Evolution, 52(4), 1998, pp. 1043–1056

DOES BATEMAN'S PRINCIPLE APPLY TO BROADCAST-SPAWNING ORGANISMS? EGG TRAITS INFLUENCE IN SITU FERTILIZATION RATES AMONG CONGENERIC SEA URCHINS

DON LEVITAN
Department of Biological Science, Florida State University, Tallahassee, Florida 32306-1100
E-mail: levitan@bio.fsu.edu

Abstract.—Evolutionary biologists generally invoke male competition and female choice as mechanisms driving sexual selection. However, in broadcast-spawning organisms sperm may be limiting and females may compete, in the Darwinian sense, for increased mating success. In this study, I investigate how species differences in egg and sperm traits result in different patterns of fertilization among three closely related sea urchins (*Strongylocentrotus purpuratus, S. franciscanus*, and *S. droebachiensis*). Field studies demonstrate that all three species achieve similar percentages of eggs fertilized when eggs and sperm are released simultaneously. However, when sperm must disperse before encountering eggs, differences arise among species such that those with the smaller eggs and faster but shorter-lived sperm achieve relatively fewer fertilizations than do species with larger eggs and slower but longer-lived sperm. A field hybridization experiment, field estimates of sperm dispersal, correlations of egg size to field rates of fertilization, laboratory studies of fertilization kinetics, and a simulation model all suggest that it is attributes of the egg (probably egg size) that are responsible for the differences. These patterns of fertilization match the species' patterns of dispersion; species that do well only when sperm and eggs are released in close proximity are more aggregated, species that do relatively well when sperm and eggs are released farther apart are more dispersed. These results are consistent with the notion that eggs of different species are adapted to maximize reproductive success under different degrees of sperm limitation and suggest that male competition and female choice may not be an appropriate dichotomy in broadcast-spawning organisms.

Key words.—Bateman's principle, echinoid, egg size, fertilization success, sexual selection, sperm limitation.

Received May 27, 1997. Accepted March 24, 1998.

Bateman's principle (Bateman 1948) suggests that, because sperm are more numerous than eggs, male reproduction is limited by access to mates and female reproduction is limited by access to resources. A corollary of this principle is that selection for increased fertilization success will act on males but not on females.

Bateman's principle has had remarkable success in explaining patterns of sexual selection, dimorphism, and allocation in the many groups in which sperm are released within a female or directly onto eggs and in self-fertilizing hermaphrodites (see, e.g., Smith 1984; Yund and McCartney 1994; McCartney 1997; Birkhead and Møller 1998). In systems where sperm or pollen is released at a distance from females, however, Bateman's principle seems less appropriate as sperm become more limiting and competition becomes less likely (Burd 1994; Levitan and Petersen 1995; Levitan 1998). Broadcast-spawning invertebrates are commonly sperm limited (Levitan 1995), so selection for increased mating success may operate on females as well as males (Levitan 1993, 1996a,b, 1998).

Because of the legacy of Bateman's principle, arguments concerning selection on female traits for increased mating success have been largely ignored (Arnold 1994a; but see Levitan [1993] for animals and Burd [1994] for plants). For example, a critical female life-history trait is offspring provisioning, yet models of optimal offspring size have been based on the success of zygotes rather than of eggs (e.g., Vance 1973; Smith and Fretwell 1974; Roff 1992; but see Levitan 1993, 1996a,b). Given the ubiquity of sperm limitation in broadcast-spawning marine invertebrates, investigating the consequences of variation in egg traits on female fertilization success and exploring alternate hypotheses that invoke fertilization dynamics to explain variation in egg traits, such as size, seem warranted.

Marine invertebrates exhibit large variation in egg size among and within developmental modes (see, e.g., Thorson 1936, 1950; Hendler 1975; Rice 1975; Chia 1976; Hermans 1979; Reaka 1979; Sastry 1979; Emlet et al. 1987). Most theoretical attention has been given to the differences in egg size between species whose larvae feed and species whose larvae do not feed (e.g., Vance 1973; Christiansen and Fenchel 1979; Strathmann 1985; Roughgarden 1989; Havenhand 1995). Less effort has been expended on investigating variation in egg size within one of these two developmental modes (Perron and Kohn 1985; Emlet et al. 1987; Hadfield and Miller 1987; Sinervo and McEdward 1988; Clarke 1993; Levitan 1993, 1996a). Only recently has a theoretical framework been offered to explain this variation (Levitan 1996a, in review).

Vance's (1973) model uses two assumptions that result in the prediction that selection on egg size will produce one or another of two extreme optima. The first assumption is that all eggs are fertilized. The second is that there is a linear relation between egg size and development time, and planktonic mortality increases with increases in development time. Recent data on echinoids suggest that both of these assumptions are suspect. Not all eggs are fertilized, and larger eggs are preferentially fertilized under conditions of sperm limitation (Levitan 1993, 1995, 1996a). In addition, a curvilinear relationship between egg size and development time may be more appropriate, in which changes in egg size have much less influence on development time in larger eggs than in smaller ones (Levitan 1996a, in review). Models that incorporate these relationships predict a continuous distribution

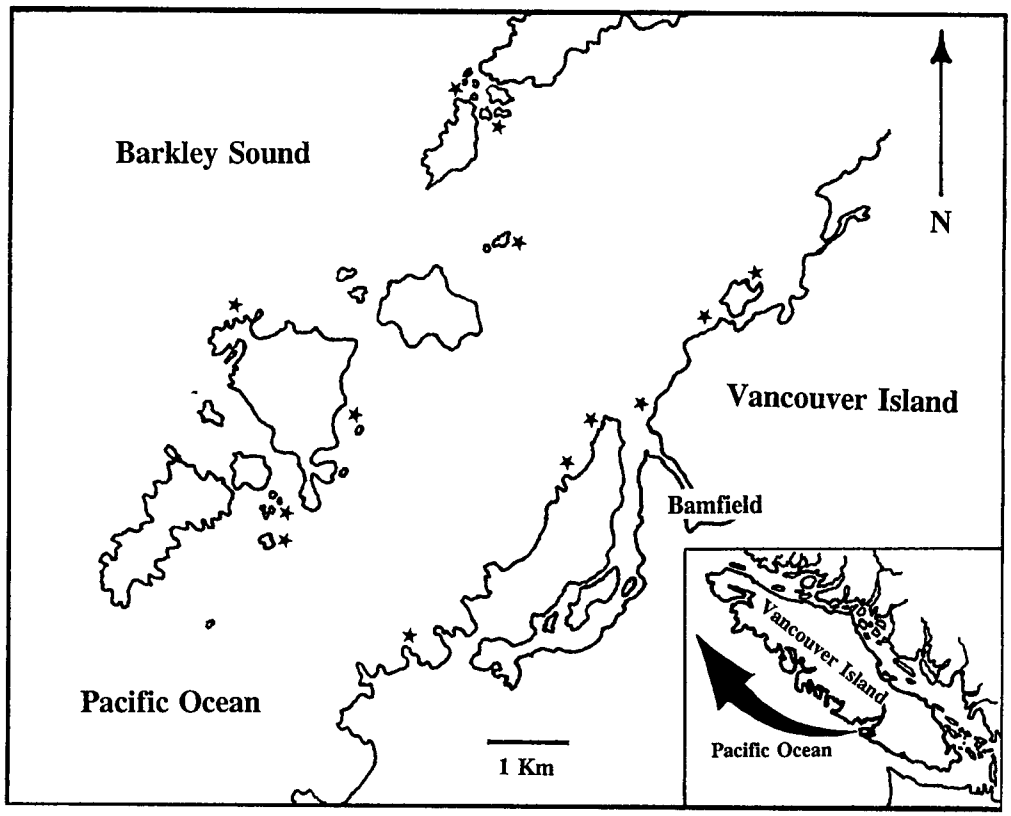

FIG. 1. Location of study sites. Vancouver Island, situated on the West Coast of Canada. Study sites are indicated by star symbols and located in the southeast corner of Barkley Sound. Sites closer to the mouth of the sound are more exposed to the swells of the open Pacific.

of potential optima instead of a dichotomous one; the optimum egg size is determined by a variety of species- and environment-specific characteristics (Levitan 1996a, in review).

The eggs of three congeneric sea urchins, *Strongylocentrotus droebachiensis, S. franciscanus*, and *S. purpuratus*, span a fivefold range in volume that is unrelated to adult body size (Levitan 1993). In spite of the large difference in parental investment per egg, all three species metamorphose at a diameter of about 0.2 mm (Emlet et al. 1987; Sinervo and McEdward 1988), so the selection for divergent egg sizes probably occurs sometime between egg production and settlement (Levitan 1996a). Because all three species have overlapping spawning times (Strathmann 1987), overlapping geographic distributions (McConnaughey and McConnaughey 1985), and similar larval design (McEdward 1986) and often develop in the same local water mass (Rumrill 1987), it is not obvious how postzygotic selection (e.g., planktonic mortality) could account for their divergent egg sizes. These species do differ in gamete traits and spawning conditions, so prezygotic factors might be responsible for selection for different egg sizes (Levitan 1993, 1996a,b).

Laboratory studies indicate that the species with the largest eggs requires the lowest concentration of sperm to achieve 50% fertilization, and the species with the smallest eggs requires the highest concentrations (Levitan 1993). Theory predicts that, given the empirical estimates for larval development and mortality, variation in sperm limitation can result in divergent selection on egg size to the extent noted among the three congeners (Levitan 1996a). What is not clear is how species-specific gamete traits influence fertilization rates in the field, where sea conditions are variable and may swamp gamete-level effects on fertilization. Here I demonstrate how species-specific gamete traits result in qualitatively different fertilization rates in the sea and show that these differences are correlated with spawning conditions such that egg traits appear to be adapted for increased zygote production for each species. The results suggest that, contrary to Bateman's principle, at least for some taxa females and eggs may be under intense selection for increased fertilization success.

