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HOW DISTRIBUTION AND ABUNDANCE INFLUENCE FERTILIZATION SUCCESS IN THE SEA URCHIN *STRONGYLOCENTROTUS FRANCISCANUS*[1]

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Abstract. Many organisms reproduce by releasing gametes into the environment. However, very little is known about what proportion of released eggs become fertilized. We examined the influence of spawning group size, degree of aggregation, position within an aggregation, and water flow, on in situ fertilization in the sea urchin *Strongylocentrotus franciscanus.* This study was conducted at a depth of 9 m on the west coast of Vancouver Island, British Columbia, Canada. Males were simulated by syringes filled with sperm; females were simulated by sperm-permeable containers filled with eggs. Individuals were placed 0.5 or 2.0 m apart within a 2 × 2 or 4 × 4 (group size of 4 or 16 individuals) experimental array. The results indicate that group size, degree of aggregation, position within a spawning group, and water flow all affect fertilization success. Fertilization success ranged from 0 to 82%. Increases in group size and aggregation, decreases in flow velocity, and central and downstream positions within an aggregation all lead to increases in fertilization success. Thus, individual reproductive performance is dependent on, and highly sensitive to, population parameters and environmental conditions.

Key words: Allee effect; density dependence; dispersion; echinoid; fertilization success; field experiment; population size; sea urchin; spawning; sperm limitation; Vancouver Island, Canada; water flow velocity.

INTRODUCTION

The free-spawning of gametes into the environment is a common mechanism of reproduction for many diverse taxa (Giese and Kanatani 1987). After release, sperm can quickly become diluted to a concentration where fertilization becomes unlikely (Pennington 1985, Denny and Shibata 1989, Levitan 1991). If there are situations where a large proportion of eggs are not fertilized, sperm limitation could be an important constraint restricting reproductive success (Mortensen 1938). The idea that sperm limitation can influence in situ fertilization has recently been addressed quantitatively in several taxa (echinoids: Pennington 1985, Levitan 1991, D. R. Levitan and C. M. Young, *unpublished manuscript,* hydroids: Yund 1990, ascidians: Grosberg 1991, fish: C. Petersen, *personal communication*). These studies suggest that fertilization is typically low due to rapid dilution of sperm.

Because fertilization success is dependent on the concentration of eggs and sperm, the distribution and abundance of spawning conspecifics may play an important role in zygote production and reproductive success. Aggregation of conspecifics has been assumed to be an important mechanism increasing the likelihood of fertilization (Pennington 1985, Giese and Kanatani 1987, Levitan 1988, 1991, Pearse et al. 1988). Yet very few studies have investigated the effect of population density on fertilization (but see Levitan [1991]), and no studies have investigated how spatial relationships between spawning organisms influence fertilization.

Most studies to date have examined how fertilization decreases with distance from a sperm source (Pennington 1985, Yund 1990, Grosberg 1991, Levitan 1991, D. R. Levitan and C. M. Young, *unpublished manuscript*) or have attempted to model fertilization success in areas of high turbulence (Denny and Shibata 1989). Here we investigate how the number of spawning individuals and their degree of aggregation influence fertilization success in the sea urchin *Strongylocentrotus franciscanus.* The results indicate that both the distribution and abundance of spawning organisms can have a profound influence on individual reproductive success and that sperm limitation may be a typical condition in many populations. This suggests that the "Allee effect" (negative density dependence, Allee 1931), typically underemphasized by many ecologists, can play an important role in the dynamics of free-spawning populations.

METHODS

Experiments were conducted in March 1990 at the mouth of Bamfield Inlet in Barkley Sound, Vancouver Island, Canada (48°50′30″ N, 125°08′00″ W). Urchins from the site were brought to the laboratory, the test diameter measured, and gametes collected using a 5 mL injection of 0.55 mol/L KCl. KCl injection induces a violent contraction of the gonad musculature and

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results in a release of mature gametes. Several injections were often needed to release all gametes. Thompson (1983) suggests that this technique is the best way to measure gamete production in urchins. Sperm volume was determined, and the sperm kept dry and cool (12°C) to maximize viability. For each experimental replicate (see below), dry sperm from 20 males were pooled and brought to the field in a jar. Eggs from one female were diluted, and ≈25 000 were pipetted into each of 20 plastic containers (66 mm in diameter, 30 mm deep, with 35-μm mesh Nitex covering the base and lid) permeable to sperm. Sealed egg-filled containers were placed in buckets filled with seawater and taken to the field.

