

The Distribution of Male and Female Reproductive Success in a Broadcast Spawning Marine Invertebrate¹

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SYNOPSIS. Many studies have addressed sexual selection in animals, but few data are available on animals that release eggs and sperm into the environment for external fertilization. Although this reproductive mode represents the ancestral condition and is still a very common reproductive strategy, it is underrepresented in empirical studies and theoretical treatments. Here I present data on the pattern of reproductive success in male and female sea urchins. The results suggest that the strength of sexual selection and the differences between the sexes in the intensity of sexual selection depend on mate density. In general, despite the high degree of multiple paternity, the variance in reproductive success appears to be lower in males and higher in females than it is in polygamous species with internal fertilization. These results may provide insight into the patterns of effective population size in marine invertebrates and also more generally the evolutionary transition from sexual monomorphism to polymorphism in adult traits.

INTRODUCTION

Despite the burgeoning literature on sexual selection in animals (Smith, 1984; Andersson, 1994; Birkhead and Møller, 1998; Shuster and Wade, 2003), very little work has been done on sedentary or sessile animals that release eggs and sperm into an aquatic medium for external fertilization (Levitan, 1998a, 2004). Although its very nature makes assessment of mating and reproductive success difficult, investigation of this form of reproduction is relevant because it is the presumed ancestral mating strategy (Franzen, 1956; Jagersten, 1972; Parker, 1984; Wray, 1995; but see Rouse and Fitzhugh, 1994) and is commonly found in most animal phyla (Giese and Kanatani, 1987). Understanding the major evolutionary transitions of isogamy to anisogamy, of external fertilization to internal fertilization, and of sexually monomorphic adults to sexually dimorphic adults probably requires an understanding of sexual selection in externally fertilizing species that closely represent the ancestral condition (Levitan, 1998a, 2004, 2005).

Darwin wrote that externally fertilizing marine invertebrates lack sexual dimorphism and do not experience sexual selection because they “are not sufficiently advanced to allow of the feelings of love and jealousy, or of the exertion of choice” (1874, p. 613; as also noted by Arnold [1994]). But evidence collected over the past two decades has indicated that, at least for females, variance can be high in the proportion of eggs released that are fertilized. This variation depends on sperm availability as determined by the distance, abundance, and behavior of spawning males (reviewed by Levitan, 1995; Yund, 2000) as well as egg and sperm traits (Levitan, 1996, 1998b, 2002a, b).

This variation in reproductive success provides ample opportunity for sexual selection (Levitan, 1998a, b).

Estimating the strength of sexual selection and how this selection can influence the evolution of male and female traits requires knowledge not only on variance in female reproductive success but also variance in male reproductive success. However, only recently has reproductive success and variance in reproductive success been measured in both males and females in an externally fertilizing species (Levitan, 2004, 2005). Here I expand the analysis of an earlier study of reproductive success in the red sea urchin, *Strongylocentrotus franciscanus* (Levitan, 2004), by examining the distribution of reproductive success among males and females and how this pattern of reproductive variance may influence sexual selection, the evolution of sexual dimorphism, and the genetic structure of external fertilizers.

Measures of reproductive success

Quantifying mating and reproductive success in externally fertilizing taxa can be challenging. The single or serial pairwise matings of internally fertilizing taxa provide, at least in principle, a simple way to determine whether any two individuals have mated or not. When organisms release sperm or pollen into the environment, this determination is more difficult, and doubly so when both sperm and eggs are released. Spawning can involve anything from a lonely individual (Levitan, 1988; Pearse *et al.*, 1988; Babcock *et al.*, 1992) to epidemic spawning events involving thousands of individuals (reviewed by Levitan, 1998a). In such cases the term “mating success” can be defined as the number of mates that simultaneously release gametes during a spawning event. When the spawning event ranges over great distances, it can be limited by the neighborhood size that encompasses the likely encounter frequency of released gametes from the perspective of a focal individual.

Here, the proxy used for female reproductive success is the fraction of a female’s eggs that are fertil-

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ized. It does not include variation in female egg production or postzygotic survivorship. The benefits of not considering female egg production include not only the logistic ease of not having to determine how many eggs are released (which would preclude any other measure of success) but also exclusion of variation in reproductive success (egg production) not likely to be under sexual selection (Arnold, 1994). The cost of this proxy is that, if species exhibit trade-offs between egg qualities that increase the likelihood of fertilization (*e.g.*, egg size, Levitan 1993, 1996, 1998*b*, 2002*a*; Marshall *et al.*, 2002; Marshall and Keough, 2003; Huchette *et al.*, 2004; and jelly-coat size, Podolsky, 2001, 2004; Levitan and Irvine, 2001) and egg number, then estimates of reproductive success may be biased, in that the reproductive success of females that release high-quality gametes might be inflated. This bias would be critical to the current study if, within species, an individual's gamete quality was correlated with mating success (the number or density of mates).

In contrast large intraspecific differences in gamete quantity are associated with variance in population density caused by non-sexually selected factors that influence egg production, such as food availability and body size (Levitan, 1989; Bureau, 1996; Wahle and Peckham, 1999), and a host of factors (age, food quality, reproductive readiness) that can affect egg production independent of population density, all of which might swamp measures of variation caused by sexual selection. Overall, the cost of overlooking possible biases seems preferable to the cost of incorporating the acknowledged and large effects of non-sexually selected factors.