METHODS

Study Site, Animals, and Species Distributions

Research was conducted in the waters surrounding the Bamfield Marine Station, Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada (Fig. 1). Depending on location and weather, the degree of wave action at this study site varies from extreme wave energy on open coast to little water movement in protected inlets.

The three congeners under study differ in adult and gamete traits. *Strongylocentrotus purpuratus*, the purple sea urchin,

TABLE 1. Mean gamete traits for *Strongylocentrotus droebachiensis*, *S. franciscanus*, and *S. purpuratus*. Data from Levitan (1993) except sperm size data (from Chia et al. 1975).

	Egg traits		Sperm traits			
			Size (mm)			
Species	Size (mm)	Fertility[1]	Head and middle piece length	Head width	Velocity (mm/s)	Longevity[2]
S. droebachiensis	0.145	0.1666	0.007	0.0015	0.088	$y = 0.308x + 3.216$
S. franciscanus	0.135	0.0512	0.006	0.0016	0.130	$y = 0.391x + 2.818$
S. purpuratus	0.084	0.0559	0.005	0.0020	0.145	$y = 0.457x + 2.798$

[1] Proportion of estimated sperm-egg collisions that result in fertilization.
[2] Sperm longevity is a function of sperm concentration. These equations are the best-fit linear regression that predicts the $\log_{10}$ sperm half-life in seconds (y) as a function of $\log_{10}$ sperm/μL (x).

reaches a maximum size of 8–9 cm (Kramer and Nordin 1978; Schroeter 1978) and has the smallest eggs and fastest but shortest-lived sperm of the three species (Table 1). *Strongylocentrotus franciscanus*, the red sea urchin, reaches a maximum size of 17 cm (Bernard and Miller 1973; Levitan et al. 1992) and has intermediate egg size, sperm velocity, and sperm longevity (Table 1). *Strongylocentrotus droebachiensis*, the green sea urchin, reaches a maximum size similar to that of *S. purpuratus* (8–9 cm; Kramer and Nordin 1978), but has the largest eggs and slowest but longest-lived sperm of these species (Table 1). Thus there is an inverse relationship between egg size and sperm velocity and between sperm velocity and sperm longevity among these species, but these differences are not related to adult body size (Levitan 1993).

Spawning times for the three species are during the winter and spring (Kramer and Nordin 1975, 1978; Rumrill 1987; Strathmann 1987). At my study site, most individuals from all three species were ripe from February through the mid-April, and *S. purpuratus* and *S. franciscanus* spawned for an additional period into early June (1989–1997, unpubl. data).

Strongylocentrotus purpuratus and *S. franciscanus* have completely overlapping distributions and are found on the West Coast of North America from Alaska to the Baja California Peninsula (Schroeter 1978; McConnaughey and McConnaughey 1985). Fossils indicate that they have coexisted over this range for between 1 and 10 million years (Kew 1920; Grant and Hertlein 1938). *Strongylocentrotus droebachiensis* has a circumpolar distribution and overlaps with the other two species north of Puget Sound (McConnaughey and McConnaughey 1985). *Strongylocentrotus purpuratus* is common in intertidal and shallow subtidal habitats (Schroeter 1978), *S. franciscanus* is occasionally seen in the lower intertidal, but is very common subtidally (Schroeter 1978), and *S. droebachiensis* is found subtidally at lower abundances than are the other two species on the West Coast of North America (Kramer and Nordin 1978; Rumrill 1987; Waddell et al. 1997).

Nearest-neighbor data were collected on the three *Strongylocentrotus* congeners during 70 dives at haphazard locations scattered throughout my study area (Fig. 1) in spring 1995, 1996, and 1997. Nearest-neighbor distances were measured from the center of one urchin, where the gonopores are located, to the center of the next closest conspecific.

Collecting Animals and Gametes

Sea urchins were collected and experiments were conducted during the springs of 1994 and 1995. Sea urchins were held in an open seawater system, fed assorted macroalgae, and used for experiments within two weeks of collection.

Sea urchins were induced to spawn with an injection of 0.55 M KCl. Sperm were collected directly off the gonopores, as they were released, with a disposable pasteur pipette and kept dry (undiluted) and on ice until used in experiments. Females were inverted into a large glass bowl filled with 5-micron–filtered sea water, and the spawned eggs were kept immersed in ambient-temperature sea water until used in experiments.

Field Experiment

In the spring of 1994, experiments were conducted on *S. franciscanus* and *S. purpuratus*. In 1995, experiments were conducted on *S. droebachiensis*, *S. purpuratus*, and the hybrid cross of *S. droebachiensis* eggs with *S. purpuratus* sperm (the reciprocal cross results in little or no fertilization; Levitan unpubl. data).

A single male and female were induced to spawn for each species tested. A sample of eggs was placed in a glass jar, so that the egg suspension had a volume of 15 mL at a concentration of approximately 1×10^5 eggs/mL. In addition, for each species, six 0.05-mL aliquots of dry sperm were placed in separate scintillation vials. Species did not differ significantly in dry sperm concentration (ANOVA, $F = 1.405$, $P = 0.254$) and averaged 3.3×10^{10} sperm/mL (SD $= 9.1 \times 10^9$). Both eggs and sperm were placed on ice and taken to the field (see Fig. 1 for field sites).

As the divers entered the water, the egg suspension was mixed with 15 mL of fluorescein dye in sea water (1 g/L of filtered sea water), placed in 10-cc syringes, and taken to the bottom at a depth of 3–10 m. When the divers were in place, technicians on the boat diluted the first of the dry sperm aliquots with 19.95 mL of fluorescein dye in sea water, placed 5 mL of this solution in a 10-cc syringe, and sent the syringe by weighted messenger down a line to the divers, who used it immediately. The reason for diluting the sperm at the last possible moment was that, while dry, sperm can last for hours to days without losing viability; once diluted and activated, sperm age within minutes (e.g., Levitan et al. 1991; Levitan 1993).

Sperm from the syringe was released upward into the water, 0.5 m above the bottom, at a rate of 1 mL/s (mean $= 1.1 \times 10^8$, SD $= 0.3 \times 10^8$ sperms/s or approximately 5×10^8 total sperm released). This release rate is within the range of sperm release rates for KCl-induced spawning in these sea

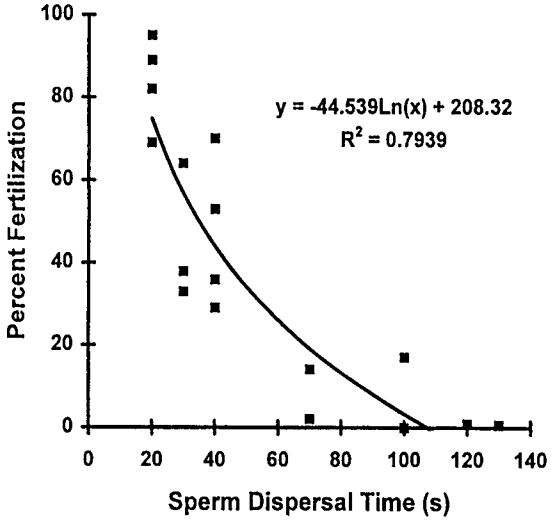

FIG. 2. Control for fertilization in the filter chamber. Sperm were released into the sea and then recollected at various sperm dispersal times. Eggs were previously introduced into the filter chambers, so fertilization occurred within the filters, not at sea. After 100 s of sperm dispersal, no fertilization was detected in the filter chambers.

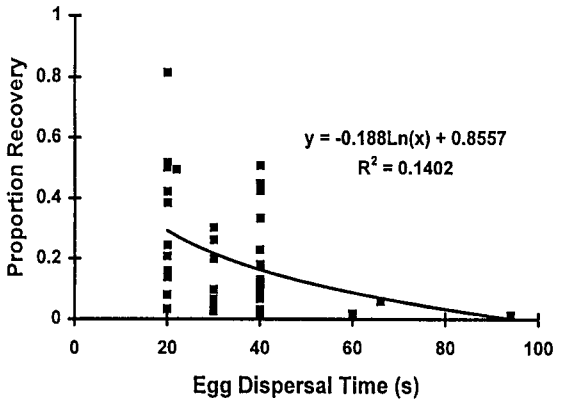

FIG. 3. Percent of eggs collected as a function of time since release into the sea. At least 100 eggs could be recovered after 120 s to provide a reasonable estimate of percent fertilization.

urchins (mean = 4×10^7, range = 1×10^5 to 3×10^8 sperm/s for these three congeners; unpubl. data). While the sperm-dye cloud diffused, it was videotaped along with a marked rule for scale. At a predetermined time (5, 20, or 80 s), 5 mL of the egg suspension was released into the center of the sperm-dye cloud at a rate of 1 mL/s. Extreme care was taken to minimize diver disturbance to the gamete cloud, and no diver disturbance was evident in the videotapes. After two minutes, the egg-dye cloud was sampled with a 5-m hose (13 mm internal diameter) connected to a 12-volt battery-operated submersible bilge pump drawing water through one of 12 1.2-L filter chambers (model OB1 OMNI-BASIC Economy full-size water filter with filter cartridge replaced with 2"-diameter PVC pipe with slots covered by 30-micron–mesh Nitex). Each of the 12 filter chambers could be opened independently, allowing for 12 experimental trials per dive (for a similar pump design, see Mundy et al. 1994). The pump was run for 30 s within the gamete cloud and then rinsed about 5 m away, outside the cloud, for 60 s. This mesh size retained eggs but allowed sperm to wash away.