We investigated the influence of the distribution and abundance of spawning urchins on fertilization success by varying the number of and distances between egg-filled containers and sperm-filled syringes in an experimental array. The egg-filled containers were placed between a weight and a float and were suspended 15 cm above the substratum. This height approximates the distance above the substratum the gametes would be released in *Strongylocentrotus franciscanus*. We realize that placing eggs in containers introduces experimental artifacts, since eggs are not normally confined. However, this technique has been compared to fertilization of free-drifting eggs and the results indicated comparable absolute values and identical relative values across treatments (Levitan 1991).

Male spawning was simulated by discharging 20 mL of dry sperm from a syringe. This volume of sperm was a typical amount released from urchins when injected with KCl (see *Results*). We realize that KCl-induced spawnings are not identical to natural spawnings; however, at present this is our best estimate of the amount of sperm released naturally (Levitan 1988). In another study (Levitan 1991), fertilization was compared when sperm were released by syringe vs. by a male induced to spawn in situ with KCl. Both methods produce similar fertilization profiles with distance from a sperm source; however, the syringe method eliminates individual male variation (which can be quite high—see *Results* and Levitan [1988, 1991]). In Levitan's (1991) study, a significant effect of population density was noted in spite of the increased variance associated with induced male spawnings. This suggests that individual variation is not so great as to obscure other factors. In the present study, we chose to eliminate this level of variation in order to specifically address the question of how two population parameters, group size and distribution, influence fertilization.

"Females" (egg-filled containers) and "males" (sperm-filled syringes) were alternated and placed in one of two array sizes at two distances between individuals (Fig. 1). This design resulted in spawning group sizes of 4 and 16 individuals (2 × 2 and 4 × 4 array) and nearest-neighbor distances of 0.5 and 2.0 m. The two levels of aggregation could be viewed as two levels of local population density of 4.0 and 0.25 urchins/m², but this is dependent on the measure of area arbitrarily chosen.

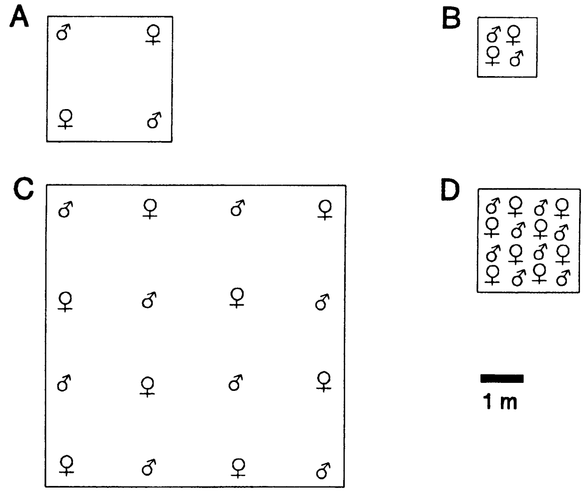

FIG. 1. Experimental design for the field experiment. Two levels of spawning-group size and degree of aggregation: (A) small dispersed group, (B) small aggregated group, (C) large dispersed group, and (D) large aggregated group. The nearest-neighbor distance between "males" and "females" was 0.5 and 2.0 m for the aggregated and dispersed populations, respectively. Dispersed and aggregated treatments can be considered density treatments (of 0.25 and 4 "individuals"/m²) when the corresponding area changes with the degrees of aggregation. "Male" symbols indicate placement of sperm-filled syringes; "female" symbols indicate placement of egg-filled containers.