The proxy used for male reproductive success is the sum, across all females with which the male has mated, of the product of the paternity share of each female and the fraction of her eggs fertilized. The benefit of this proxy is that the currency for male and female reproductive success is the same. A unit value of 1.0 is equal to the full fertilization of a single female's eggs. Although the currency is the same, the possible range of values is quite different. The value for a female can range only from 0 to 1, whereas that for a male can range from 0 to the full fertilization of all females participating in a spawning event (potentially >1,000).

Reproductive success is a function of the distribution, abundance, and quality of adults and gametes of the same and the opposite sex, as well as the pattern of water flow that transports, mixes, and dilutes the gametes. During a spawning event, the eggs from a female may simultaneously be fertilized by sperm from numerous males, and the share of paternity might or might not be highly skewed. An individual could have high mating success yet have very low reproductive success (*e.g.*, take part in a large spawning event but be largely outcompeted for fertilizations) or have very low mating success and very high reproductive success (complete fertilization with a nearby mate). All these factors suggest that mating success

may have no simple relationship with reproductive success.

METHODS

This study used microsatellite markers in the temperate sea urchin *Strongylocentrotus franciscanus* to examine the reproductive success of males and females. The work was conducted at the mouth of Bamfield Inlet, British Columbia, Canada. Details can be found in earlier publications (Levitan, 2004). Here, I elaborate on the variance and distribution of fertilization success in males and females. In the experiment reported here, sea urchins were induced to spawn *in situ* over a range of densities and population sizes. Animals were picked up, turned over and injected with KCl in the soft tissue surrounding the mouth, and placed back on the sea floor. On different days individuals were induced to spawn over a range of population densities and sizes that reflect natural variation in densities within a 5 × 5-m area. For this species, the neighborhood size that influences fertilization success appears to be at this spatial scale, as larger spawning events do not increase the likelihood of fertilization for a female within this area (Levitan, 2002*a*).

After the sea urchins had spawned for 30 min, eggs were collected in the water column above each female. Tube feet were also collected from all spawning sea urchins for genotyping. In the laboratory the eggs were inspected after 3 hr for fertilization and early development, and then after 3 days larvae were individually frozen. The experiment was replicated 35 times over a range of mate densities. I analyzed 6 to 15 microsatellite loci (McCartney *et al.*, 2004) of all adults (N = 428) and 20 larvae per female (N = 3,425) to determine parentage (Levitan, 2004).

RESULTS

The average female fertilization success depended on the density of spawning males (Fig. 1). At low density, sperm were limiting, and fertilization success tended to be low. As density increased, the average percentage of eggs fertilized increased to near 100%. At higher densities, polyspermic fertilizations resulted in developmental failure as confirmed by examination of stained sperm-egg fusions under fluorescent and confocal microscopy (Levitan, 2004).

A weak correlation was apparent between the density and number of spawning mates (0.33). This weak relationship resulted in part because either a few or a relatively large number of individuals were induced to spawn in either the full 5 × 5-m area or a smaller subsection of the area. This was done in order to tease apart the effects of neighbor distance and the number of individuals on fertilization. Males and females did not differ significantly in reproductive success and followed the same trajectory as a function of the number of mates with success peaking at intermediate levels (Fig. 2). The reduction in female reproductive success at high levels of mating success is a result of polyspermy and the similar reduction in male reproductive

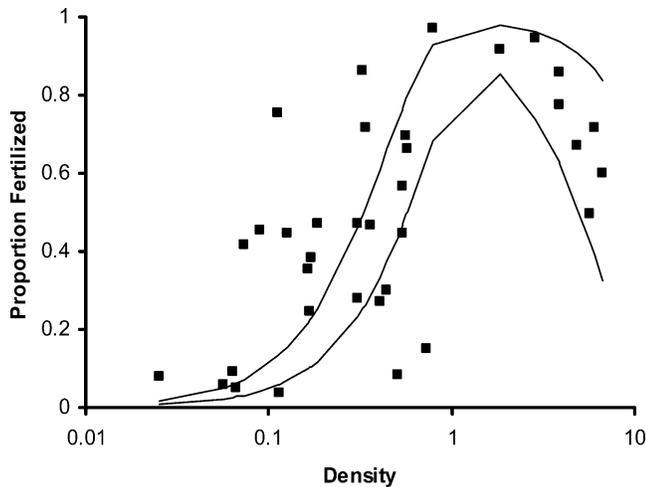


FIG. 1. Average female fertilization success and the density of males. Lines indicate upper and lower 95% confidence intervals around the mean as predicted by a fertilization-kinetics model. Fertilization success is lower at low density because of sperm limitation and at high density because of polyspermy (from Levitan, 2004).

success is, at least in part, caused by the correlation between the numbers of males and females (0.45). The overall spawning sex ratio across all spawning events in this study was not significantly different from 1:1 and did not vary as a function of the number or density of spawning individuals (Levitan, 2004).

The standardized fertilization variance (variance divided by the squared average) was independent of mate density ($P > 0.3$) for males, but dependent on mate density in a complex way for females ($P < 0.001$ for a fourth order polynomial). Male and female variances were only unequal at intermediate mate densities. At lower or higher mate densities male and female variances in fertilization success were surprisingly similar (Fig. 3). At low mate density, both males and females experienced similar variation in reproductive success because of sperm limitation. For both sexes fertilization success depended strongly on individual proximity to mates and variation in sea conditions that influenced the mixing and dispersal of gametes. As average female fertilization success exceeded 50%, the variance in female fertilization success decreased, because sperm began to saturate more females, but male variance remained high, because some males were more successful than others. As mate density increased further, average female fertilization success decreased—because of polyspermy—and variance in female reproductive success increased.

