

Influence of Body Size and Population Density on Fertilization Success and Reproductive Output in a Free-Spawning Invertebrate

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Abstract. Gamete production and fertilization influence zygote production. While gamete production is correlated positively with body size, individual fertilization success may be a function of population density. Usually it is assumed that when high population density leads to reduced body size and gamete production, per capita zygote production is diminished. This field study of the sea urchin *Diadema antillarum* Philippi provides a test of this assumption. Three experiments were conducted to determine the effect of male spawning on fertilization success. In the first experiment, unfertilized eggs were placed in Nitex bags at three distances up and downstream from a spawning male. In the second experiment, unfertilized eggs were released and captured at three distances downstream from a sperm source. In both experiments, fertilization decreased with distance from the sperm source. The final experiment tested the influences of male size and population density on fertilization success; the effect of density was significant, but size was not. A simple model estimates the average number of zygotes produced by females of average size under different density regimes: at high population density, increased fertilization success can compensate for decreased gamete production. Small individuals at high population density may have similar per capita zygote production as large individuals at low population density. Thus, estimates of reproductive output based on body size or gamete production alone can be misleading.

Introduction

One of the major generalizations in population biology is that, within a species, larger body size confers greater

reproductive success (Williams, 1975). This generalization is based, in part, on evidence indicating that body size and gamete production are directly proportional (*e.g.*, Vertebrates: Bagenal, 1966; Invertebrates: Paris and Pitelka, 1962; Rinkevich and Loya, 1979; Suchanek, 1981; Angiosperms: Sarukhan, 1980; Algae: Vernet and Harper, 1980). However, estimating zygote production, or more generally reproductive success, from gamete production alone can be inappropriate and misleading. If gametes are shed into the surrounding medium, fertilization success, and thus zygote production, can be profoundly influenced by the abundance and behavior of conspecifics. While gamete production is correlated positively with body size, individual fertilization success may be a function of population density (discussed by Mortensen, 1938; Thorson, 1946; Denny and Shibata, 1989; Strathmann, 1990; empirical evidence provided by Pennington, 1985). An individual spawning a large number of gametes in isolation has poor reproductive success; yet estimates of fecundity (production of offspring) are generally based on gamete number or gonad size (*e.g.*, Paine, 1969; Sutherland, 1970, 1972; Branch, 1975; Wu, 1980; Suchanek, 1981; Jackson, 1985). The ecological and evolutionary interpretation of these data can be misleading if the significance of fertilization success is ignored.

Estimating fecundity from body size or gamete number can be particularly misleading when organisms exhibit an inverse relationship between body size and population density (*e.g.*, plants—Harper, 1977; animals—Paine, 1969; Sutherland, 1970, 1972; Branch, 1975; Wu, 1980; Suchanek, 1981; Lawrence and Lane, 1982; Sebens, 1983a). In such cases, there may be an important trade-off between (a) large size with high individual gamete production at low population density, and (b) smaller size

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with lower gamete production at higher population density. An inverse relationship between size and density may be a result of resource limitation or other factors such as variation in recruitment and survivorship (Sebens, 1983b). Regardless of the mechanism, if body size is inversely related to population density, and density is important to fertilization success, then body size alone is a poor predictor of zygote production. If a gain in fertilization success balances the cost of reduced gamete production, then small organisms living at high population density may be just as fecund as large organisms living at low population density.

This study provides empirical evidence on the relative influence of male body size and population density on fertilization success and fecundity in the sea urchin *Diadema antillarum*. Because an inverse relationship between mean body size and population density has been documented for *Diadema* (St. Croix—Carpenter, 1981; Barbados—Hunte *et al.*, 1986; St. John—Levitan, 1988a), it is possible that small urchins at high density would have average per capita zygote production similar to large urchins at low density. I first determine an appropriate method for a field assay of fertilization success in free-spawning invertebrates, and then examine the relative influence of male body size and male population density on the fertilization of eggs. Finally, I present a model and its assumptions to calculate the average number of zygotes being produced by females at various population densities.

