelly significantly alters the conditions of selection for large ovum size. Third, the presence of a jelly coat increases stabilizing selection on ovum size, especially at low sperm concen-

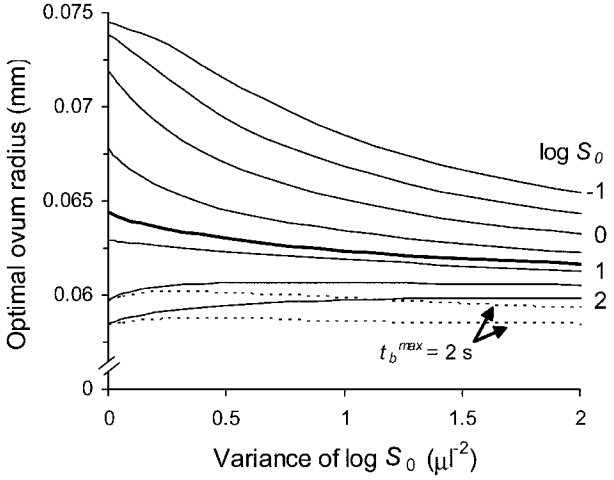

Figure 8: Changes in optimal ovum size as a function of variance in initial sperm concentrations. Mean initial sperm concentrations ($\log S_0$), shown beside curves, change in half–order of magnitude steps ($\log S_0' = 0.836$ is also shown by the bold curve). For solid curves, $t_b^{max} = 0$. Dashed curves show the result of including polyspermy risk ($t_b^{max} = 2$ s) at the two highest sperm concentrations.

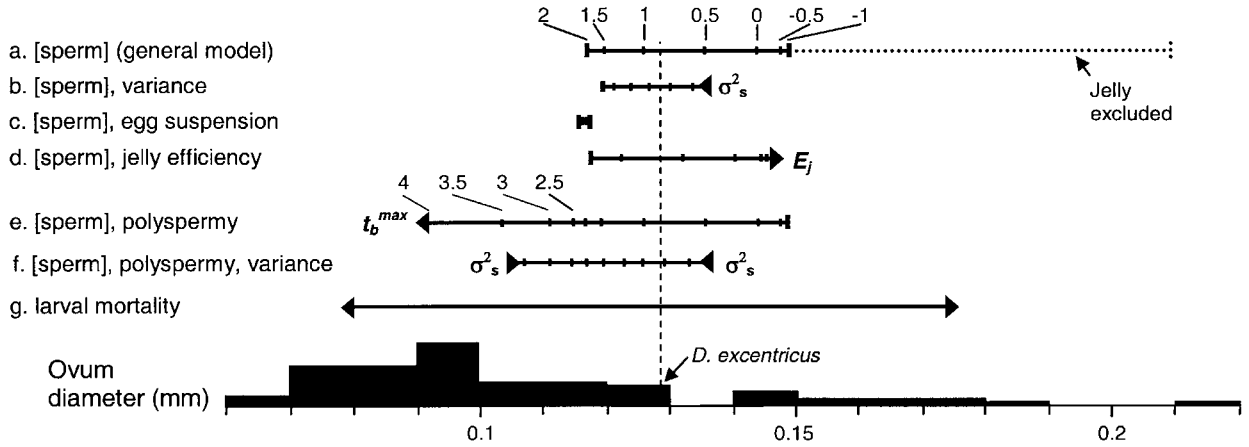

Figure 9: Summary of optimal ovum size ranges relative to standard eggs for different model assumptions. Parameters varied in the model are listed beside each range. Note that initial sperm concentrations ($\log S_0$), shown by tick marks, range from -1 to 2 μL^{-1}, except for models that include polyspermy (maximum = 4 μL^{-1}) and for the model *g*, where sperm concentration was held constant ($S_0 = S_0'$). Where parameters differed from the general model, values used were as follows: larval mortality, $M' \pm 1$ SD = 0.037–0.220 d^{-1}; jelly fertilization efficiency, $E_{j'} = 0.4$; polyspermy, $t_b^{max} = 2$ s; variance in sperm concentration, $\sigma_s^2 = 1$ μL^{-2}. Heavy bars are range boundaries that would not change appreciably given more extreme values for the parameter listed. Arrows indicate the direction of further change at range boundaries given even more extreme values for the parameter listed. The dotted range shows how optimal size is extended in the general model when investment in jelly is excluded. The histogram shows the frequency distribution of ovum sizes for a sample of 78 obligate planktotrophic echinoid species where both ovum size and mode of development were certain (from Emlet et al. 1987).

trations, indicating that jelly alters the strength of selection for large ovum size (fig. 10). In summary, results of the model show that jelly coats lead to a narrower range of optimal ovum sizes, require more stringent conditions to favor large sizes, and stabilize selection for the reduced size range.