The mating system in this example is highly polygamous. Multiple paternity was detected in 98% of females and multiple maternity was detected in 83% of males. Even more striking was the proportion of individuals that mated with each other. On average, 65% of males produced at least some offspring with every female in a spawning event. Similarly 53% of females produced at least some offspring with every male in a spawning event. This percentage, for both males and

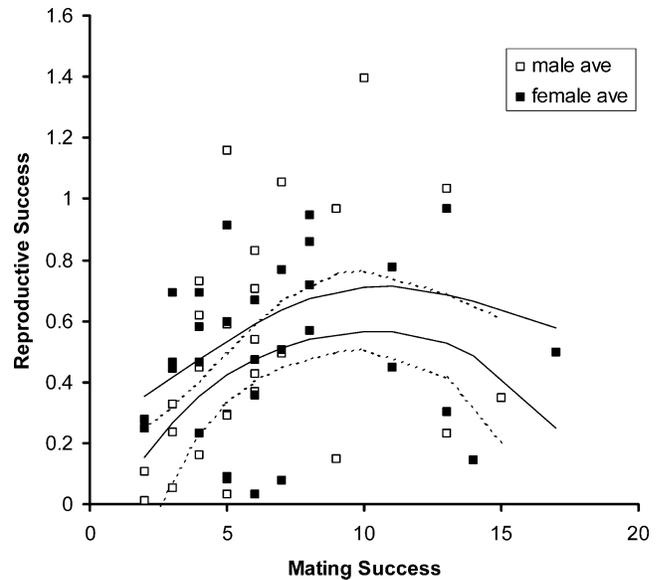


FIG. 2. Average reproductive success and mating success. Averages calculated from all the males or females that spawned in each independent spawning event ($N = 35$ events). Reproductive success is the fraction of a female's eggs that are fertilized; mating success is the number of mates in the spawning event. Open symbols represent males, and solid symbols represent females. Dotted (males) and solid (females) lines are the upper and lower 95% confidence intervals based on a polynomial regression ($P = 0.0003$ and 0.0014 for linear and polynomial components for males and 0.0001 and 0.0001 for the same components in females). Males and females show similar reproductive success, and both show peaks at intermediate levels of mating success.

females, was inversely related to the number of spawning males; the vast majority of individuals produced offspring with every spawning mate when the number of spawning males was low (Fig. 4). There was no

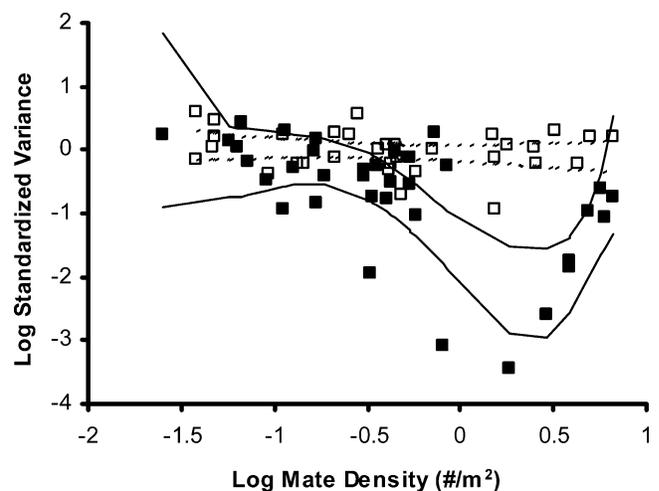


FIG. 3. Standardized reproductive variance and mate density. Open symbols represent males, and filled symbols represent females. Dotted (males) and solid (females) lines are the upper and lower 95% confidence intervals based on a polynomial regression. The sexes differ in standardized variance only at intermediate mate densities. This figure differs slightly from the figure in Levitan (2004) because a calculation error was addressed.