Materials and Methods

Determination of fertilization success

Fertilization success was assessed by two techniques during the summer of 1988 at Lameshur Bay, St. John, U.S. Virgin Islands. The first experiment investigated the effects of distance, flow, and current direction on fertilization success. A large male urchin (65–70 mm test diameter) was placed subtidally in 4–6 m of water. The direction and speed of the water flow was determined by releasing fluorescein dye 15 cm off the bottom with a syringe and recording the time taken for the center of the cloud to move 1 m. Nitex bags (35 micron mesh), 5 × 3 cm in size, were filled with 0.5 ml of unfertilized eggs (approximately 10⁶ eggs) and placed upstream and downstream from the urchin at 1, 3, and 5 m distances (one bag at each distance). The bags, held between a weight and a float, were suspended 15 cm above the bottom. The mesh size of the bags was small enough to hold the 80–100 micron eggs, yet large enough to allow sperm (sperm head approximately 3 microns; Harvey and Anderson, 1943) to enter the bags. The male urchin was then injected with 0.5 M KCl to induce spawning. After 20 min, the egg bags were collected and rinsed in seawater. Two hours after the field work, 250 eggs from each bag were inspected

in the laboratory for the presence of a fertilization membrane. The experiment was replicated ten times.

In the second experiment, I investigated fertilization success of free-drifting eggs. Sperm and eggs were collected less than 1 h before experiments were conducted by injecting urchins with KCl and then collecting the released gametes with a pipet held directly above the gonopores. Sperm were kept in concentrated form (dry) and the eggs were placed in a 300 ml jar filled with seawater to maximize viability. Samples of eggs were fertilized with sperm, just prior to and directly after the experiments, as a control for gamete viability. All controls with sperm were over 99% fertilized and without sperm were 0% fertilized. A syringe filled with 3.0 ml of dilute eggs (approximately 3 × 10⁶) and another filled with 1.5 ml of concentrated sperm (approximately 3 × 10¹⁰—Tyler *et al.*, 1956) were taken to a sandy bottom (4–6 m). The speed and direction of water flow were measured with fluorescein dye as described above. The syringe containing sperm was placed next to a syringe containing fluorescein dye; both were held 15 cm above the bottom. At either the 0.1, 1.0, or 3.0 m downstream interval, the syringe containing eggs was held 15 cm above the bottom. Directly downstream of the egg syringe was a 35 micron mesh plankton net (mouth opening diameter: 0.5 m, 300 ml glass jar at terminal end). The sperm and fluorescein dye were released simultaneously. When the edge of the dye cloud passed over the egg syringe, the eggs were released; 1 min later, the plankton net was brought to the surface. Within 30 s, the egg samples were poured over 35 micron mesh Nitex and rinsed with seawater to remove excess sperm. The eggs were re-suspended in seawater, fixed in formalin (after 2 h), and assayed for the presence of a fertilization membrane (250 eggs per sample). The experiment was replicated five times.

Population density and body size

A field experiment to test the effect of male size and population density on fertilization was conducted between February and August 1986, in Lameshur Bay. There was no apparent unidirectional current, and wave surge was minimal. Urchins from one of three size classes (40–50, 50–60, 60–70 mm test diameter) were haphazardly placed in subtidal arenas at one of three population densities (1, 4, 16 males/m²). This size range represented 78% of the 1986 population structure (Levitan, 1988b). The range of population density was 6–20 urchins/m² before and 0.2–0.7/m² after the 1983 mass mortality of *Diadema* (Levitan, 1988a,b; Karlson and Levitan, 1990). Arenas were placed 15 m apart on a natural sand bottom at a depth of 4–6 m. An arena is simply an area of bottom defined by four egg-containing Nitex bags placed in a square. The urchins were injected with 0.5 M KCl to induce spawning. If an

Table I

Effect of distance, up and down stream position, and current velocity on the percentage (arcsine transformed) of eggs being fertilized

SV	DF	SS	MS	F
Distance	2	0.455	0.228	
Position	1	0.051	0.051	
Current	1	0.052	0.052	14.28***
Interaction	2	0.005	0.002	3.19 NS
Error	53	0.844	0.016	3.23 NS
Total	59	1.406		0.14 NS

*** = $P < .001$, NS = not significant.

Eggs were held in Nitex bags. Analysis of covariance with two main effects; distance between urchin and bags, and up-current or down-current position. The current velocity was the covariate.

urchin did not spawn or if it was female, it was replaced. All urchins, within an arena, were induced to spawn within 1 min. Control arenas with no males were used to check for ambient sperm in the water. Spawning lasted approximately 5 min. After 20 min, the egg bags were collected and rinsed in seawater. Within 2 h, 250 eggs per bag were assayed for the presence of a fertilization membrane. The 4 Nitex bags per arena were pooled to give 1000 eggs per replicate. There were 8 to 12 replicates for each level of male size and density. One set of replicates (3 male sizes \times 3 male densities) was attempted each day.