After each trial, another dry sperm sample was diluted and sent to the divers until all sperm dispersal times were run for all species (and hybrid cross in 1995). Eggs from each trial were collected in a separate filter chamber. After the dive, the samples were returned to the lab for determination of the percent of fertilized eggs out of a sample of at least 100 eggs.

An InterOcean S4 current meter was used to estimate variation in flow velocity and wave height at 0.5-s intervals throughout the experimental time period (on some of the 1994 trials and all of the 1995 trials). The current meter was placed 5 m away from the experiments to reduce the possibility of diver influence on flow-rate estimates.

The video images were recorded approximately 5 m from the sperm cloud at the same height as the cloud and thus provide a two-dimensional image (vertical axis and one horizontal axis) that was assumed to be proportional to the three-dimensional volume of the cloud. For analysis of sperm dispersal, the images were traced at 0, 2.5, 5, 10, 20, 40, and 80 s (or on clear images, with scale bar included, closest to those times) onto acetate sheets. These tracings were then digitized to produce calculations of the area of the sperm cloud. Sperm dispersal rate was calculated as the slope of the sperm-cloud area as a function of time.

Field Controls

Experiments were conducted to insure that fertilization was taking place in the ocean rather than inside the filter chambers. In the field, virgin eggs were introduced directly into the hose of the submersible pump. The pump was stopped, and then 5 mL of sperm mixed with dye was released (ca. 4×10^9 sperm/s or 2×10^{10} total sperm released) into the ocean. At one of a variety of sperm dispersal times, the sperm cloud was sampled with the pump. The experiment was then repeated at a different sperm dispersal time and the sample collected in another filter chamber until all 12 filter chambers were filled for that dive. Any fertilization in these experiments must have occurred in the filter chambers. When sperm dispersed for over 100 sec, no fertilization was detected in the chambers (Fig. 2). In the field experiments the minimum time that sperm dispersed before being collected was 125 s (5-s sperm dispersal + 120-s sperm-egg contact time). In addition, the concentration of released sperm in the field experiments was more than an order of magnitude less than that in these controls, an extra margin of dilution to insure that fertilization in the field experiments occurred in the ocean rather than in the filter chambers. Longer sperm-egg contact times were not practical because the proportion of eggs recollected dropped sharply with egg dispersal time (Fig. 3).

Laboratory Experiment on Sperm-Egg Contact Time

Sperm were serially diluted in glass beakers in a volume of 100 mL of sea water. Between 4000 and 8000 eggs were placed in plastic vials the bottoms of which had been replaced with 30-micron Nitex mesh, so that lifting the vial out of a

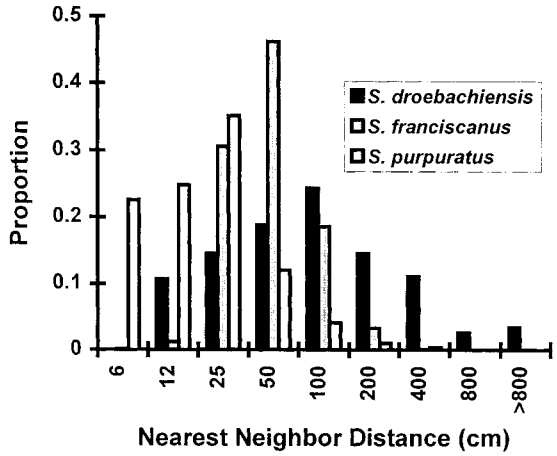

FIG. 4. Distribution of nearest-neighbor distances for three *Strongylocentrotus* species in Barkley Sound. Data collected during 70 dives throughout study area (Fig. 1). Note that distance doubles in each size class.

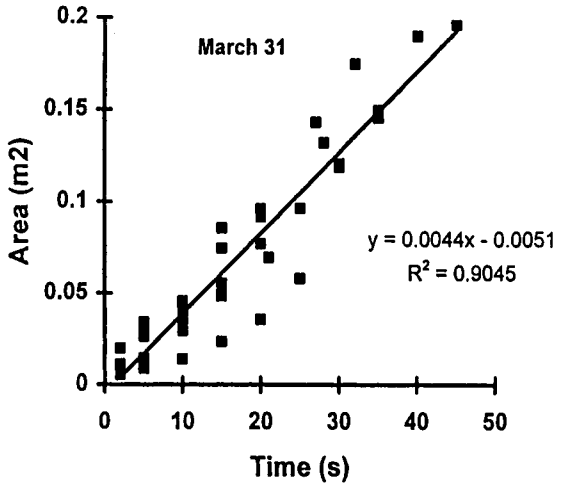

FIG. 5. Area of the sperm cloud as a function of time since release on 31 March 1995. Sperm-cloud area calculated from video images. Sperm dispersal rate is the slope of this relationship. Sperm dispersal rate was calculated for each experimental day.

beaker containing a sperm dilution would quickly separate the eggs from the sperm. These vials were placed in the beakers containing sperm for 10 or 100 sec, removed, rinsed five times with filtered sea water, and placed in beakers with filtered sea water to incubate for three hours. In a third treatment, serially diluted sperm were place in scintillation vials with eggs in 10 mL of sea water and left for the full three-hour period. Experiments were conducted in a shallow sea table with flowing ambient-temperature sea water (9–10°C). Sperm concentration was estimated from the 1000-fold dilution of dry sperm (eight replicate counts on a hemocytometer), and egg concentration was estimated from the stock egg solution (three replicate counts of 0.1 mL). After three hours the percent of eggs fertilized was determined, and the concentration of sperm needed to fertilize 50% of eggs (f_{50}) was calculated by means of a fertilization kinetics model (Vogel et al. 1982; see below). All three species were tested (13–20 replicates per species).

Calculation of f_{50}

The data from the sperm-egg contact-time experiment were used to generate an index of gamete performance, the amount of sperm needed to fertilize 50% of the eggs under laboratory conditions (f_{50}). I calculated this value by fitting the laboratory data to a gamete-kinetics models (Vogel et al. 1982), using the Marquart method of nonlinear regression (SAS Institute 1988). This model predicts the proportion of fertilized eggs (φ_∞) from the initial concentration of sperm (S_0, sperm/μL) and eggs (E_0, eggs/μL), sperm-egg contact time (t), rate of sperm-egg collision (β_0, mm^3/s; calculated from the product of the sperm velocity and egg cross-sectional area, Table 1), and fertilization constant (β, mm^3/s; fitted through iteration):

$$\varphi_\infty = 1 - \exp\left[-\frac{\beta S_0}{\beta_0 E_0}(1 - e^{-\beta_0 E_0 t})\right]. \quad (1)$$

RESULTS

Distribution of Urchins

Nearest-neighbor distances were measured for 2283 individuals (*S. purpuratus*, $n = 590$; *S. franciscanus*, $n = 1459$; *S. droebachiensis*, $n = 234$). *Strongylocentrotus purpuratus* has the nearest neighbors (median 13 cm, mean 19 cm), followed by *S. franciscanus* (median 33 cm, mean 40 cm) and *S. droebachiensis* (median 60 cm, mean 134 cm; Fig. 4). The nearest-neighbor distances are directly correlated with egg size and sperm longevity and inversely correlated with sperm velocity in these species (see Table 1 for gamete traits).

Sperm Dispersal Rate

Field trials were conducted on 28 days at a depth between 3 m and 8 m. Daily average flow varied from 2 cm/s to 23 cm/s, and instantaneous flow varied from 0 cm/s to 85 cm/s.

Sperm dispersal rate was calculated from the slope of the relationship between sperm-cloud area and time for each experimental day. Species did not differ in size of the sperm cloud as a function of time (ANCOVA with time since sperm release as the covariate, species effect was ns in 1994, $P = 0.9848$, and in 1995, $P = 0.4274$, but the effect of date and the covariate of time were significant, $P = 0.0001$ for all cases). To provide the most robust estimate of daily sperm dispersal rate, the data from all trials and species each day were pooled (e.g., see Fig. 5). The rate at which the sperm cloud expanded each day was related to mean instantaneous (0.5-s interval) current velocity during the experimental time period (Fig. 6).

Sperm dispersal rate explained between 28% and 55% of the daily differences in mean fertilization rate for each species or hybrid cross (Fig. 7). Sperm dispersal rate was used as a covariate in analyses of species differences in fertilization rates.

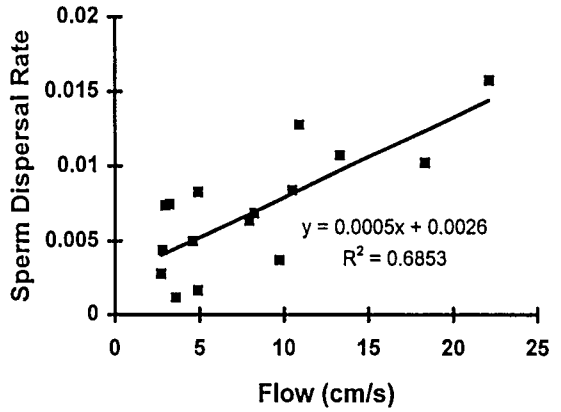

FIG. 6. Sperm dispersal rate and flow velocity. Sperm dispersal rate was calculated as in Fig. 5; flow velocity is the average 0.5-s flow velocity for each experimental date. Flow was recorded with an InterOcean S4 current meter placed 0.5 m above the bottom and 5 m from the experimental location.