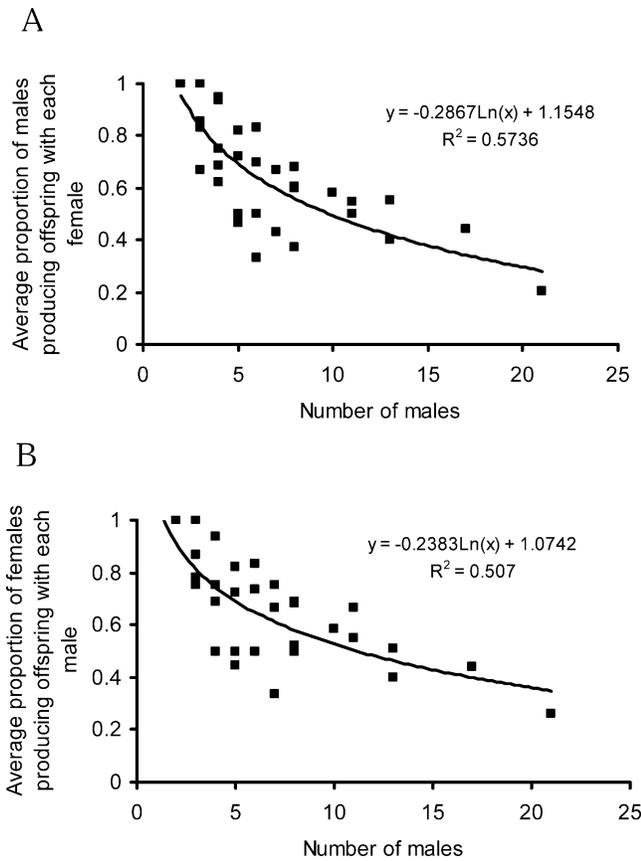


FIG. 4. The proportion of individuals that mate as a function of the number of males. A. Average proportion of males that produce offspring with each female in a spawning event. B. Average proportion of females that produce offspring with each male in a spawning event. When few males spawn, all males produced offspring with all females. As the number of males increased, a lower proportion of males produced offspring with each female and a lower proportion of females produced offspring with each male.

significant relationship as a function of the number of spawning females ($P > 0.6$ for both males and female). In part, the decrease in percentage of individuals mating with each other at high male numbers is a detection issue, as the number of spawning males approaches the number of larvae analyzed for parentage. However, this is not the only reason, because males, with the highest paternity share per female, lose shares as the number and density of male competitors increases (see Figure 7 in Levitan, 2004). This suggests that the level of polygamy is a function of sperm availability.

Given the degree of polygamy and thus the opportunity for competition and choice, it is interesting that the distributions of reproductive success of males and females were similar; particularly at low or high mate densities, where sperm were limiting or debilitating. Only at intermediate densities did the distribution of reproductive success match that typically seen in polygamous mating systems (Fig. 5). The similarity of the male and female fertilization variances, particularly at low and high mate density, was caused by two fac-

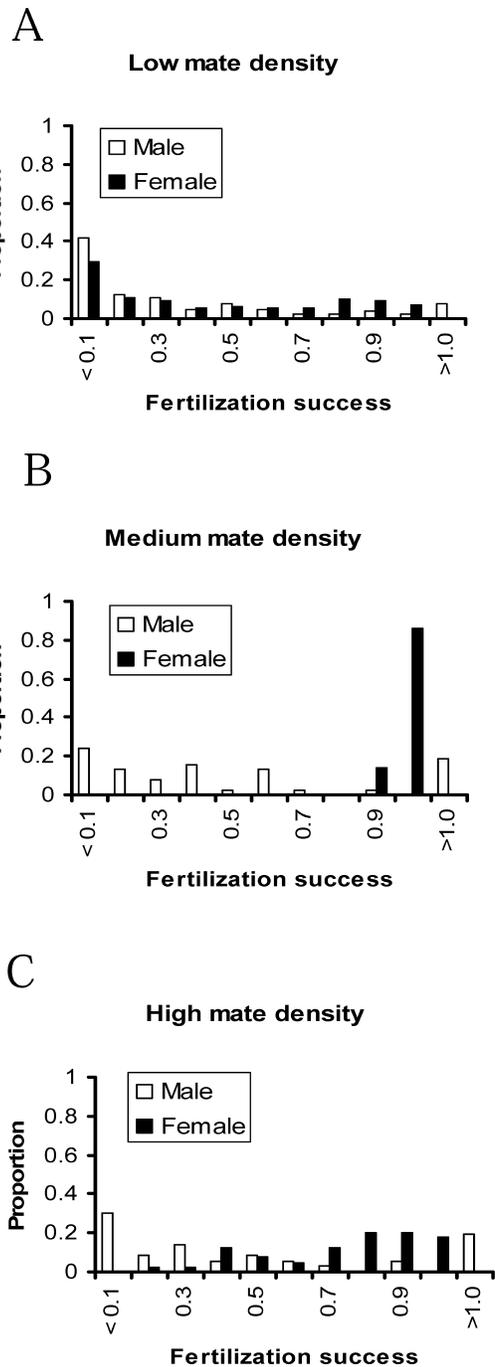


FIG. 5. Distribution of reproductive success for males and females at (A) low, (B) medium, and (C) high mate densities. The distribution of reproductive success is similar for males and females at both low and high mate densities.

tors: (1) an increase in female variation associated with either sperm limitation or polyspermy and (2) relatively low variability in male success compared to that in mating systems with big winners and losers (see, *e.g.*, Bateman, 1948; Clutton-Brock, 1988). This low variability may be associated with the inability of males to exclude other males from access to a female's eggs,

the absence of female control over which males and sperm fertilize her eggs, or both.

DISCUSSION

Distribution of reproductive success

A basic premise of Bateman's principle is that, because females invest more in each offspring, females quickly reach an asymptote in the relationship between reproductive success and mating success; a female can quickly accumulate all the sperm needed to fertilize the limited number of eggs she can properly produce and care for. The result is generally low variance in female reproductive success. In contrast, males, because they invest relatively little in each offspring, can continue to produce offspring with additional matings and often have high variance in reproductive success, as some males garner disproportionate shares of matings with females while others either directly or indirectly are outcompeted for mating opportunities (Andersson, 1994; Arnold, 1994; Birkhead and Møller, 1998). Although these sex roles are occasionally reversed, and males are burdened with parental duties while females gain more from additional matings (Berglund *et al.*, 1986; Jones *et al.*, 2000), the general pattern for organisms that copulate or pseudocopulate is that the production of offspring depends strongly on the number of mates for one sex (usually males). For the other sex, the number of matings is less important to offspring production (Bateman, 1948; Clutton-Brock, 1988). The degree of this importance depends on a female's ability to store sperm relative to the time and investment in each bout of reproduction.