Arenas, in the above experiment, were 1 m² at low density and 0.25 m² for medium and high density treatments (*i.e.*, 1 urchin per arena at low density, 1 and 4 urchins per arena at medium and high density). This was done because it was impossible to place $\frac{1}{4}$ of an urchin in the small arena and impractical to place (and spawn within the experimental time frame) 16 males in a large arena. Although both methods (varying urchin number and area) are true density manipulations, this design confounds the effect of number and distance between males and eggs at the low and medium densities. In another study (Levitan *et al.*, 1991), the relative influence of varying urchin number and distance was examined. The results suggest that both factors are important. When a few rare organisms clump, and spawn, the probability of fertilization increases slightly. When many organisms are at high density, and spawn, the probability of fertilization increases greatly. Thus, the use of a small number of spawning urchins underestimates the importance of any density effect noted.

Results and Discussion

Determination of fertilization success

At the low flow recorded in Lameshur Bay (0.009, SE = 0.003 m/s), current speed did not have a significant

effect on fertilization success. Furthermore, fertilization success was not significantly different in up-current and down-current positions at the same distances (Table I). Diffusion and wave surge exposed the sperm to both up-current and down-current egg bags. Perhaps at higher current speeds these effects would be important. Yund (1990) also found no difference between up-current and down-current rates of fertilization in hydroids during periods of slack tide. Pennington's (1985) study indicated that current speeds greater than 0.2 m/s decreased fertilization success. An inverse relationship between flow and percent fertilization was also noted in *Strongylocentrotus franciscanus* (Levitan *et al.*, 1992). Recent models indicate that high turbulence quickly dilutes gametes below the concentration where fertilization is likely (Denny, 1988; Denny and Shibata, 1989).

The distance from the egg bags to the male urchin had a significant effect on fertilization success (Table I). This result, also seen in the work of Pennington (1985) and Yund (1990), reflects a dilution of sperm as it diffuses over larger volumes. It is not due to advection, because a similar fertilization profile occurred in both directions. This result was compared with the free-drifting egg experiment (Fig. 1) and indicates that this latter experiment also had a significant distance effect (Table II). Over comparable distances, the free-drifting eggs had 2.7 times the fertilization rate of eggs held in Nitex bags (2.75 and 2.62 times greater at 1 and 3 m, respectively). However, the amount of sperm released was 3.6 times greater in the drifting egg experiment (an average of 0.42 ml for 67.5 mm urchins *versus* 1.5 ml released by syringe).

Both the Nitex bag and the free-drifting egg experiments might have artifacts associated with the methods that affect fertilization success. With Nitex bags, the presence of the

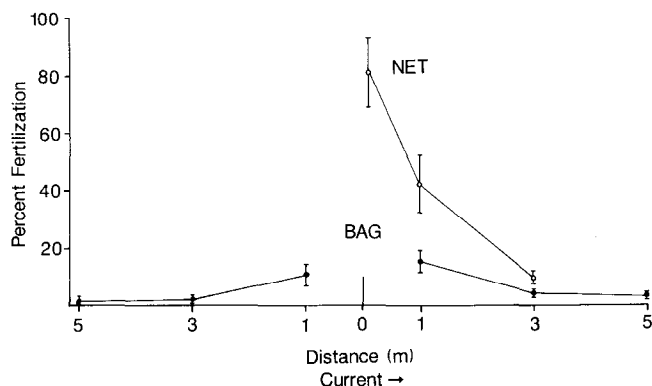


Figure 1. Relationship between percent fertilization and distance from a sperm source. Closed symbols represent eggs held in Nitex bags; open symbols represent free drifting eggs collected in a plankton net. On average, the plankton net experiment used 3.6 times the amount of sperm as the bag experiment. Water current flows left to right. Means and standard errors are plotted.