Species Differences in Field Fertilization Rates

Twelve to 15 trials of each tested species were conducted each year. Fertilization rates of *S. purpuratus* in the two years were surprisingly similar (Table 2). Because *S. purpuratus* did not show year-to-year variation, all species and hybrid trials were considered in one analysis.

Sperm dispersal time is the interval from sperm release to egg release and was experimentally fixed at 80, 20, or 5 s. The percent of eggs fertilized decreased as a function of sperm dispersal time (Fig. 8). The important response variables are comparative fertilization success when spawning is simultaneous (eggs and sperm are released simultaneously in the same location) and changes in this comparative success with the degree of synchrony (difference in time of spawning or distance between individuals). The former is the intercept and the latter is the slope of the relationship between sperm dispersal time and fertilization. Species differences in the slopes and intercepts were analyzed with ANCOVA (Table 3). Species differed significantly in the slope of the relationship between sperm dispersal time and fertilization (Fig. 8). *Strongylocentrotus droebachiensis* had the smallest rate of decrease in the percent of eggs fertilized, followed by *S. franciscanus,* and *S. purpuratus* had the greatest. The hybrid cross of *S. droebachiensis* eggs with *S. purpuratus* sperm had a rate of decrease not significantly different from that of *S. droebachiensis* (or *S. franciscanus*) but significantly different from that of *S. purpuratus* (Table 3). Species did not differ significantly in the intercept of the relationship between fertilization success and sperm dispersal time, but the intercept of the hybrid cross was significantly lower than that of *S. purpuratus* (Table 3). Sperm dispersal rate (the expansion rate of the sperm cloud) was a significant covariate in the test on the intercepts (rate of fertilization decrease as a function of

TABLE 2. Average fertilization success of *Strongylocentrotus purpuratus* in 1994 and 1995.

Sperm dispersal time	1994	1995
5 s	71%	71%
20 s	48%	50%
80 s	11%	11%

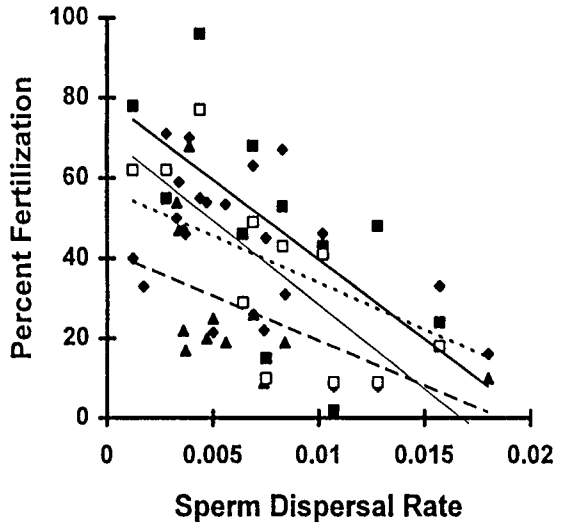

FIG. 7. Average fertilization and sperm dispersal rate. Each point on the graph is the average female fertilization success for that species and date (mean of three sperm dispersal times). Diamonds and dotted line are *Strongylocentrotus purpuratus*, triangles and dashed line are *S. franciscanus*, solid squares and bold line are *S. droebachiensis*, and open squares with fine line are the hybrid of *S. droebachiensis* eggs with *S. purpuratus* sperm.

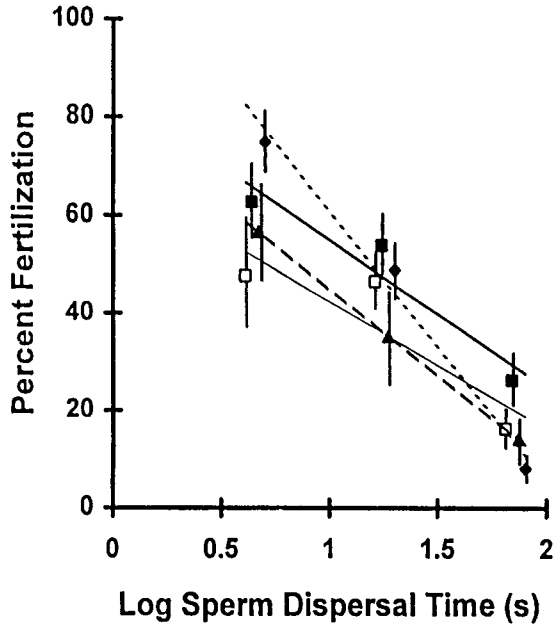

FIG. 8. Fertilization and sperm dispersal time. Sperm dispersal time is the period of sperm dispersal before eggs are introduced into the sperm cloud. Once eggs are released, the sperm and eggs always interact for two minutes before eggs are recollected. Each datum is the mean and standard error for that species across all experimental dates (n = 12–20). All statistics conducted on arcsine-transformed fertilization data. Values are back-transformed for plot. Symbols as in Figure 7.

TABLE 3. Analysis of covariance tests for species differences in the field experiment. The response variables were the slope and intercept of the relationship between sperm dispersal time (log transformed) and fertilization success (arcsine transformed). The covariate is the sperm dispersal rate (Rate). Results of Student-Newman-Keuls pairwise tests are listed on the side of each ANCOVA.

						SNK test			
Source	df	SS	MS	F	$P > F$	Group	Mean	n	Species
Slope									
Species	3	1.574	0.525	5.850	0.0016	A	−0.648	24	*S. purpuratus*
Rate	1	0.012	0.012	0.014	0.7105	B	−0.377	12	*S. franciscanus*
Error	53	4.752	0.090			B	−0.317	11	*S. droebachiensis*
Total	57	6.376				B	−0.256	24	Hybrid
Intercept									
Species	3	3.211	1.070	4.360	0.0081	A	1.528	24	*S. purpuratus*
Rate	1	2.240	2.240	9.130	0.0039	A B	1.079	12	*S. franciscanus*
Error	53	12.998	0.245			A B	1.170	11	*S. droebachiensis*
Total	57	8.772				B	0.912	11	Hybrid

sperm dispersal time) but not the slopes (Table 3). Not only was the slope of this relationship insensitive to the sperm dispersal rate (the degree of water mixing), but there was a near-perfect correlation between the mean slope for each species and mean egg cross-sectional area (Fig. 9).

Sperm-Egg Contact-Time Experiments

In the laboratory, when eggs were exposed to sperm for shorter periods of time, fertilization success decreased (Fig. 10). The amount of sperm needed for 50% fertilization increased by up to a maximum of 2.9 orders of magnitude when sperm-egg contact time decreased from 100 to 10 s and a maximum of 3.8 orders of magnitude when sperm-egg contact was decreased from 3 h to 10 s. The amount of change in the f_{50} depended on both the change in sperm-egg contact time (from 10 to 100 s or from 10 s to 3 h) and the species examined (Fig. 10D). A two-way ANOVA indicated a significant interaction between species and the amount of change in sperm-egg contact time (Table 4), so species differences were analyzed in separate one-way ANOVAs for each sperm-egg contact time comparison, and a significant species effect was noted in each case (Table 4). In all significant comparisons, the species with the smaller eggs was more sensitive to changes in sperm-egg contact time than was the species with larger eggs. In comparisons between species when sperm-egg contact time varied between 10 s and 100 s, there was a significant pairwise difference between *S. droebachiensis* and the other two species (Table 4). In comparisons between species when sperm-egg contact time varied between 10 s and 3 h, there was a significant pairwise difference between *S. purpuratus* and the other two species (Table 4).

Theoretical Predictions of Effect of Changes in Sperm-Egg Contact Time

The field experiment revealed that the species differed in the sensitivity of fertilization success to changes in sperm diffusion time. When individuals spawned simultaneously, species did not differ significantly in fertilization rate (ns difference in intercepts, Table 3), but as the sperm dispersal time increased, species differences became significant (sig-

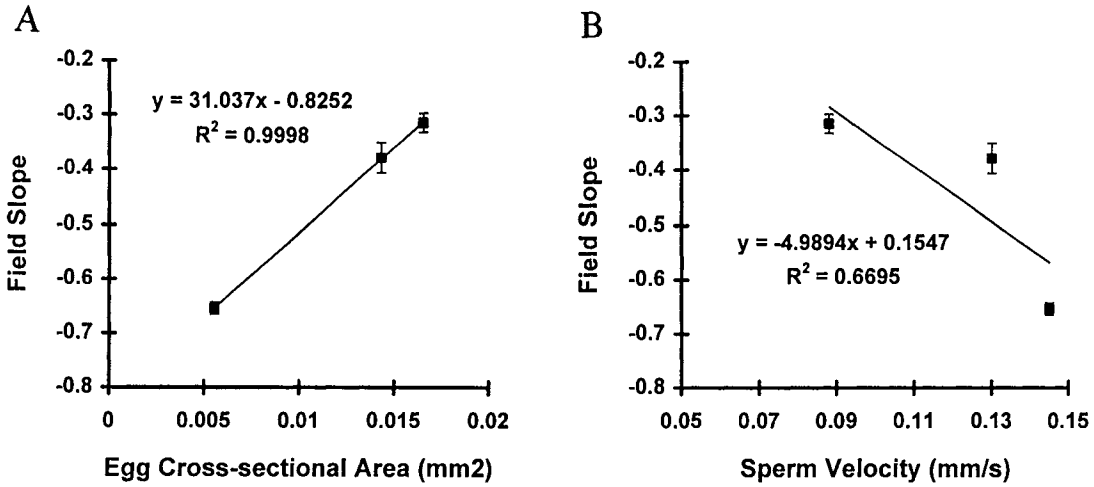

FIG. 9. Slope of the relationship between female fertilization success and sperm dispersal time (Fig. 8) plotted against mean egg cross-sectional area (A) and sperm velocity (B). Mean and standard error plotted; values for egg size and sperm swimming velocity from Table 1. R^2-values calculated from mean data for each species.