How these considerations translate into actual differences in the patterns of reproductive success between copulating males and females depends on the mating system (Shuster and Wade, 2003). In purely monogamous systems with one-to-one sex ratios, the distributions of male and female matings and reproductive successes are identical. When one or the other sex has access to multiple partners, however, then male (or sperm) competition, female choice, and sexual conflict can lead to dramatic gender differences in the distribution of reproductive success, and males typically have much greater variance than females (Clutton-Brock, 1988).

In contrast, male and female variances in reproductive success in the present study are surprisingly similar, especially given the high degree of polygamous mating. Unlike typical Bateman gradients (in which reproductive success is a function of mating success; Arnold and Duvall, 1994; Andersson and Iwasa, 1996; Jones *et al.*, 1999), which show different positive slopes of the dependence of reproductive success on mating success, the present data indicate similar intermediate peaks for both sexes (Fig. 2). When too many individuals spawned, reproductive success decreased because of polyspermy (Levitan, 2004). Although male reproductive success tended to reach a higher

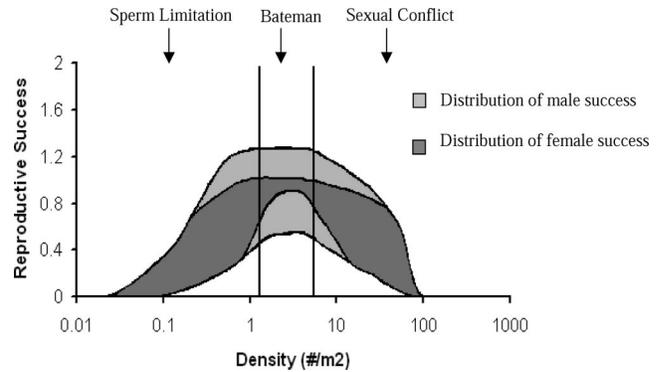


FIG. 6. Conceptual illustration of the distribution of male and female mating success. Three zones with different selective pressures are noted: sperm limitation, "Bateman," and sexual conflict. The variances are only unequal in the Bateman zone. At the extremes, the variances are similar for males and females but the selective pressures may be quite different. At low densities both males and females may be under selection for increased mating success, whereas at high densities, males may be selected for increased mating success while females try to resist matings.

peak and lower extremes than did female reproductive success, these differences are not significant.

A more detailed look at the variance in reproductive success indicates that only at intermediate levels of mate density did sexual selection abate for females. At high and low densities for females, and at all densities for males, sexual selection appeared to be intense. At low densities, it was attributable to sperm limitation, and at high densities it was manifested as sexual conflict. The general prediction of Bateman's principle (that of high reproductive variance in males and low variance in females) held only at a fairly narrow range of mate densities (Figs. 5, 6).

Consequences of reproductive variation to population structure

In contrast to polygamous mating systems with internal fertilization, the data presented here suggest relatively high female variance (at all but intermediate densities, where sperm are neither limiting or debilitating) and relatively low male variance (the notable lack of big winners and losers at all densities) (Fig. 5). The higher variation in female fertilization in broadcast than in internal fertilizers has been recognized previously (*e.g.*, by Levitan and Petersen, 1995; Bishop, 1998; Yund, 2000). Numerous studies have demonstrated that female fertilization success can vary between 0 and 100% of eggs fertilized (reviewed by Levitan, 1995, 1998a; Yund, 2000). However the lack of big winner and loser males is a novel finding, only apparent by the use of molecular markers to establish paternity.

The relatively high variance in female fertilization success has added to the argument that the low genetic diversity and low ratio of effective to actual population size in high-fecundity broadcast-spawning taxa is caused by high reproductive variance (Hedgcock, 1994). This has been termed the sweepstakes hypoth-

esis, under which few individuals dominate reproductive events, resulting in high levels of genetic drift. The sweepstakes hypothesis predicts two genetic consequences. The first is temporal genetic subdivision among cohorts of recruits that can be manifested as a Wahlund effect (finding heterozygote deficiencies in the overall population because the genetically subdivided cohorts are lumped together). The second is lower genetic diversity in these cohorts than in the full adult population. Some evidence supports the first prediction (Johnson and Black, 1982; Li and Hedgecock, 1998), but alternative hypotheses have been suggested, including variation in selective pressures (Johnson and Black, 1984) and spatial variation in the source of recruits (Flowers *et al.*, 2002) that can also result in temporal subdivision. A test of the second prediction failed to show a significant difference between the genetic diversity of recruitment pulses and the adult population (Flowers *et al.*, 2002). Together these results suggest that the validity of the sweepstakes hypothesis requires further scrutiny.

The basic premise of the sweepstakes hypothesis is that, in high-fecundity populations, a small minority of individuals can repopulate the next generation of adults and that these lucky individuals represent a small subset of the full genetic variation in the population. Sweepstakes may not occur, if despite high early-life-stage mortalities, the surviving individuals come from a wider sampling of parental genotypes, because the relatively high variance in female reproductive success (compared with internally fertilizing taxa) is compensated for by relatively low variance in male reproductive success. The outcome of broadcast spawning may be a decrease rather than an increase in reproductive variance compared with that of copulating species.