Table II

Percent (arcsine transformed) eggs fertilized in free-drifting eggs

SV	DF	SS	MS	F
Distance	3	2.081	1.041	13.60**
Current	1	0.020	0.020	0.26 NS
Error	11	0.842	0.076	
Total	14	2.975		

** = $P < .01$, NS = not significant.

Analysis of covariance with one main effect; distance between released eggs and sperm. The current velocity was the covariate.

mesh impedes the flow through the containers, while holding the eggs stationary increases the amount of water and sperm sampled by eggs. With the free-drifting eggs, the release of gametes through syringes might increase estimates of fertilization because the sperm were extruded at a high rate (Denny and Shibata, 1989) and the eggs were released and captured in the center of the passing sperm plume. If, on balance, the Nitex method underestimates fertilization and the free-drifting method overestimates fertilization, then Figure 1 represents the upper and lower bounds of actual fertilization success at these current velocities. Most importantly, finding the same pattern of decreasing fertilization success with distance, using different techniques, provides the robust conclusion that relative fertilization rates can be assayed in the field. The Nitex bag method is convenient, and provides a clear relative measure of fertilization success.

Population density and body size

Over natural ranges of population density and body size, male population density had a highly significant effect on the percent of eggs fertilized, while male body size had no significant effect on the percent of eggs fertilized (Table III). The ranges of the two factors were 47-fold for size (measured as a function of gonad volume; see Levitan, 1989, for body and gonad size regression) and 16-fold for density. Thus, even though the experiment varied individual size more than density, male size did not significantly influence fertilization. The mean percent fertilization measurements (size classes pooled for each male density) were 0.1, 7.3, 18.0, and 45.0% for 0, 1, 4, and 16 males/m², respectively (Fig. 2). Density was manipulated in two ways, by varying area between low and medium density, and varying urchin number between medium and high density treatments. Both manipulations resulted in significant differences (all three densities were different from one another; 95% confidence interval test). This suggests that both the number and distribution of point sources of sperm release are important factors in fertilization success.

Table III

Effect of population density and body size on the percentage of eggs being fertilized

SV	DF	SS	MS	F
Density	2	8389.82	4149.91	57.20***
Size	2	399.38	199.69	2.72 NS
Interaction	4	227.85	56.96	0.78 NS
Error	84	6160.52	73.34	

*** = $P < .001$, NS = not significant.

Two-way ANOVA of arcsine transformed data (percent fertilization). Factors were male density and male body size.

The finding that male size had no effect on fertilization can be related to the distribution of sperm sources. Sperm dilutes quickly over the two-dimensional area inhabited by urchins as it disperses through the three-dimensional volume of water. The number and position of sperm sources may be more important than the amount of sperm released from any given source. Another possibility involves the high variance associated with gamete production in male *Diadema* (Levitan, 1988c). In that study, KCl injections were made in the same manner but on a slightly larger size range of urchins (30–80 mm test diameter) than the present study. The results indicated a significant positive relationship of sperm release to body size with high variance ($\log \text{gametes} = \log \text{size } 2.30 - 4.58$, $R^2 = 0.10$, $n = 134$).

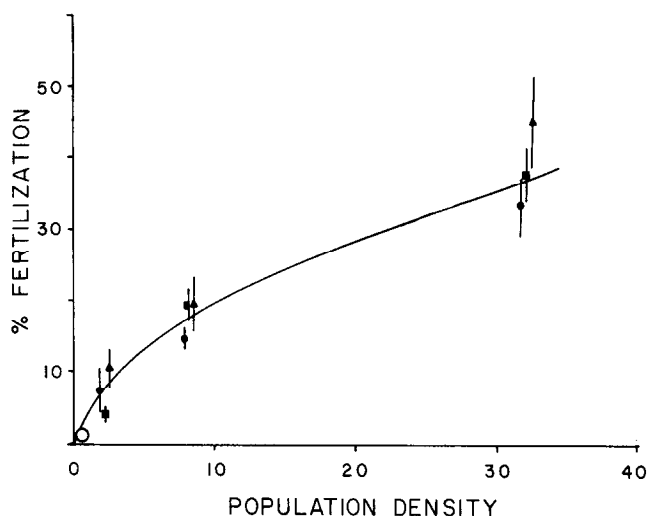


Figure 2. Relationship between population density of *Diadema* and percent fertilization of eggs. Population density is graphed as two times the male density, since the sex ratio of *Diadema* in Lameshur Bay was 1:1. The mean value and standard error are shown for each body size at each density ($n = 8-12$ for each value). Circles, squares, and triangles are 40–50, 50–60, and 60–70 mm test diameter urchins, respectively. The large circle is the control with no urchins. Regression calculated from individual data points; $\log \text{percent fertilization} = 0.72 \log \text{density (m}^{-2}) + 0.49$, $R^2 = 0.72$, $P < 0.0001$, $n = 96$.