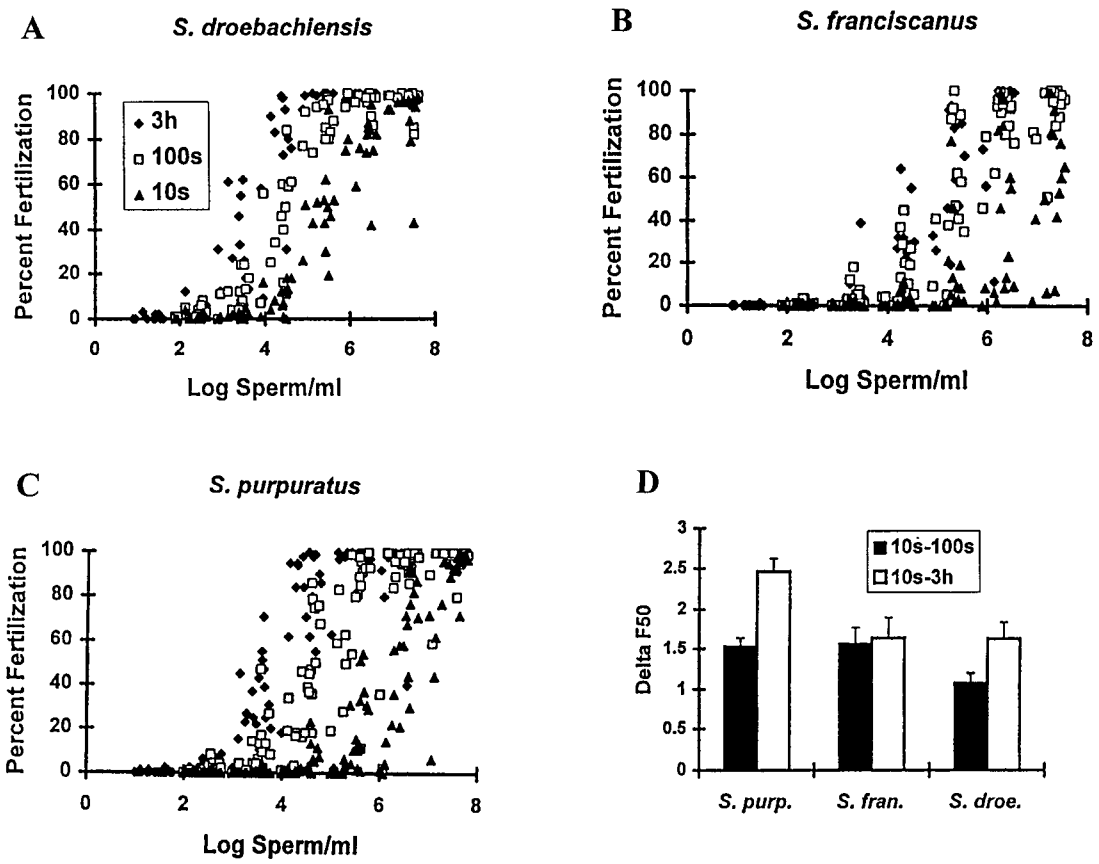

FIG. 10. Influence of sperm-egg contact time on fertilization success. (A) *Strongylocentrotus droebachiensis*; (B) *S. franciscanus*; (C) *S. purpuratus*; (D) histogram of mean and standard error of the difference in the log-transformed change in f_{50} among species and comparing 10 s to 100 s and 10 s to 3 h.

TABLE 4. Two-way analysis of variance testing the effects of species (*S. purpuratus, S. franciscanus, S. droebachiensis*) and the difference in sperm-egg contact time (100 s vs. 10 s or 3 h vs. 10 s) on the difference in the amount of sperm needed to fertilize 50% of eggs. Because of a significant interaction, independent tests were conducted for each sperm-egg contact-time comparison. Student-Newman-Keuls pairwise tests are reported for each ANOVA.

						SNK test			
Source	df	SS	MS	*F*	*P* > *F*	Group	Mean	*n*	Species
Two-way ANOVA									
Species	2	6.903	3.451	7.04	0.0015				
Time	1	5.894	5.894	12.02	0.0008				
Interaction	2	3.051	1.526	3.11	0.0494				
Error	88	43.13	0.490						
Corrected Total	93	60.51							
100 s vs. 10 s									
Species	2	2.031	1.016	3.45	0.0406	A	1.572	14	*S. franciscanus*
Error	44	12.96	0.295			A	1.538	20	*S. purpuratus*
Corrected Total	46	14.99				B	1.088	13	*S. droebachiensis*
3 h vs. 10 s									
Species	2	7.922	3.961	5.78	0.0059	A	2.463	20	*S. purpuratus*
Error	44	30.17	0.686			B	1.637	14	*S. franciscanus*
Corrected Total	46	38.097				B	1.627	13	*S. droebachiensis*

nificant differences in slopes, Table 3). These differences are correlated with egg size (Fig. 9). When the sperm dispersal time increases, two factors simultaneously influence fertilization success; the sperm cloud is more diffuse, reducing gamete concentration, and the time period during which sperm can interact with eggs is reduced. This second factor is less obvious but is apparent because the controls indicate that, after 120 s of sperm diffusion, sperm are too dilute to achieve fertilization. If sperm and eggs are released simultaneously, then sperm and eggs can interact for a maximum of 120 s before the sperm are too diffuse to fertilize eggs. If sperm disperse for 80 s before the eggs are introduced, then no more than 40 s are available for fertilization and probably much less, because the controls that yielded zero fertilization at 120 s used sperm concentrations an order of magnitude higher than those in the field experiment.

The structure of Vogel et al.'s (1982) fertilization kinetics model and the empirical results from the laboratory suggest that changes in sperm-egg contact time can influence patterns of fertilization. I conducted simulations with equation (1) and using parameters based on the field experiment to determine whether the interaction of sperm-egg contact time, sperm concentration, and egg size could explain species differences in the relationship between sperm dispersal time and fertilization success found in the field experiment (Figs. 8, 9). To determine whether species differences in fertilization success could be caused by egg size differences, rather than some other gamete attribute, I held all gamete parameters except egg size constant in the model. Parameters were based on *S. droebachiensis* values for β/β_0 (0.1666), β_0 was calculated from *S. droebachiensis* sperm velocity (0.088 mm/s) and from egg cross-sectional areas based on the three congeners (0.084, 0.135, 0.145 mm diameter; Levitan 1993); β was calculated as $0.1666 \times \beta_0$. Egg concentration was set at 100/μL on the basis of the empirical value in the field experiment. Sperm concentration varied, and the model was tested at two sperm-egg contact times, 120 s (representing males and females spawning together or zero sperm dispersal time) and 5 s (males and females spawning apart or a greater sperm dispersal time). The results indicate that under these parameters, when sperm and eggs interacted for 120 s, the three egg-size simulations resulted in similar fertilization profiles as a function of sperm concentration (Fig. 11), but when sperm and eggs interacted for only 5 s, simulations with smaller eggs had lower fertilization success for a particular sperm concentration than did simulations with larger eggs (Fig. 11).

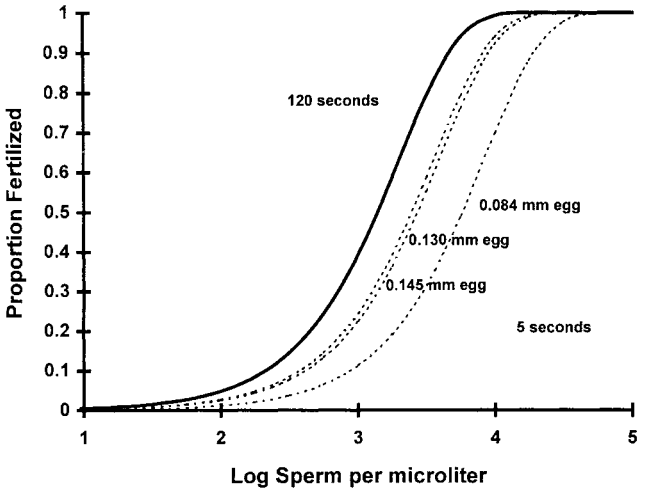

FIG. 11. Simulation of the influence of egg size on fertilization success when sperm-egg contact time is either 120 s (bold line, same for three egg sizes tested) or 5 s (dotted lines). Plot generated from Vogel et al.'s (1982) fertilization kinetics model (eq. 1). Egg concentration is 100/μL. All species parameters are based on *Strongylocentrotus droebachiensis* (Table 1), and egg size is varied in the model to represent the egg sizes for the three *Strongylocentrotus* species tested.

DISCUSSION

Gametes from closely related species interact differently to produce zygotes in the sea. Although previous studies have documented species-specific gamete traits (e.g., Gray 1955; Amy 1983; Emlet et al. 1987; Franzén 1987; Eckelbarger et al. 1989; Levitan 1993) and gamete performance in the laboratory (Branham 1972; Levitan 1993), this is the first to document that these differences result in performance differences in the field. The differences in fertilization success in the field appear to be biologically significant because of their magnitude (e.g., greater than threefold difference at the 80-s sperm dispersal time) and because they were evident despite the wide fluctuations in flow velocity (daily average flow varied from 2 cm/s to 23 cm/s, and instantaneous readings from 0 cm/s to 85 cm/s) and intraspecific variations in gamete performance (Levitan 1996b) that might swamp more subtle species differences in performance. These dramatic effects suggest that selection on gamete attributes under natural conditions is likely to be intense.