This possibility is not obvious, because the potential range of reproductive variance in males is much greater than that in females because males produce and release many orders of magnitude more gametes than do females. In three sea-urchin species, *Strongylocentrotus purpuratus*, *S. franciscanus*, and *S. droebachiensis*, an individual releases around 1 million eggs or 100 billion sperm per spawning event (D.R.L., unpublished data). Therefore the range of potential reproductive success is approximately 5 orders of magnitude greater for males than females. The evidence from the present study is that this potential is far from being reached and that male variance is much less than is potentially possible.

A possible scenario for which the sweepstakes hypothesis would hold is one in which small discrete patches of newly fertilized embryos are produced by only a few adults and produce pulses of larvae genetically distinct from other such patches. Many of these patches will suffer catastrophic mortality, and pulses of new recruits will be genetically similar and distinct from other temporal pulses that suffered their own unique pattern of reproduction and mortality.

In the present study, however, even though female

reproductive success was variable, single females produced offspring with a large number of mates even during the fairly small and constrained experimental spawning events (Fig 4). Natural spawning events can involve many thousands of individuals (Levitan, 2002a) and the result of these events may be pulses of millions of larvae made up of fairly even contributions from each spawning individual (see Fig. 5). The result would be, even at small spatial scales, pulses of newly fertilized embryos that are genetically diverse. In spite of high larval mortality rates, in the absence of selection on particular genotypes, the resultant juvenile cohort could well have representative genotypes from and genetic diversity similar to that of the adult population (a result noted by Flowers *et al.*, 2002).

Although a single study (Levitan, 2004) only provides the narrowest of views of male and female reproductive success, it does provide a starting point that suggests that the assumptions of the sweepstakes model must be tested further.

Sexual selection and sexual dimorphism

The high degree of multiple paternity noted in *S. franciscanus* allows for the possibility that fertilization is a random mixing process. If male and female successes are independent of trait values, then the variance in reproductive success may not indicate sexual selection (Shuster and Wade, 2003) but simply reflects random variation in the placement of males and females in a spawning event and water flow. Two lines of evidence suggest, however, that trait values can influence fertilization success for both males and females. First, lab and field studies indicate that gamete traits influence patterns of fertilization. These traits include sperm velocity (Levitan, 2000), egg and jelly-coat size (Levitan, 1993, 1996, 1998b, 2000, 2002a; Levitan and Irvine, 2001; Farley and Levitan, 2001; Podolsky, 2001, 2004; Marshall *et al.*, 2002; Marshall and Keough, 2003; Huchette *et al.*, 2004), and egg receptivity (Levitan, 1993, 2002b). Gamete traits that increase the likelihood of sperm and egg collision, or fertilization given a collision, perform better under conditions of sperm limitation (Levitan, 1998b, 2002a). Individuals in a population can also vary in gamete-recognition proteins (Metz and Palumbi, 1996; Debenham *et al.*, 2000), and preliminary laboratory observations suggest that a male that shares a gamete-recognition gene with a female will garner a greater paternity share than will a male with more dissimilar genes (Palumbi, 1999).

Individuals within populations differ in gametic traits, and this variation can influence fertilization success under field conditions (Levitan, 1996, 1998b). Even on the wave-swept shores of the outer west coast of Canada, the majority of the variance in fertilization success in a field experiment was explained by gamete quality (Levitan, 1996). These patterns in the relationship between specific gamete traits and fertilization success are also noted across related species. Gamete

traits that increase fertilization success under conditions of sperm limitation occur in the least common (and most sperm-limited) species, and traits that do so when sperm are abundant occur in the most common (and least sperm-limited) species (Levitan, 2002a).

The second line of evidence is that the behavior of adults may also be a target of sexual selection. Thorson (1950) noted that, although in numerous instances males and females spawn synchronously, when the sexes differ in time of spawning, the males usually spawn first. This observation has been corroborated by further data (reviewed by Levitan, 1998a, Levitan, 2005) and applies also to externally fertilizing dioecious algae (Clifton, 1997). The notion that sexual selection acts on the timing of spawning is supported by experiments that demonstrate the cost of spawning late for males (loss of paternity shares to earlier-spawning males) but not females (Levitan, 2005). The optimal spawning strategy of males depends on the degree of sperm competition. Spawning earlier for protracted periods before egg release can provide a bet hedging advantage when individuals are widely spaced. Spawning more explosively for shorter periods before egg release can provide a competitive advantage for closely spaced individuals (Levitan, 2005). Benthic invertebrates, that often spawn distant to one another, such as sea urchins, seem to exhibit the former strategy. Fish, that spawn in close proximity, seem to exhibit the latter strategy (Levitan, 2005).

The rare cases in which females spawn before males seem to be restricted to pair-spawning species in which males release sperm onto eggs after they have been released (e.g., some brittle stars, sea stars, horseshoe crabs, and fish, reviewed by Levitan, 1998a, 2005). Interestingly, cases in which females spawn first are also associated with the rare instances of sexual dimorphisms in body and gonad size. Pairing with a mate sets up the arena for adult interactions among mates and competitors for mates. These are the conditions under which the sexes would be subject to differences in selection on adult morphological traits, setting the stage for the evolution of the sexual dimorphism that is noted in taxa that copulate or pseudocopulate (Levitan, 1998a, 2004). Sexual selection can act on both externally and internally fertilizing taxa, but it is the evolution of pair spawning and copulatory behavior (that transition itself a product of sexual selection; see Parker, 1984; Levitan, 1998a) that resulted in the expansion of sexual selection to act on adult morphological traits (Levitan, 2005).