Zygote production model

Percent fertilization was estimated rather than total number of fertilized eggs produced per individual. Below is a model that estimates average individual zygote production for average-size individuals at different population densities. This model provides information on the relative zygote production of individuals from different populations. It does not estimate differences between individuals within a spawning event.

Estimates of zygote production of average-size females at different densities were made from the following equations. Average female size at a specific density was estimated by:

log body size (mm)

$$= -0.28 \log \text{ population density (m}^{-2}\text{)} + 1.87,$$

$$R^2 = 0.79, P < .001, n = 7 \text{ sites,}$$

(Lameshur Bay field distribution; Levitan, 1988a). (1)

The expected number of eggs released into the water by spawning females was estimated by:

$$\log \text{ volume of eggs (ml)} = 3.56 \log \text{ size (mm)} - 6.59,$$

$$R^2 = 0.35, P < 0.001, n = 74 \text{ (1 ml of eggs} = 2.1$$

$$\times 10^6 \text{ eggs, from Levitan, 1988c). (2)}$$

Average zygote production was estimated by calculating the percent of the released eggs fertilized at that specific density:

$$\log \text{ percent fertilization} = 0.72 \log \text{ density (m}^{-2}\text{)}$$

$$+ 0.49, R^2 = 0.72, P < 0.0001, n = 96. \text{ (Fig. 2). (3)}$$

This relationship and the variance associated with this calculation are plotted in Figure 3.

Figure 3 indicates a surprisingly even trade-off between gamete production and gamete fertilization with increasing density. Small individuals at high density, on average, produce a similar number of zygotes as larger individuals at low density. The model indicates that decreased fertilization success can offset increased individual gamete production of large individuals at low population density.

Model assumptions

Generalizing from this model to actual spawning events should be done with caution, and involves the following assumptions: (1) synchrony of spawning and the pattern of dispersion during spawning are independent of population density, (2) different size urchins at different densities spawn in the same manner and frequency, (3) there is no competition for sperm by eggs, and (4) survivorship of adult urchins is size-independent (to generalize beyond one spawning event).

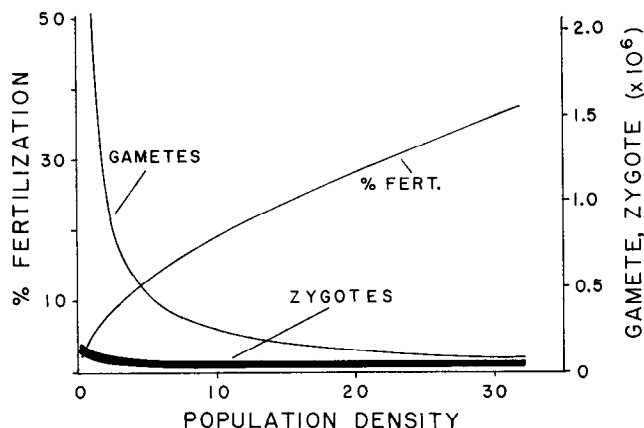


Figure 3. Trade-off between gamete production of average-size females (gametes) and gamete fertilization (% fert.). "Gametes" is calculated as the mean number of eggs being released into the water by a mean-size female urchin at that density (body size determined by equation 1, the amount of gametes released by that size female determined by equation 2). "% Fert." is calculated as the mean percent of eggs fertilized at that density (equation 3, Fig. 2). "Zygotes" is calculated as the product of "Gamete" and "% Fert.," and is plotted (by the thickness of the line) as the 95% CI calculated from the variance of the two regression lines [$SE \log \text{ zygotes} = (\text{variance} [\log \text{ gametes}] + \text{variance} [\log \text{ percent fertilized}])^{0.5}$].