Gamete arrays were placed at a depth of 9 m on a cobble- and sand-covered horizontal shelf that was bordered on the shallow side by a rocky boulder field covered with the kelp *Macrocystis*, and on the deep side by a gradually steepening sandy slope. The arrays were spaced 30 m apart along the shelf, with their position varying randomly each day. Individually numbered egg-filled containers were first placed in each array. Sperm (20 mL) were then released up into the water column from syringes in the male positions, at a 15 cm height, within each array. All sperm within each array were released within 1 min. Care was taken to create as little disturbance as possible during the release of sperm. All four array types were run within 15 min. The egg-filled containers remained in position for 30 min. This time period was chosen since dilute sperm from *S. franciscanus* have a half-life of <20 min (Levitan et al. 1991). Additionally, fertilization generally occurs within the first few seconds of immersion within a sperm plume (Levitan et al. 1991). After the sperm were released, flow direction and velocity were visualized by releasing a plastic bag filled with seawater and enough sand to achieve neutral buoyancy. Flow velocity was estimated as the mean distance travelled during 1 min at 10 to 50 cm above the substrate (up to four replicate flow estimates per time period).

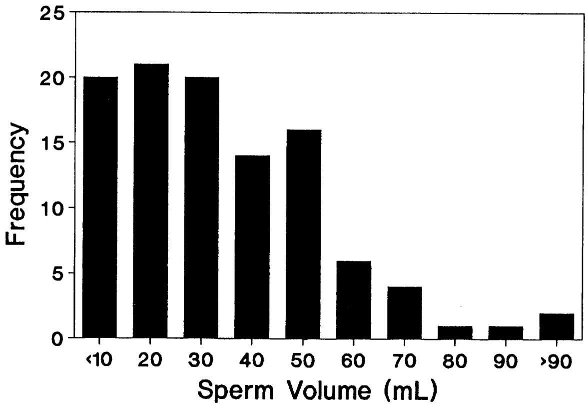

FIG. 2. Frequency distribution of the volume of sperm released by male *Strongylocentrotus franciscanus* injected with KCl.

TABLE 1. *Strongylocentrotus franciscanus*; Two-way analysis of covariance testing percentage fertilization (arcsine-transformed); main effects were spawning-group size and degree of aggregation, with current velocity as the covariate. Each datum is the average fertilization for each treatment application (five replicates × four treatments = 20).

Source of variation	df	SS	MS	*F*	*P*
Covariate					
Current	1	0.226	0.226	16.015	.001
Main effects					
Group size	1	0.156	0.156	11.061	.005
Distance	1	0.209	0.209	14.786	.002
Group × distance	1	0.005	0.005	0.355	.566 NS†
Error	15	0.212	0.014		
Total	19	0.808			

† NS = not significant.

At the end of the 30-min interval, egg-filled containers were collected and returned to buckets filled with clean seawater (i.e., collected before the sperm were released). A separate bucket was used for each treatment. Eggs were incubated in the laboratory for 3 h before a subsample of 250 eggs per container was investigated for the presence of a fertilization membrane or further developmental stages. Data were expressed as percentage fertilized and were arcsine-transformed for statistical analysis. Replicates of the experiment were conducted on five separate days.

RESULTS

Laboratory spawning

Over 200 urchins were injected with KCl; 52% of the urchins were male. This percentage did not differ significantly from a 1:1 sex ratio ($\chi^2 = 0.22$, 1 df, $P > .6$).

The volume of sperm released following KCl injection was 30.2 ± 22.5 mL ($\bar{X} \pm$ SD, Fig. 2). This is equivalent to $\approx 3.0 \times 10^{11}$ spermatozoa released per spawning event (cf. 10^{10} sperm/mL from hemocytometer counts—Levitan et al. 1991). Most of the sperm were released during the first few minutes, but small amounts were occasionally extruded after two hours. The three most frequently occurring size classes of sperm release were 0–10, 10–20, and 20–30 mL, with a median value of 28 mL. There was no significant relationship between the amount of sperm released and male body size over the size range examined (Fig. 3).

In the field experiment, we released slightly less sperm than the median value determined above (20 vs. 28 mL). Although fertilization is relatively insensitive to the amount of sperm released from a single point source (Levitan 1991, D. R. Levitan and C. M. Young, *unpublished manuscript*), our underestimate of sperm release might result in slightly lower fertilization than more massive releases.