The differences noted among species do not result from species-specific differences in adult morphology, reproductive allocation, or behavior. Gametes from all species were released in a uniform manner at a uniform concentration. Even differences in spawned materials other than gametes, like viscosity differences in semen (Thomas 1994a,b), are likely to have been diminished because sperm were diluted and well mixed with sea water and dye before release. Controls (Fig. 2) indicate that differences in fertilization success were manifested in the ocean rather than during collection or transport in filter chambers. Species-specific differences in fertilization were entirely a result of species-specific differences in gamete traits such as morphology, physiology, and behavior.

Differences in gamete performance were correlated with differences in gamete traits. The species with the smallest eggs and fastest but shortest-lived sperm (*S. purpuratus*) exhibited the steepest decline in fertilization success with increased sperm dispersal time. The species with the largest eggs and slowest but longest-lived sperm (*S. droebachiensis*) exhibited the shallowest such decline. The species with intermediate traits (*S. franciscanus*) exhibited an intermediate decline. These differences could be attributed to sperm traits, egg traits, or some more complex sperm-egg interaction. One possible hypothesis is that, because sperm age more quickly at low concentrations, longer-lived sperm would have higher fertilization success with increased sperm dispersal time. A

second hypothesis is that fast sperm would cause the sperm cloud to disperse faster than do slow sperm, resulting in a more rapid decline in fertilization success with increased sperm dispersal time. A third hypothesis is that larger eggs provide a larger target for sperm and are fertilized at a higher rate, particularly when the time available for sperm-egg interactions is short. Six lines of evidence support the last hypothesis.

First, although sperm longevity decreases with sperm concentration, sperm half-life has never declined below five minutes in laboratory studies of these three species (Levitan 1993). Therefore, although sperm longevity may be important in explaining patterns of fertilization with sperm dispersal time in nature, it is not likely to explain the patterns noted in the present experiment, where sperm had a maximum time of 120 s before they were too dilute to have a significant chance of finding an egg.

Second, video tapes of the dispersing sperm cloud revealed no significant species-specific differences in the rate at which sperm dispersed. A nearly 10-fold difference in sperm concentration among species would be needed to produce the differences of 9–26% in fertilization success noted at the 80-s sperm dispersal time (e.g., see Fig. 10 for the relationship between fertilization and sperm concentration). For sperm concentration to be decreased 10-fold, the sperm cloud would have to be an order of magnitude larger in volume, presenting a 366% larger profile (assuming a spherical shape). Yet the videotapes revealed no hint of a difference among species in dispersal rate. Although the species differ significantly in sperm velocity (0.088 mm/s to 0.145 mm/s average velocity; Levitan 1993), sperm often swim in circles or spirals and do not seem to travel great linear distances (Miller 1985 for echinoderms; pers. obs. for the three species studied here). Turbulent water flow is the likely major cause of sperm dispersal, and differences in sperm velocity have a negligible effect at this scale.

Third, the field hybridization experiment indicates that, regardless of the species of the sperm donor, the slope of the relationship between fertilization success and sperm dispersal time is determined by the species of the egg donor (Fig. 8). Some attribute of the egg is responsible for the species-specific slopes noted in the field experiment.

Fourth, the correlation between mean egg cross-sectional area and the mean slope of the relationship of fertilization and sperm dispersal time is nearly perfect, whereas sperm swimming velocity is a poor predictor of this relationship (Fig. 9). This point may explain why the slope for *S. purpuratus* differed significantly from those for the other two species, but no significant slope differences could be detected between the two other species; their egg sizes are more similar, and the magnitude of the effect was proportional to the differences in egg sizes. Regardless of whether gametes move in relation to each other primarily because of sperm swimming behavior or microscale turbulence, the rate at which sperm collide with eggs is a function of the projected size of the target, the egg cross-sectional area. Although a correlation among three species is not in itself strong evidence, it is supported by laboratory experiments and theory.

Fifth, computer simulations predict a large effect of egg size at short sperm-egg interaction times and a smaller or no effect at longer times. Given enough time and longevity, sperm will eventually find and attach to an egg, regardless of the target size, but as searching time (or longevity) decreases, the *rate* of collision increasingly influences fertilization success. Under the field conditions in this experiment and the parameters used in the model, sperm longevity is not an issue, but searching time is restricted because within 120 s sperm become too diffuse to achieve fertilization. The model prediction that fertilization success will not be sensitive to egg size when sperm and eggs interact for 120 s is consistent with our field-experiment result showing no species differences in the intercept of the relationship of fertilization success and sperm dispersal time (Table 3). The intercept represents a maximum sperm-egg contact time of 120 s. The model prediction that fertilization success will be sensitive to egg size when sperm and eggs interact for 5 s is consistent with the field-experiment result showing species differences in that slope (Table 3). Differences among species became more pronounced with decreases in sperm-egg contact time.

Finally, laboratory fertilization assays indicate that sperm-egg contact time influences fertilization to a greater extent in species with smaller eggs than in species with larger eggs. This result provides empirical support for the predictions made by the computer simulations. In constrast to the simulations, species differ in factors other than egg size. These include sperm velocity, the receptiveness of the egg surface to sperm, and the thickness of the jelly coat (Levitan 1993, 1996a). Sperm velocity is inversely related to egg size in these species (Levitan 1993) and if important would result in a trend opposite to that noted. Egg receptivity—the proportion of sperm collisions that result in fertilization—is not correlated with egg size in these species (Levitan 1993). Jelly-coat thickness is correlated with egg size in these species (unpubl. data) and may be partially responsible for the patterns noted (see, e.g., Podolsky 1995; Podolsky and Strathmann 1996), but a similar effect of sperm-egg contact time on fertilization success has been noted when jelly coats have been removed (unpubl. data). Jelly coats in these *Strongylocentrotus* species also shear off eggs quickly in moving sea water (unpubl. data), making their influence on fertilization in nature difficult to assess. Gamete traits other than egg size may influence rates of fertilization but need not be invoked to explain the species differences in fertilization noted in the lab and field, given the results of the computer simulation.

The present weight of evidence suggests that attributes of the egg influence species-specific fertilization rates in the field. These differences are correlated with egg size (Fig. 9) and can be explained by egg-size differences (Fig. 11). Egg size has been correlated with fertilization success among species (Levitan 1993), within species (Levitan 1996a), and within females (Levitan 1996a) in the laboratory and among (this study) and within (Levitan 1996a) species in the field.

If larger eggs lead to greater fertilization success, why are not all eggs at some maximum size? If the energy allocated to reproduction is constant, then increases in egg size must be balanced by decreases in egg number. An optimal egg-size model indicates that, when empirical estimates of development time and egg size and planktonic mortality are used for this species group, intermediate eggs sizes are predicted (Levitan 1996a,b). The optimal intermediate size var-

ies as a function of ambient sperm concentration; greater sperm limitation results in larger predicted optimal egg size (Levitan 1996a,b).

Variation in sperm availability is certainly not the only mechanism that can shift optimal egg size. Temperature during development, planktonic food availability, and larval mortality rates can also, in theory, cause shifts in echinoid egg size (Levitan, in review). Because these congeners cooccur and share spawning times, the influence of sperm availability on selection on egg size may be more apparent than in other taxa where the planktonic environment varies among species (Levitan 1996a). One possible exception is *S. droebachiensis,* which has a more northern and circumpolar distribution than do the other two species. The lower water temperatures at higher latitudes may contribute to the larger egg sizes noted in this species (Levitan, in review). Regardless, the point is not that sperm availability determines egg size but that it may influence selection on egg size. In other taxa, confounding factors may obscure patterns associated with sperm availability.

The primary determinant of sperm availability is the distribution and abundance of spawning conspecifics (Levitan 1995). These three congeners differ in adult dispersion and habitat use. *Strongylocentrotus purpuratus*, the species with the smallest eggs and fastest sperm, lives intertidally and in shallow subtidal habitats. In Barkley Sound, this species has the most clumped distribution (Fig. 4); individuals are usually piled together in clumps that are wedged into cracks and crevices in rock surfaces. *Strongylocentrotus franciscanus*, the species with intermediate gamete traits, lives subtidally, at high density but spaced at greater intervals than is *S. purpuratus* (Fig. 4). *Strongylocentrotus droebachiensis*, the species with the largest eggs and slowest but longest-lived sperm, is also subtidal and has the greatest distance between conspecifics in Barkley Sound (Fig. 4).

In situ levels of female fertilization success have been measured from KCl-induced spawnings of these three species at their natural population densities and habitats in Barkley Sound. *Strongylocentrotus purpuratus* has the highest levels of fertilization (mean 91% in subtidal populations and 99% in intertidal populations), followed by *S. franciscanus* (61%) and *S. droebachiensis* (56%). These levels are correlated with nearest-male distance and male population density (Levitan 1996c, unpubl. data).

These patterns of dispersion and fertilization indicate that gamete attributes of these species are well suited to species-specific spawning conditions. Investment in larger eggs by *S. purpuratus* would not pay off because it is for the most part not sperm limited and is less likely than the other two species to spawn under dispersed conditions. For *S. droebachiensis*, the payoff of producing larger eggs is substantial because it is sperm limited and the gametes of this species are more likely to encounter one another under more dispersed conditions. *Strongylocentrotus franciscanus* has intermediate levels of fertilization and adult aggregation; its payoff for investment in larger eggs is intermediate. By trading off egg size and egg number, each species can optimize the production of offspring as a function of fertilization and postzygotic success.