The first assumption involves the distribution and synchrony of spawning urchins and how this varies under different density regimes. Patterns of spawning synchrony and aggregation were investigated in Lameshur Bay following the mass mortality of *Diadema* (discussed below) when population density was relatively low (Levitan, 1988c). Spawning was weakly linked to the lunar cycle and occurred sporadically on all but the last five days of the lunar month. The degree of aggregation did not change over the lunar cycle and nearest neighbor distances (average of 75 cm) did not change as a function of reproductive readiness. Over 100 observations of *Diadema* spawnings indicate that individuals generally spawned alone [*i.e.*, no other urchins spawning within sight (5–10 m); Levitan, 1988c; pers. obs.]. On the one occasion, I observed two individuals spawning in contact with one another, they were both male. Thus, although a nearest neighbor distance of 75 cm is closer than expected by chance (random distribution would be 130 cm—Levitan, 1988c), the likelihood of two neighbors spawning at the same time was only 5% (Levitan, 1988c). Further, there is only a 50% chance that the nearest neighbor is of the opposite sex. This suggests that the model overestimates fertilization success at low density.

Published data also exists for *Diadema* in Lameshur Bay previous to the mass mortality, when density was 13/m² (Randall *et al.*, 1964). This is consistent with later estimates of 14/m² in Lameshur Bay the year before the mass mortality (Levitan, 1988a, b). Randall and his col-

leagues suggested that *Diadema* were aggregated independent of spawning activities (see also Pearse and Arch, 1969) and often had spines touching. They observed 13 spawning events: 10 were individuals spawning alone and 3 were small group spawnings (4–10 individuals with spines touching). The pattern of spawning was again weakly associated with the lunar cycle (significance test by Iliffe and Pearse, 1982). The evidence suggests that the pattern of spawning and aggregation does not change over a range of densities. If small group spawnings and occasional large spawning aggregations were more common at high density, this would only magnify the influence of density on fertilization success (*i.e.*, if spawning pheromones are effective only above a critical concentration), and increase the importance of a trade-off between gamete production and fertilization as suggested by the model. Low *Diadema* population density is not just an artifact induced by the mass mortality. Population density previous to the mass mortality varied widely and regionally ($0.04\text{--}25.8/\text{m}^2$: Bauer, 1980; $< 1\text{--}72/\text{m}^2$: Hay 1984).

The second assumption concerns size-dependent spawning. Experimental density manipulations indicated that body size is a good predictor of gonad volume and gamete release across densities (Levitan, 1989). There is also no influence of body size on the likelihood of spawning when injected with KCl (Levitan, 1988c). Whether this also holds true for natural spawning events is unknown and would be very difficult to establish. However, there is no evidence to date that suggests that these patterns vary with body size or population density.

The third assumption concerns the influence of egg number on fertilization success. Laboratory studies of *Strongylocentrotus franciscanus* conducted by placing eggs in small vials that would enhance sperm competition found no evidence of decreasing fertilization, at a constant sperm concentration, when egg number was increased 800% (Levitan *et al.*, 1991). Levitan *et al.*, using a fertilization kinetics model (Vogel *et al.*, 1982), also demonstrated that fertilization was insensitive to egg number at the concentrations likely to be found in the field.

The final assumption concerns relative survivorship patterns between large and small urchins across densities. These values are important for extending the results of one spawning to predicting lifetime reproductive output. Over the entire lifespan of an urchin, from egg to adult, an increasing survivorship pattern would be appropriate, due to high larval and post-larval mortality. However, the present model deals strictly with urchins after the age (and size) of first reproduction (approximately 25 mm for *Diadema*—Levitan, 1988c). Adult urchins in general (Ebert, 1982), and specifically *Diadema antillarum* (Karlson and Levitan, 1990), appear to exhibit size-independent survivorship. Further, experimental evidence indicates that

Diadema does not exhibit density-dependent mortality induced by food limitation (Levitan, 1989).

Investigation of these assumptions indicates that the model may be quantitatively imprecise due to factors associated with spawning synchrony and aggregation. However, the evidence suggests that the conclusion of a trade-off between gamete production and gamete fertilization, associated with population density, is correct; individuals at low density are larger, but individuals at high density have a higher likelihood of fertilization. It is important to note that larger individuals, within a spawning event, would produce more zygotes than smaller individuals.

Example of the model

These experiments suggest that population density has a major influence on fertilization success and production of offspring in *Diadema*. An appraisal of fecundity (production of offspring) based on body size or gamete production in this species, without considering the compensatory effects of fertilization success, would be inappropriate. The following example demonstrates how misleading estimates of fecundity can be, when based solely on body size.