Field experiment

A two-way analysis of covariance tested percentage fertilization (arcsine-transformed) with spawning-group size and degree of aggregation as the main effects, and current velocity as the covariate. Results indicated that both the main effects and the covariate were highly significant (Table 1). Fertilization success increased with an increase in spawning-group size and degree of aggregation (Fig. 4) and a decrease in current velocity (Fig. 5). "Females" that were downstream or in the center of a spawning group had higher fertilization success as compared to upstream or peripheral females (Fig. 6). These positional effects were less pronounced in aggregated populations (Table 2). The highest single measurement of fertilization was 82.2%, found in the center of a large aggregated group; the lowest measurement was 0%, found on the upstream side of a small dispersed group. The overall mean fertilization was 18.3% for all arrays combined.

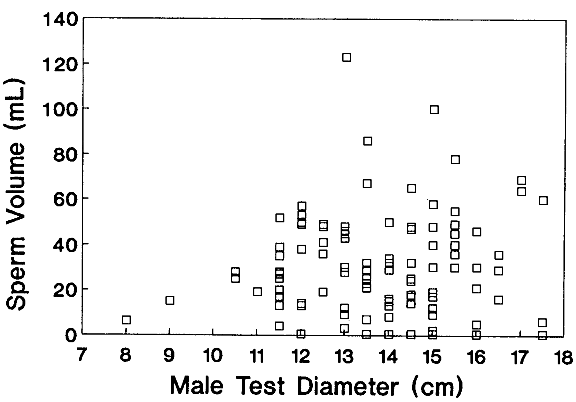

FIG. 3. Relationship between male test diameter and the volume of sperm released by adult *Strongylocentrotus franciscanus*. Regression was non-significant ($R^2 = 0.025$, $P > .62$, $N = 105$).

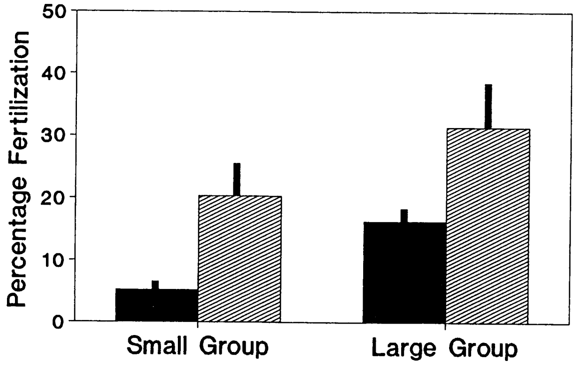

FIG. 4. Percentage of eggs fertilized as a function of spawning-group size and degree of aggregation. Solid bars are dispersed treatments; hatched bars are aggregated treatments. Mean and standard error are plotted ($N = 5$).

TABLE 2. Positional effects on percentage fertilization in *Strongylocentrotus franciscanus*. There were five replicates. Up- and down-current positions are divided into two even groups; center and periphery positions are divided into the center two and peripheral six positions; see Fig. 1 for arrays. Unequal sample sizes in the large arrays are due to containers in which eggs were lost.

	Up	Down	Center	Periphery
A) Small dispersed	1.7	8.7	…	…
SE	1.2	4.6		
N	5	5		
B) Small aggregated	20.6	20.0	…	…
SE	6.7	6.5		
N	5	5		
C) Large dispersed	12.4	20.2	23.7	14.1
SE	2.7	3.1	4.2	2.4
N	18	19	9	28
D) Large aggregated	27.3	35.8	38.8	29.2
SE	4.9	4.8	8.6	3.6
N	19	20	10	29

DISCUSSION

Water flow and sperm dilution

Fertilization decreased with increasing water flow, due to the rapid dilution of sperm. This result has been consistently found in other in situ studies of fertilization success with unidirectional flow. At a distance of 1 m from a sperm source, fertilization success was estimated to be as follows: At slack water, Yund (1990) found fertilization to be >80%. In gentle wave surge and current velocities <0.01 m/s, Levitan (1991) estimated fertilization to be 20–40%. At current velocities of <0.2 m/s, Pennington (1985) measured fertilization to be 20% and at velocities >0.2 m/s, fertilization was 5%.