In contrast with the effect of sperm conditions, variation in larval mortality more strongly affects variation in ovum size (fig. 9, model *g*). The span of the optimal size range was three times greater varying M alone as compared with varying S_0 alone. In contrast, optimal jelly coat thickness varied only slightly as a function of M at S_0' but strongly as a function of S_0 at M' (fig. 7). This contrast shows that jelly investment is principally influenced by spawning conditions, while ovum investment is influenced most strongly by larval mortality conditions. Furthermore, by reducing the cost of extended development, a low mortality rate extends the range of predicted sizes to more closely match a range typical of broadcast-spawning echinoids (fig. 9).

Prezygotic Selection and the Evolution of Anisogamy

The trade-off between fertilization and fecundity that governs zygote production is central to evaluating whether prezygotic factors could drive an increase in egg size (Levitan 1993; Podolsky and Strathmann 1996) and underlies the evolution of anisogamy (Levitan 1996*a*; Randerson and Hurst 2000). For target size advantages alone to favor increases in ovum size, sperm limitation would need to result in fertilization benefits that exceeded fecundity costs. Podolsky and Strathmann (1996) showed that if organic content scales isometrically with ovum volume, then increases in ovum size lead to reduced zygote production, regardless of sperm concentration. Below a critical scaling exponent ($c = 0.65$), however, zygote production for *Dendraster excentricus* became a positive function of ovum size, and large egg size could evolve in the absence of postzygotic benefits. The substantial drop in this exponent when jelly coats are included ($c = 0.05$) shows that jelly severely restricts patterns of investment where fertilization benefits could drive increases in ovum size. Even when jelly makes fertilization highly inefficient ($E_{j'} = 0.4$), scaling requirements remain restrictive ($c = 0.35$) compared with exponents reported for interspecific comparisons. In a summary of such data for echinoderms, Jaeckle (1995) reported an overall scaling exponent of $c = 0.853$ among planktotrophic species. This consequence of producing an external coat reinforces the conclusion that target size benefits are unlikely to explain the evolution of anisogamy (Randerson and Hurst 2000).

External coats can be viewed as an alternative way to enlarge an egg's target size while reducing its organic density. In *D. excentricus*, a standard jelly coat increases the target size of a standard egg 5.9-fold but reduces whole-

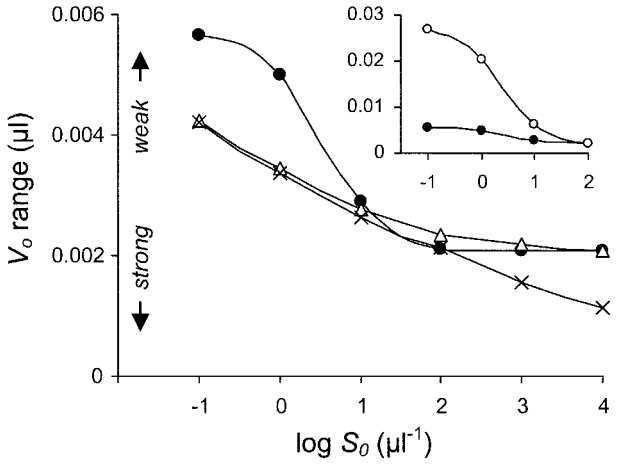

Figure 10: Strength of stabilizing selection, as measured by the range of ovum sizes that produce 75% or more of the maximum N_m at each sperm concentration. (Because fitness curves are propotionally similar, the choice of percentage is arbitrary.) A smaller V_o range indicates stronger stabilizing selection. Curves shown are for the general model (*filled circles*; model *a* in fig. 9), the model with sperm variance (*open triangles*; model *b* in fig. 9), and the model with sperm variance and polyspermy (*crosses*; model *e* in fig. 9). The inset shows values (note change in scale) for the general model (*filled circles*) and a model with jelly coats excluded (*open circles*; *dotted range* in fig. 9).