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REFERENCES

- Andersson, M. A. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey.
- Andersson, M. and Y. Iwasa. 1996. Sexual selection. *Trends Ecol. Evol.* 11:A53–A58.
- Arnold, S. J. 1994. Bateman's principles and the measurement of sexual selection in plants and animals. *Am. Nat.* 144:S126–S149.
- Arnold, S. J. and D. Duvall. 1994. Animal mating systems—a synthesis based on selection theory. *Am. Nat.* 143:317–348.
- Babcock, R., C. Mundy, J. Keesing, and J. Oliver. 1992. Predictable and unpredictable spawning events: *In situ* behavioural data from free-spawning coral reef invertebrates. *Invertebr. Reprod. Dev.* 22:213–228.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- Berglund, A., G. Rosenqvist, and I. Svensson. 1986. Reversed sex roles and parental energy investment in zygotes of two pipefish (Syngnathidae) species. *Mar. Ecol. Prog. Ser.* 29:209–215.
- Birkhead, T. and A. Møller. 1998. *Sperm competition and sexual selection*. Academic Press, San Diego.
- Bishop, J. D. D. 1998. Fertilization in the sea: Are the hazards of broadcast spawning avoided when free-spawned sperm fertilize retained eggs? *Proc. R. Soc. London Ser. B Biol. Sci.* 265:725–731.
- 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, British Columbia.
- Clifton, K. E. 1997. Mass spawning by green algae on coral reefs. *Science* 275:1116–1118.
- Clutton-Brock, T. H. 1988. *Reproductive success*. The University of Chicago Press, Chicago.
- Darwin, C. 1874. *The descent of man, and selection in relation to sex*. 2nd ed. J. Murray, London.
- Debenham, P., M. A. Brzezinski, and K. R. Foltz. 2000. Evaluation of sequence variation and selection in the bindin locus of the red sea urchin, *Strongylocentrotus franciscanus*. *J. Mol. Evol.* 51:481–490.
- Farley, G. S., and D. R. Levitan. 2001. The role of jelly coats in sperm-egg encounters, fertilization success, and selection on egg size in broadcast spawners. *Am. Nat.* 157:626–636.
- Flowers, J. M., S. C. Schroeter, and R. S. Burton. 2002. The recruitment sweepstakes has many winners: Genetic evidence from the sea urchin *Strongylocentrotus purpuratus*. *Evolution* 56:1445–1453.
- Franzen, A. 1956. On spermiogenesis, morphology of the spermatozoon and biology of fertilization among invertebrates. *Zool. Bidr. Upps.* 31:1–28.
- Giese, A. C., and H. Kanatani. 1987. Maturation and spawning. In A. C. Giese, J. S. Pearse, and V. B. Pearse (eds.), *Reproduction of marine invertebrates*, Vol. IX. *Seeking unity in diversity*, pp. 251–329. Blackwell Scientific/Boxwood Press, Palo Alto/Pacific Grove, California.
- Hedgecock, D. 1994. Does variance in reproductive success limit effective population sizes of marine organisms? In A. R. Beaumont (ed.), *Genetics and evolution of aquatic organisms*, pp. 122–134. Chapman and Hall, London.
- Huchette, S. M. H., J. P. Souldard, C. S. Koh, and R. W. Day. 2004. Maternal variability in the blacklip abalone, *Haliotis rubra* Leach (Mollusca: Gastropoda): Effect of egg size on fertilization success. *Aquaculture* 231:181–195.
- Jagersten, G. 1972. *Evolution of the metazoan life cycle*. Academic Press, New York.
- Johnson, M. S. and R. Black. 1982. Chaotic genetic patchiness in an intertidal limpet, *Siphonaria* sp. *Mar. Biol.* 70:157–164.
- Johnson, M. S., and R. Black. 1984. Pattern beneath chaos: The effect of recruitment on genetic patchiness in an intertidal limpet. *Evolution* 38:1371–1383.