In 1983, *Diadema* population density declined 95–99% throughout the Caribbean (Lessios *et al.*, 1984). Since then, there has been a significant increase in mean body size (from 30 to 60 mm test diameter, at Lameshur Bay by June 1987) of the surviving *Diadema*. The median weight of individual *Diadema* has increased 10-fold since the mass-mortality (from 20 to 200 g live weight). During the same period, median gonad volume has increased 200-fold (from 0.05 to 10.0 ml; Levitan, 1988b). Predictions have been made that since growth rates and gamete production are high for this urchin, *Diadema* would rapidly return to former densities (Hughes *et al.*, 1985). However, recruitment since the mass-mortality continues to be at a low level (Hughes *et al.*, 1987; Lessios, 1988; Levitan, 1988b).

Individual zygote production can be estimated before and after the mortality event. In Lameshur Bay, 95% of the 1983 urchin population was between 20 and 40 mm in size and at a density of $15/\text{m}^2$. In 1987, at the same location, 70% of the population was between 60 and 80 mm in size and at a density of $0.2/\text{m}^2$ (Fig. 4). A 70 mm female releases an average of 2.0×10^6 eggs into the water, while a 30 mm female releases only 0.1×10^6 eggs (equation 2). However, fertilization success is estimated to be only 1% at a density of $0.2/\text{m}^2$ compared to 22% at $15/\text{m}^2$ (equation 3). Small females at high density are producing slightly more zygotes than the large females at low density (2.2×10^4 versus 2.0×10^4 zygotes per individual). Poor fertilization success at low population density might be contributing to the poor recruitment seen since the mass mortality.

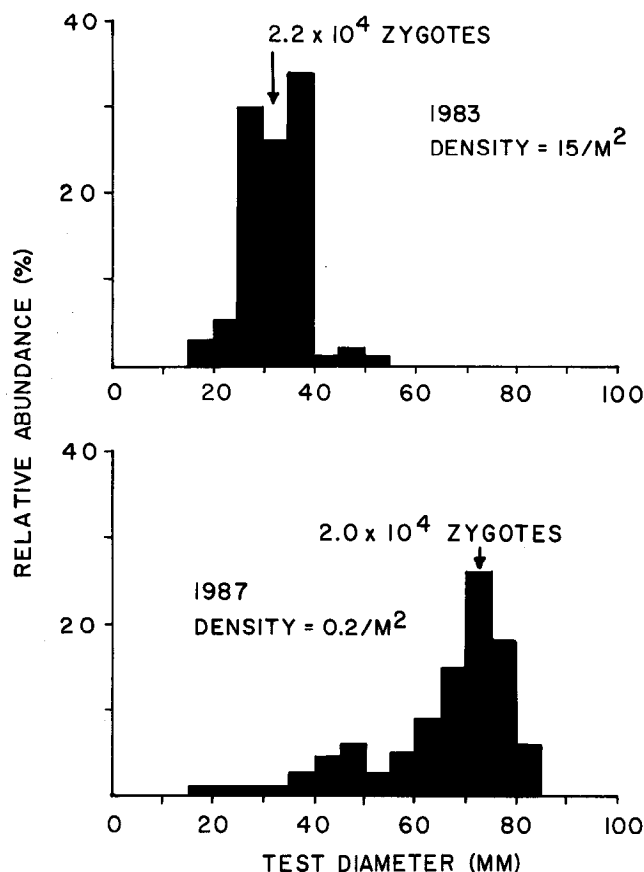


Figure 4. Size-frequency distribution and population density of *Diadema antillarum* before (1983) and after (1987) the mass mortality on a reef in Lameshur Bay, St. John, U. S. V. I. Mean zygote production of the median size urchins are estimated from equations 2 and 3.

Conclusions

Many mobile invertebrates and fish aggregate or swarm during spawning (Levinton, 1982; Pennington, 1985). A temporary spawning aggregation would increase the likelihood of fertilization at low population density and reduce the nutritional costs of living at high density. Plants and sessile animals may suffer the consequences of isolation the most, and may be under high selection pressure to reproduce asexually, self-fertilize, or be hermaphroditic.

This study suggests that the influence of population density on fertilization success should be recognized and incorporated into an assessment of an organism's reproductive potential. This may change our perception of a "good" habitat and a "successful" organism. The assumption that large body size and high gamete production translate into high reproductive success may be incorrect when the importance of fertilization success is ignored.

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