egg organic density to only 8.4% of the standard ovum. An equivalent gain in target size through ovum hydration would heavily dilute cell contents and potentially alter cell physiology (Craik and Harvey 1987; Thorsen et al. 1996). Separating the physical and energetic aspects of size, and discarding the physical component early in development, allows eggs to avoid such a compromise. These results suggest why increases in external coats may be favored over changes in internal composition or ovum enlargement if sperm limitation were responsible for driving the evolution of gamete dimorphism.

Dusenbery (2000) offered a different prezygotic hypothesis for the evolution of anisogamy on the basis of the assumption that energy-rich eggs would improve sperm-egg contact by allowing for the production of sperm attractants. Although widespread, sperm attraction has not been detected in *D. excentricus* or most echinoids (Miller 1985), and its absence in promoting sperm-egg contact was verified experimentally in the echinoid *Lytechinus variegatus* (Farley and Levitan 2001). The release of such attractants could add to or surpass the effect of an external coat in enhancing the effective target size (Jantzen et al. 2001). Accessory structures could also act in concert with attractants by providing a matrix for storage and release (Suzuki 1989; Jesu-Anter and Carroll 2001) or by slowing egg sinking and altering the distribution of attractants around eggs (Mitchell et al. 1985). If the cost of attractants and hydrodynamic influences on their function continue to be better estimated (Jantzen et al. 2001), future models should incorporate attractant production to assess its contribution to life-history trade-offs.

Extraembryonic Investment and Life-History Evolution

By decoupling physical and energetic size, egg coats play an important but neglected role in life-history evolution by altering optimal patterns of resource allocation. In *D. excentricus*, the jelly coat comprises 10%–16% of the organic cost of an egg, similar to values reported for *Arbacia punctulata* (7%; Bolton et al. 2000) and *Sterechinus neumayeri* (17%; Marsh and Manahan 2000). When fertilization is limited by a sperm-egg encounter, investment in jelly returns a profit by increasing the conversion of gametes into zygotes; under sperm saturation, the investment returns a loss by reducing the conversion of resources into gametes. As a result, external coats buffer the evolution of ovum size from ecological effects of spawning conditions (fig. 9) and can maintain energetically smaller ova by reducing one cost of small egg size (Hart 1995). The contribution of sperm attractants to target size would reinforce this conclusion (Jantzen et al. 2001). Similarly, if eggs pool after spawning or are released in viscous strings (Thomas 1994; Meidel and Yund 2001; Yund and Meidel 2003), individual ovum size should contribute little to sperm-egg collision and would be expected to evolve more strictly in response to postzygotic factors.

The expectation that costs of extraembryonic material are balanced by fitness benefits, in terms of offspring number or quality, has been demonstrated rarely in marine invertebrates (Pechenik 1979) and only in relation to postzygotic risks. For example, in benthic egg masses, the spacing of embryos by gel enhances development rate and embryo survival by allowing adequate oxygen diffusion (Strathmann and Strathmann 1989), but gel can account for 30%–60% of mass DOW, imposing an upper limit on egg mass size (Lee and Strathmann 1998). Similarly, Perron (1981) found a positive correlation between development time (=risk of benthic predation) and thickness of encapsulating structures (=degree of protection) in 10 *Conus* species, indicating that resource allocation had responded to embryonic risks. Costs of capsular material in *Conus* (Perron 1981) and *Thais lamellosa* (Stickle 1973) were also high, ranging from 20% to 50% of the total reproductive allocation. These patterns of investment parallel those in terrestrial plants, where a large portion of the reproductive allocation can be devoted to fruits and flowers (Bell 1985; Cruden and Lyon 1985; Charnov and Bull 1986) or, more analogously, to structures that aid

receipt of wind-borne pollen (Niklas and Paw U 1982; Whitehead 1983).