In the present study, with unidirectional water flow from 0.002 to 0.047 m/s, and in another study (D. R. Levitan and C. M. Young, *unpublished manuscript*) with unidirectional water flow from 0.06 to 0.12 m/s, a significant inverse relationship was found between flow and fertilization success. The very low fertilization success predicted by Denny and Shibata (1989) was due to the highly turbulent flow conditions they modeled (velocities up to 5 m/s). Care must be taken, therefore, when extrapolating results from fertilization experiments or models to other environments with different flow conditions.

Fertilization can drop from 100 to 0% over a two to three order decrease in the magnitude of sperm concentration (Vogel et al. 1982, Pennington 1985, Levitan et al. 1991). Laboratory studies with *Strongylocentrotus franciscanus* determined that fertilization dropped from 80 to 3% with a decrease in sperm concentration from 10^4 to 10^2 sperm/mL (Levitan et al. 1991). Evidence from the field suggests that, as a consequence of dilution over time, fertilization success declines quickly several metres away from a sperm source (Pennington 1985, Yund 1990, Grosberg 1991, Levitan 1991, D. R. Levitan and C. M. Young, *unpublished manuscript*). In the Bahamas, under a current regime similar to the present study, *Clypeaster rosaceus* sperm concentration decreased five orders of magnitude in the short time it took the sperm plume to travel 2 m (D. R. Levitan and C. M. Young, *unpublished manuscript*). Denny and Shibata (1989) estimated even higher dilution effects in their model for wave-swept shores. They predicted that under these conditions, increases in population density would have little impact on reproductive success, since dilution was so great that only males several centimetres apart from a female would have any influence on fertilization. In turbulent flow and a unidirectional current, they estimated that 100 males placed at 1-cm intervals up-

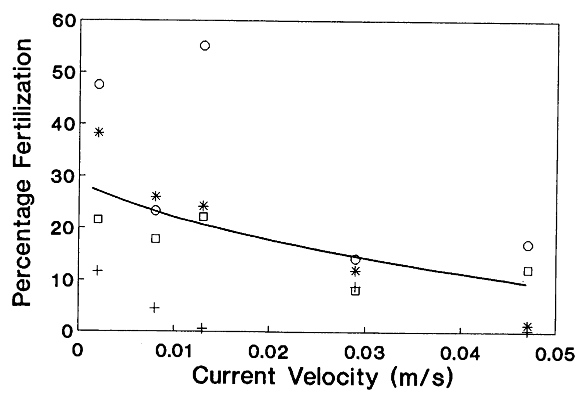

FIG. 5. Percentage of eggs fertilized as a function of current velocity. Symbols represent each treatment group: ○ = aggregated large and * = aggregated small populations; □ = dispersed large and + = dispersed small populations. Regression is of mean percentage fertilization (treatments pooled for each time period) plotted against average current velocity for each experimental time period. Regression equation: fertilization (%) = exp(−29.354 × current velocity + 3.367); $R^2 = 0.88$, $P = .0002$.