These results beg the question of why species with larger eggs are not more aggregated. Increased population density can lead to higher fertilization success but lower gamete production; thus increased aggregation may not result in increased fitness when food is limiting (Levitan 1991; Levitan and Young 1995). The two species with larger eggs (*S. droebachiensis* and *S. franciscanus*) live in a subtidal habitat where increases in density of the abundant *S. franciscanus* lead to decreased gonad size in this species as a result of food depletion (Bureau 1996). *Strongylocentrotus droebachiensis*, the species with the largest eggs, faces the additional problem of being relatively rare (Rumrill 1987; Waddell et al. 1997; Levitan, unpubl. data). Male number and male distance to females are both important determinants of female fertilization success, so rare species may not be able to overcome sperm limitation completely by forming small groups (Levitan et al. 1992). *Strongylocentrotus purpuratus,* the species with the smallest eggs, live in shallow or intertidal wave-exposed environments that are a refuge from the intense grazing activity of the competitively dominant *S. franciscanus* (Schroeter 1978) and are generally in tight clumps covered with drift algae (pers. obs.). Population dynamics, species interactions, and environmental constraints on adults appear to determine the species microhabitat distribution, and gamete attributes may have adapted to these conditions.

The correlation of sperm traits with egg traits and adult distribution suggests a gradient from sperm competition to sperm limitation among these species. Sperm velocity, although it has a negligible effect on movement at larger spatial scales, might be important at the scale of gamete interactions and sperm competition. When sperm are at high concentration and close to eggs, fast sperm are more likely to collide with eggs than are slow sperm. If the negative correlation between velocity and longevity represents an energetic trade-off, males experiencing intense sperm competition and ephemeral virgins would be more successful with fast but short-lived sperm. At the other extreme, males under conditions of sperm limitation would be more successful with long-lived sperm that remain viable until contact with eggs occurs and are less likely be outcompeted at the last moment by a faster competitor because sperm densities are low. When *S. purpuratus* spawns in tide pools or in tight clumps, competition is possible, and selection should favor small eggs and fast sperm. When *S. droebachiensis* spawns at great distances from conspecifics, sperm longevity would be beneficial, and selection should favor large eggs and long-lived sperm.

The patterns of sea urchin distribution and abundance found in Barkley Sound appear typical of those on the West Coast of North America (Kramer and Nordin 1978; Schroeter 1978; Waddell et al. 1997), but are not invariate throughout these species' geographic ranges. Population density of *S. droebachiensis* is higher on the East Coast of North America (see, e.g., Himmelman 1986). Interestingly, eggs in these populations may be smaller (0.125–0.145 mm; R. Wahle, pers. comm.; 0.130 mm; M. Lesser and C. Walker, pers. comm.; but also 0.138–0.179 mm; R. Vadas and B. Beal, pers. comm.) and more similar in size to those of *S. franciscanus*, which has similar population densities on the West Coast. The larger issues of the historic population sizes of these species (Mann and Breen 1972; Estes and Palmisano 1974; Elner and Vadas 1990) and the time scales at which

populations fluctuate relative to the rate of gamete character evolution are more difficult to evaluate. Spatial and temporal variation is likely in all factors influencing selection on gamete characters. Optimal values are moving targets, and these life-history characters may not be at equilibrium.

Fertilization Ecology and Bateman's Principle

When female reproduction is limited by sperm availability, selection on females and eggs for increased fertilization success is likely to be important. Broadcast-spawning invertebrates are commonly sperm limited and show high variance in female fertilization success (Levitan 1995). This variance presents the opportunity for selection to operate. In the *Strongylocentrotus* species, egg traits appear to be adapted to the spawning conditions typical for each species. Current evidence suggests that egg size is the trait responsible for differential fertilization, but even if its influence results from tight genetic linkage to another egg trait, these results still demonstrate that variance in female gametic traits results in variance in female fertilization success. The simple dichotomy of sperm competition and female choice invoked to explain patterns of sexual selection may be less appropriate for broadcast-spawning organisms.

Instead of a dichotomy between male competition and female choice, it may be more appropriate to think of sexual selection in broadcast spawners as a theoretical surface of gamete interactions on which one axis is the ratio of sperm to eggs and the other the absolute concentration of gametes (Levitan 1998). The first axis determines the balance between sperm and egg competition, and the second the likelihood of direct or indirect competition for fertilizations. Direct competition is the case in which a spermatozoan (or egg) is unable to fertilize an egg (or spermatozoan) because a zygote has already formed. Indirect competition is that between gametes that never interact. Gametes better at fertilization have a higher fitness than those performing more poorly. The importance of this distinction is that when gamete collisions are relatively rare indirect competition can result in selection for greater fertilization success in both sexes. When gamete collisions are frequent and one gamete type is relatively rare, then the common gamete experiences direct competition and the rare gamete may choose among competitors. Bateman's principle applies to the latter situation.

When either gamete collisions are rare or sperm and eggs are equally abundant, then the intensity of sexual selection will be symmetrical, and selection for sexual dimorphism should be reduced (for a similar argument based on symmetrical mating success, see Arnold 1994b). Because sperm generally greatly outnumber eggs (but for *Drosophila* with few large sperm, see Pitnick et al. 1995), it is expected that direct sperm competition is more likely than direct egg competition. However, given the turbulent and heterogeneous patterns of water movement, gamete interactions can often be rare and egg competition—although not as likely as sperm competition—becomes a largely unexplored possibility (e.g., when diffuse sperm passes by a clump of eggs; Levitan 1998).

Increased symmetry in the intensity of sexual selection provides a potential explanation for the near absence of sexual dimorphism in broadcast-spawning marine invertebrates (Levitan 1998). The rare instances of sexual dimorphism in body size noted in broadcasting-spawning invertebrates seem to be correlated with a high degree of pair spawning and in some cases documented sperm competition (Levitan 1998). In pseudocopulating and copulating taxa, sexual dimorphism in body size is extremely common (Levitan 1988). These patterns support the notion that high levels of fertilization and sperm competition result in increased sexual dimorphism and that, as sperm become more limiting, Bateman's principle becomes less applicable. One possible exception to this rule is the divergence in gamete size between sexes in all animals, but recent theory suggests that sperm limitation coupled with selection on increased zygote size can result in anisogamy without direct sperm competition or Bateman's principle (Levitan 1996b, 1998).

Evidence of selection on egg characteristics for increased fertilization success in three congeners is not reason to reject Bateman's principle in broadcast-spawning species. However, these results, coupled with the mounting evidence of sperm limitation in this diverse group, suggest that it may be appropriate to intensify our evaluation of how sexual selection operates in this important and probably ancestral mating system.

Acknowledgments

I thank H. Brook, D. Bureau, J. Dalby, G. Farley, S. Kinsey, D. Levitan, T. McGovern, B. Prather, B. Schlining, K. Schlining, and K. Silvestre for field and laboratory assistance. M. Lesser, R. Vadas, R. Wahle, and C. Walker generously provided unpublished data on egg sizes of eastern North American populations of sea urchins. A. Spencer, the staff, and especially the late John Boom of the Bamfield Marine Station greatly facilitated this research. T. McGovern, M. McCartney, M. Ruckelshaus, A. Thistle, J. Travis, and A. Winn made many helpful suggestions on the manuscript. This work was supported by the National Science Foundation and the Bamfield Marine Station.

Literature Cited

Amy, R. L. 1983. Gamete sizes and developmental time tables of five tropical sea urchins. Bull. Mar. Sci. 33:173–175.

Arnold, S. J. 1994a. Is there a unifying concept of sexual selection that applies to both plants and animals? Am. Nat. 144:S1–S12.

———. 1994b. Bateman's principles and the measurement of sexual selection in plants and animals. Am. Nat. 144:S126–S149.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila.* Heredity 2:349–368.

Bernard, F. R., and D. C. Miller. 1973. Morphometric data for a preliminary investigation on the red sea urchin resources of British Columbia (*Strongylocentrotus franciscanus* Ag.). Fisheries Research Board of Canada, Manuscript Report Series 1256. Pacific Biological Station, Nanaimo, BC.

Birkhead, T. R., and A. Møller, eds. 1998. Sperm competition and sexual selection. Academic Press, New York.

Branham, J. M. 1972. Comparative fertility of gametes from six species of sea urchins. Biol. Bull. 142:385–396.

Burd, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. Bot. Rev. 60:83–139.

Bureau, D. 1996. Relationship between feeding, reproductive condition, jaw size and density in the red sea urchin, *Strongylocentrotus franciscanus.* M.Sc. thesis, Simon Fraser University, Vancouver, BC.

CHIA, F.-S. 1976. Sea anemone reproduction: patterns and adaptive radiations. Pp. 261–270 *in* G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum, New York.

CHIA, F.-S., D. ATWOOD, AND B. CRAWFORD. 1975. Comparative morphology of echinoderm sperm and possible phylogenetic implications. Am. Zool. 15:533–565.

CHRISTIANSEN, F. B., AND T. M. FENCHEL. 1979. Evolution of marine invertebrate reproduction patterns. Theor. Popul. Biol. 16: 267–282.

CLARKE, A. 1993. Reproductive trade-offs in caridean shrimps. Funct. Ecol. 7:411–419.

ECKELBARGER, K. J., C. M. YOUNG, AND J. L. CAMERON. 1989. Modified sperm in echinoderms from the bathyal and abyssal zones of the deep sea. Pp. 67–74 *in* J. S. Ryland and P. A. Tyler, eds. Reproduction, genetics and distribution of marine organisms. Olsen and Olsen, Fredensborg, Denmark.

ELNER, R. W., AND R. L. VADAS, SR. 1990. Inference in ecology: the sea urchin phenomenon in the northwestern Atlantic. Am. Nat. 136:108–125.