Results of the model make several ecological predictions concerning relative investment in ova and coats. For example, animals that routinely spawn in areas where gametes concentrate, such as tide pools, would be expected to allocate relatively less to coats than those spawning where sperm are diluted (Denny et al. 1992). Another potential benefit of jelly, in protecting ova from shear forces, could also be favored under conditions of turbulence and rapid sperm dilution (Thomas et al. 1999), although the resilience of jelly coats under such conditions has been questioned (Farley and Levitan 2001). Relative allocation could also be influenced by development temperatures. All else being equal, high temperatures should speed development and reduce larval mortality, leading to the production of smaller eggs (Levitan 2000*a*) and larger jelly coats (fig. 7). Latitudinal gradients in ovum size support this prediction in some spawning invertebrates (Hagström and Lönning 1967) but not in others (e.g., *Anthopleura elegantissima* and *Platynereis bicanuliculata* in Strathmann 1987), and the pattern for many fishes is opposite (Fleming and Gross 1990; Beacham and Murray 1993; Johnston and Leggett 2002). Latitudinal comparisons require caution because the evolutionary effects of temperature could be confounded with latitudinal changes in the densities of predators, prey, or spawning conspecifics (Thorson 1950; Highsmith 1985) as well as with proximate effects of temperature on cell size (Van Voorhies 1996; Woods 1999). Comparative data on the relative sizes of external coats are lacking for these ecological comparisons.

The model results highlight two other patterns important to gamete evolution. First, although investment in low-cost accessory structures leads to higher optimal rates of fertilization, the egg size that is optimal ensures complete fertilization only at the very highest sperm concentrations (fig. 3*B*). Earlier work provided both theoretical (Ball and Parker 1996) and empirical (Warner et al. 1995; Shapiro and Giraldeau 1996) support for male adaptive infertility, the hypothesis that males competing for fertilizations should often evolve spawning strategies that fail to achieve complete fertilization of eggs. Considering a different set of trade-offs, the model presented here provides a complementary argument that female gametes also should fail to evolve to sizes that ensure complete fertilization. Together, these results indicate how incomplete fertilization can result from an adaptive allocation of resources by both males and females, a prediction that is consistent with field data (Levitan and Petersen 1995; Yund 2000) showing that fertilization is highly variable and often incomplete (Mortensen 1938).

Second, the model predicts that evolutionary shifts in ova and coats will be positively correlated under most conditions—given changes in sperm concentration at all larval mortalities, in sperm variance, and in larval mortality at most sperm concentrations. One exception occurs when varying larval mortality at high sperm concentrations (fig. 7), but jelly contributes little to target size under these conditions. Empirically, a positive correlation between ovum and jelly volumes among species (see appendix) is consistent with this pattern (jelly coats: $r_s = 0.81$, $P < .001$, $N = 17$; polyplacophoran hulls: $r_s = 0.98$, $P < .0001$, $N = 8$; all species: $r_s = 0.8$, $P < .001$, $N = 32$). Similar patterns of positive covariation in jelly and ovum size have been noted both within and between females of *D. excentricus* (Levitan and Irvine 2001; Podolsky 2001). It is important to note that the analyses of interspecific data were not corrected for phylogeny, positive covariation could result from positive genetic or environmental correlations between ovum and jelly volumes, and more definitive tests of model predictions would involve analyses of residuals in relation to environmental differences among species.

Life-history consequences presented here may apply broadly to marine organisms in which broadcast spawning is widespread and external egg coverings are typical (Breder and Rosen 1966; Giese and Kanatani 1987). It is important to reemphasize that this analysis does not presume that egg coats evolved or have been maintained solely to enhance rates of sperm-egg encounter (Podolsky 2002). Rather, the analysis gauged the scope for ovum size evolution if sperm limitation and egg target size were major determinants of sperm-egg encounter under natural spawning conditions. The results reflect disproportionate change in external coat size and limited change in ovum size under a broad range of conditions and assumptions, even when jelly coats reduce fertilization efficiency. Likewise, although the primary goal of the model was not to explain variation in the size of accessory structures, the degree of target size enhancement by jelly (maximum 11-fold; general model) is close to measures for eggs of planktotrophic marine invertebrates (maximum 12.25-fold; see appendix). Thus, model predictions of jelly to ovum ratios encompass a range similar to those found in nature.

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