- Jones, A. G., G. Rosenqvist, A. Berglund, and J. C. Avise. 1999. The genetic mating system of a sex-role-reversed pipefish (*Syngnathus typhle*): A molecular inquiry. *Behav. Ecol. Sociobiol.* 46:357–365.
- Jones, A. G., G. Rosenqvist, A. Berglund, S. J. Arnold, and J. C. Avise. 2000. The Bateman gradient and the cause of sexual selection in a sex-role-reversed pipefish. *Proc. R. Soc. London Ser. B Biol. Sci.* 267:677–680.
- Levitan, D. R. 1988. Asynchronous spawning and aggregative behavior in the sea urchin *Diadema antillarum* Philippi. In R. D. Burke (ed.), *Echinoderm biology, Proceedings of the 6th International Echinoderm Conference*, pp. 181–186. Balkema, Rotterdam.
- Levitan, D. R. 1989. Density-dependent size regulation in *Diadema antillarum*: Effects on fecundity and survivorship. *Ecology* 70: 1414–1424.
- Levitan, D. R. 1993. The importance of sperm limitation to the evolution of egg size in marine invertebrates. *Am. Nat.* 141:517–536.
- Levitan, D. R. 1995. The ecology of fertilization in free-spawning invertebrates. In L. McEdward (ed.), *Ecology of marine invertebrate larvae*, pp. 123–156. CRC Press, Boca Raton, Florida.
- Levitan, D. R. 1996. Effects of gamete traits on fertilization in the sea and the evolution of sexual dimorphism. *Nature* 382:153–155.
- Levitan, D. R. 1998a. Sperm limitation, sperm competition and sexual selection in external fertilizers. In T. Birkhead and A. Møller (eds.), *Sperm competition and sexual selection*, pp. 173–215. Academic Press, San Diego.
- Levitan, D. R. 1998b. Does Bateman's principle apply to broadcast-spawning organisms? Egg traits influence *in situ* fertilization rates among congeneric sea urchins. *Evolution* 52:1043–1056.
- Levitan, D. R. 2000. Sperm velocity and endurance trade-off and influence fertilization in the sea urchin *Lytechinus variegatus*. *Proc. R. Soc. London B Biol. Sci.* 267:531–534.
- Levitan, D. R. 2002a. Density-dependent selection on gamete traits in three congeneric sea urchins. *Ecology* 83:464–479.
- Levitan, D. R. 2002b. The relationship between conspecific fertilization success and reproductive isolation among three congeneric sea urchins. *Evolution* 56:1599–1609.
- Levitan, D. R. 2004. Density-dependent sexual selection in external fertilizers: Variances in male and female fertilization success along the continuum from sperm limitation to sexual conflict in the sea urchin *Strongylocentrotus franciscanus*. *Am. Nat.* 164: 298–309.
- Levitan, D. R. 2005. Sex specific spawning behavior and its consequences in an external fertilizer. *Am. Nat.* 165:682–694.
- Levitan, D. R. and S. D. Irvine. 2001. Fertilization selection on egg and jelly-coat size in the sand dollar *Dendraster excentricus*. *Evolution* 55:2479–2483.
- Levitan, D. R. and C. Petersen. 1995. Sperm limitation in the sea. *Trends Ecol. Evol.* 10:228–231.
- Li, G. and D. Hedgecock. 1998. Genetic heterogeneity, detected by PCR-SSCP, among samples of larval Pacific oysters (*Crassostrea gigas*) supports the hypothesis of large variance in reproductive success. *Can. J. Fish. Aquat. Sci.* 55:1025–1033.
- McCartney, M. A., K. Brayer, and D. R. Levitan. 2004. Polymorphic microsatellite loci from the red urchin, *Strongylocentrotus franciscanus*, with comments on heterozygote deficit. *Mol. Ecol. Notes* 4:226–228.
- Marshall, D. J. and M. J. Keough. 2003. Sources of variation in larval quality for free-spawning marine invertebrates: Egg size and the local sperm environment. *Invertebr. Reprod. Dev.* 44:63–70.
- Marshall, D. J., C. A. Styan, and M. J. Keough. 2002. Sperm environment affects offspring quality in broadcast spawning marine invertebrates. *Ecol. Lett.* 5:173–176.
- Metz, E. C. and S. R. Palumbi. 1996. Positive selection and sequence rearrangements generate extensive polymorphism in the gamete recognition protein bindin. *Mol. Biol. Evol.* 13:397–406.
- Palumbi, S. R. 1999. All males are not created equal: Fertility differences depend on gamete recognition polymorphisms in sea urchins. *Proc. Natl. Acad. Sci. USA* 96:12632–12637.
- Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. In R. L. Smith (ed.), *Sperm competition and the evolution of animal mating systems*, pp. 1–60. Academic Press, Orlando, Florida.
- Pearse, J. S., D. J. McClary, M. A. Sewell, W. C. Austin, A. Perez-Ruzafa, and M. Byrne. 1988. Simultaneous spawning of six species of echinoderms in Barkley Sound, British Columbia. *Invertebr. Reprod. Dev.* 14:279–288.
- Podolsky, R. D. 2001. Evolution of egg target size: An analysis of selection on correlated characters. *Evolution* 55:2470–2478.
- Podolsky, R. D. 2004. Life-history consequences of investment in free-spawned eggs and their accessory coats. *Am. Nat.* 163: 735–753.
- Rouse, G. and K. Fitzhugh. 1994. Broadcasting fables: Is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. *Zool. Scr.* 23:271–312.
- Shuster, S. M. and M. J. Wade. 2003. *Mating systems and strategies*. Princeton University Press, Princeton, New Jersey.
- Smith, R. L. (ed.) 1984. *Sperm competition and the evolution of animal mating systems*. Academic Press, Orlando, Florida.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25:1–45.
- Wahle, R. A. and S. H. Peckham. 1999. Density-related reproductive trade-offs in the green sea urchin, *Strongylocentrotus droebachiensis*. *Mar. Biol.* 134:127–137.
- Wray, G. A. 1995. Evolution of larvae and developmental modes. In L. McEdward (ed.), *Ecology of marine invertebrate larvae*, pp. 412–448. CRC Press, Boca Raton, Florida.
- Yund, P. O. 2000. How severe is sperm limitation in natural populations of marine free-spawners? *Trends Ecol. Evol.* 15:10–13.