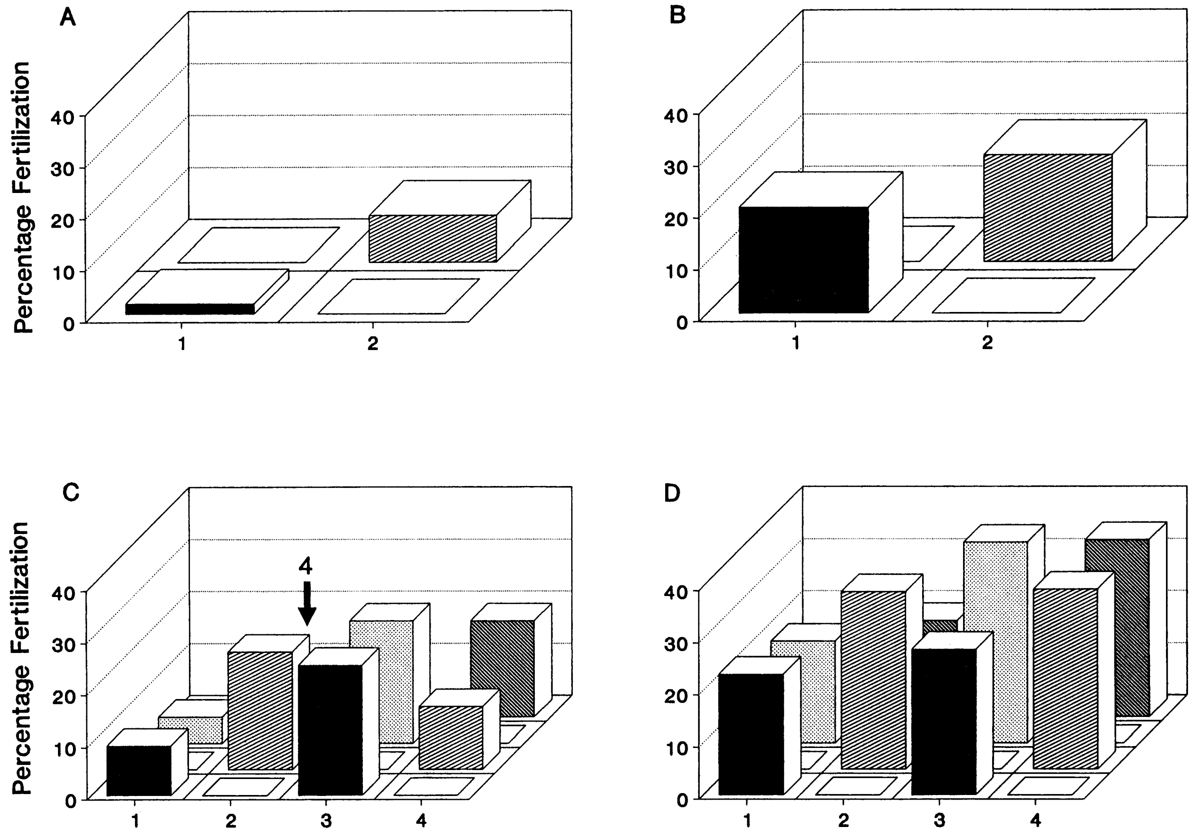

FIG. 6. Positional effects on fertilization in the four treatment groups. Current flow is from left to right. Histograms indicate spatial patterns of arrays. Bars indicate "female" positions (mean response), and positions with 0% fertilization indicate "male" positions. (A) Small dispersed group. (B) small aggregated group. (C) large dispersed group (arrow indicates 4% fertilization of hidden bar in back row). (D) large aggregated group.

stream from a single female would only result in a fertilization success of 2–3%. The present study suggests that under normal flow conditions associated with the spawning season of *S. franciscanus* on the west coast of Vancouver Island, the number and distribution of spawning conspecifics can have an important impact on fertilization.

Distribution, abundance, and the Allee effect

The results of this study clearly indicate the importance of population parameters on individual reproductive success. An individual in the center of a large spawning aggregation has been shown to have greater reproductive success compared to other individuals at more distant positions or involved in smaller spawning events. Individual fertilization success ranged from 0 to 82% depending on the number of spawning individuals, degree of aggregation, individual position in relation to the spawning group and flow, and flow velocity. The wide range of results suggests that individual fertilization success is very sensitive to changes in population parameters and environmental conditions.

Strongylocentrotus franciscanus is abundant in the shallow subtidal zones of the Pacific Northwest. In Barkley Sound density averages 6.8 urchins/m^2 (range 0–50 urchins/m^2, J. Watson, *unpublished data*). Based on our data and assuming synchronous spawning, *S. franciscanus* in this area may experience fairly high, but not complete, fertilization success. In other areas where this urchin is less dense (J. Watson, *personal communication*), fertilization success could be much reduced and present a major bottleneck limiting the production of larvae. Less abundant species that freely spawn gametes into the environment may be severely constrained by sperm limitation and may lead to recruitment limitation in some marine populations.