EMLET, R. B., L. R. MCEDWARD, AND R. R. STRATHMANN. 1987. Echinoderm larval ecology viewed from the egg. Pp. 55–136 *in* M. Jangoux and J. M. Lawrence, eds. Echinoderm studies. Vol. 2. Balkema, Rotterdam.

ESTES, J. A., AND J. F. PALMISANO. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

FRANZÉN, A. 1987. Spermatogenesis. Pp. 1–47 *in* A. C. Giese, J. S. Pearse, and V. B. Pearse, eds. Reproductions of marine invertebrates. Vol. 9. Boxwood Press, Pacific Grove, CA.

GRANT, U. S., AND L. G. HERTLEIN. 1938. The west American Cenozoic Echinoidea. Univ. Calif. Publ. Math. Physics 2:1–225.

GRAY, J. 1955. The movement of sea-urchin spermatozoa. J. Exp. Biol. 32:775–801.

HADFIELD, M. G., AND S. E. MILLER. 1987. On developmental patterns of opisthobranchs. Am. Malacol. Bull. 5:197–214.

HAVENHAND, J. N. 1995. Evolutionary ecology of larval types. Pp. 79–122 *in* L. McEdward, ed. Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL.

HENDLER, G. 1975. Adaptional significance of the patterns of ophiuroid development. Am. Zool. 15:691–715.

HERMANS, C. O. 1979. Polychaete egg sizes, life histories, and phylogeny. Pp. 1–9 *in* S. Stancyk, ed. Reproductive ecology of marine invertebrates. Univ. of South Carolina Press, Columbia, SC.

HIMMELMAN, J. H. 1986. Population biology of green sea urchins on rocky barrens. Mar. Ecol. Prog. Ser. 33:295–306.

KEW, W. S. W. 1920. Cretaceous and Cenozoic Echinoidea of the Pacific Coast of North America. Berkeley Univ. Publ. Bull. Dept. Geol. 12:23–236.

KRAMER, D. E., AND D. M. A. NORDIN. 1975. Physical data from a study of size, weight and gonad quality for the red sea urchin (*Strongylocentrotus franciscanus* Agassiz) over a one-year period. Fisheries Research Board of Canada, Manuscript Report Series 1372.

———. 1978. Physical data from a study of size, weight and gonad quality for the green sea urchin (*Strongylocentrotus droebachiensis*) over a one-year period. Fisheries Research Board of Canada, Manuscript Report Series 1476.

LEVITAN, D. R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biol. Bull. 181:261–268.

———. 1993. The importance of sperm limitation to the evolution of egg size in marine invertebrates. Am. Nat. 141:517–536.

———. 1995. The ecology of fertilization in free-spawning invertebrates. Pp. 123–156 *in* L. McEdward, ed. Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL.

———. 1996a. Predicting optimal and unique egg sizes in free-spawning marine invertebrates. Am. Nat. 148:174–188.

———. 1996b. Effects of gamete traits on fertilization in the sea and the evolution of sexual dimorphism. Nature 382:153–155.

———. 1996c. Distribution, abundance, and water flow influence fertilization success in natural assemblages of sea urchins. Am. Zool. 36:12A.

———. 1998. Sperm limitation, gamete competition and sexual selection in external fertilizers. Pp. 173–215 *in* T. R. Birkhead and A. Møller, eds. Sperm competition and sexual selection. Academic Press, New York.

LEVITAN, D. R., AND C. PETERSEN. 1995. Sperm limitation in the sea. Trends Ecol. Evol. 10:228–231.

LEVITAN, D. R., AND C. M. YOUNG. 1995. Reproductive success in large populations: empirical measures and theoretical predictions of fertilization in the sea biscuit *Clypeaster rosaceus*. J. Exp. Mar. Biol. Ecol. 190:221–241.

LEVITAN, D. R., M. A. SEWELL, AND F. S. CHIA. 1991. Kinetics of fertilization in the sea urchin *Strongylocentrotus franciscanus*: interaction of gamete dilution, age, and contact time. Biol. Bull. 181:371–378.

———. 1992. How distribution and abundance influences fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecology 73:248–254.

MANN, K. H., AND P. A. BREEN. 1972. The relationship between lobster abundance, sea urchins, and kelp beds. J. Fish. Res. Bd. Can. 29:603–609.

MCCARTNEY, M. A. 1997. Sex allocation and male fitness gain in a colonial, hermaphroditic marine invertebrate. Evolution 51: 127–140.

MCCONNAUGHEY, B. H., AND E. MCCONNAUGHEY. 1985. Pacific Coast. Knopf, New York.

MCEDWARD, L. R. 1986. Comparative morphometrics of echinoderm larvae. II. Larval size, shape, growth, and the scaling of feeding and metabolism in echinoplutei. J. Exp. Mar. Biol. Ecol. 96:267–286.

MILLER, R. L. 1985. Demonstration of sperm chemotaxis in Echinodermata: Asteroidea, Holothuroidea, Ophiuroidea. J. Exp. Zool. 234:383–414.

MUNDY, C. N., R. C. BABCOCK, I. ASHWORTH, AND J. SMALL. 1994. A portable discrete-sampling submersible plankton pump. Biol. Bull. 186:168–171.

PERRON, F. E., AND A. J. KOHN. 1985. Larval dispersal and geographic distribution in coral reef gastropods of the genus *Conus*. Pp. 95–100 *in* Proceedings of the fifth international coral reef congress, Tahiti.

PITNICK, S., T. A. MARKOW, AND G. S. SPICER. 1995. Delayed male maturity is a cost of producing large sperm in *Drosophila*. Proc. Natl. Acad. Sci. USA 92:10614–10618.

PODOLSKY, R. D. 1995. Effects of the echinoid egg jelly coat on fertilization through changes in effective egg size. Am. Zool. 35:54A.

PODOLSKY, R. D., AND R. R. STRATHMANN. 1996. Evolution of egg size in free-spawners: consequences of the fertilization-fecundity trade-off. Am. Nat. 148:160–173.

REAKA, M. L. 1979. The evolutionary ecology of life history patterns in stomatopod Crustacea. Pp. 235–259 *in* S. Stancyk, ed. Reproductive ecology of marine invertebrates. Univ. of South Carolina Press, Columbia, SC.

RICE, M. E. 1975. Sipuncula. Pp. 67–127 *in* A. C. Giese and J. S. Pearse, eds. Reproduction in marine invertebrates. Vol. 2. Academic Press, New York.

ROFF, D. A. 1992. The evolution of life histories. Chapman and Hall, New York.

ROUGHGARDEN, J. 1989. The evolution of marine life cycles. Pp. 270–300 *in* M. W. Feldman, ed. Mathematical evolutionary theory. Princeton Univ. Press, Princeton, NJ.

RUMRILL, S. 1987. Predation upon echinoderm embryos and larvae. Ph.D. diss., Univ. of Alberta, Edmonton, Alberta, Canada.

SAS INSTITUTE. 1988. SAS/stat user's guide. Rel. 6.03 ed. SAS Institute, Cary, NC.

SASTRY, A. N. 1979. Pelecypoda (excluding Ostreidae). Pp. 113–292 *in* A. C. Giese and J. S. Pearse, eds. Reproduction in marine invertebrates. Vol. 5. Academic Press, New York.

SCHROETER, S. C. 1978. The role of competition in determining the distribution and abundance of purple sea urchins, *Strongylocentrotus purpuratus* (Stimpson). Ph.D. diss., Univ. of California, Santa Barbara, CA.

SINERVO, B., AND L. R. MCEDWARD. 1988. Developmental consequences of an evolutionary change in egg size: an experimental test. Evolution 42:885–899.

SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. Am. Nat. 108:499–506.

SMITH, R. L. 1984. Sperm competition and the evolution of animal mating systems. Academic Press, Orlando, FL.

STRATHMANN, M. 1987. Phylum Echinodermata, class Echinoidea. Pp. 511–534 *in* M. Strathmann, ed. Distribution and development of marine invertebrates of the northern Pacific Coast. Univ. of Washington Press, Seattle.

STRATHMANN, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annu. Rev. Ecol. Syst. 16:339–361

THOMAS, F. I. M. 1994a. Transport and mixing of gametes in three free-spawning polychaete annelids, *Phragmatopoma californica* (Fewkes), *Sabellaria cementarium* (Moore), and *Schizobranchia insignis* (Bush). J. Exp. Mar. Biol. Ecol. 197:11–27.

———. 1994b. Physical properties of gametes in three sea urchin species. J. Exp. Mar. Biol. Ecol. 194:263–284.

THORSON, G. 1936. Reproduction and larval development of Danish marine bottom invertebrates. Medd. Dan. Fisk. Havunders. Serie Plankton 4:1–523.

———. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25:1–45.

VANCE, R. R. 1973. On reproductive strategies in marine bottom invertebrates. Am. Nat. 107:339–352.

VOGEL, H., G. CZIHAK, P. CHANG, AND W. WOLF. 1982. Fertilization kinetics of sea urchin eggs. Math. Biosci. 58:189–216.

WADDELL, B. J., R. I. PERRY, G. SCHARF, AND G. ROSS. 1997. Surveys on green sea urchin (*Strongylocentrotus droebachiensis*) populations in Queen Charlotte Strait, British Columbia, October 1995 and March 1996. Canadian Technical Report of Fisheries and Aquatic Sciences 2143.

YUND, P. O., AND M. A. MCCARTNEY. 1994. Male reproductive success in sessile invertebrates: competition for fertilizations. Ecology 75:2151–2167.

Corresponding Editor: S. Palumbi