Both the number and distribution of spawning individuals influenced fertilization. Behavioral modifications can affect the distribution, but not the number of individuals; a small number of rare organisms may clump, but population size will still be small, thus limiting fertilization success. The costs associated with spawning at low population density or in a small population represent a form of the "Allee effect" (Allee 1931). This effect, also known as negative density dependence, leads to reduced population growth and possible local extinction.

Historically the Allee effect has been underemphasized in ecological studies, while positive density-dependent factors have received much attention (e.g., studies of intraspecific competition). This may be due to the influence of terrestrial ecologists studying animals with internal fertilization (noting that plant ecologists have recognized the importance of pollen limitation for several years; e.g., Schemske et al. 1978, Willson et al. 1979, Schemske 1980, Weller 1980, Bierzychudek 1981). For organisms with internal fertilization, difficulties in finding a mate may not represent a severe problem, except in the most sparse populations (acknowledging that unsuccessful matings can occur at all densities and population sizes). However, for organisms with external fertilization, finding a suitable mate does not ensure mating success. Even in relatively large aggregations with synchronous spawning, a large percentage of viable eggs are not fertilized, due to sperm limitation (Fig. 7). The Allee effect may be important in marine, freshwater, and many plant populations.

Unfortunately, the propensity for ecologists to concentrate on positive density dependence has carried over into marine and aquatic systems, where a large proportion of organisms exhibit external fertilization (see Strathmann [1990] for a comparison of terrestrial and aquatic reproduction). These studies provide excellent accounts of how increased population density results in decreased body size, reduced gamete production, and/or increased mortality (e.g., Harger 1970, Sutherland 1970, Menge 1972, Paine 1976, Keller 1983), but do not address the problem of gamete dilution and fertilization success. A rare study (Suchanek 1981) that mentions fertilization success predicts that larger individuals at low density produce 90-fold more offspring than smaller individuals at high density, *assuming* equal fertilization. The present study suggests that assuming equal fertilization probabilities when population density is unequal may not be valid.

The trade-off between increases in intraspecific competition and fertilization success (positive and negative density dependence) as population density increases has been investigated in the sea urchin *Diadema antillarum* (Levitan 1991). In that study the cost of reduced gamete production due to intraspecific competition was balanced by increased gamete fertilization. At high densities, average body mass was an order of magnitude smaller than at low density, yet individual zygote production was estimated to be similar across densities.

The present study indicates the importance of population parameters and flow conditions on fertilization. We still need to know a great deal more about synchrony in spawning, patterns of gamete dispersal, and the fate of zygotes in the field. Accurate estimates of these parameters are needed to determine the fecundity and settlement success of free-spawning organisms and to compare this mode of reproduction to other life history strategies.

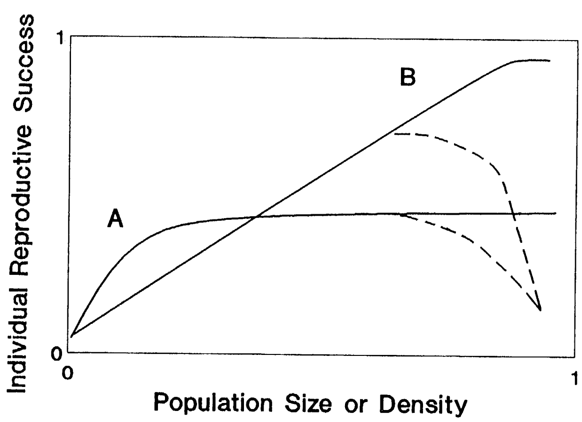

FIG. 7. The "Allee effect" and its application to organisms with internal and external fertilization. (A) An internally fertilizing organism. At low density or population size, difficulty in mate-finding results in reduced reproductive success. When mates are no longer limiting, reproductive output remains constant unless density-dependent processes limit survivorship or gamete production (– – –). (B) An externally fertilizing organism. Reproductive output continues to increase until all eggs are fertilized or unless density-dependent processes limit survivorship or gamete production (– – –).

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