6 Sperm Limitation, Gamete Competition, and Sexual Selection in External Fertilizers

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INTRODUCTION

External fertilization is a common and widespread reproductive strategy in aquatic environments (Giese and Kanatani 1987) and is generally thought to be ancestral to internal modes of reproduction (Jägersten 1972; Parker 1984; Wray 1995; but see Rouse and Fitzhugh 1994). Therefore, estimates of male and female fertilization success in external fertilizers may provide not only information on sperm competition for the majority of animal phyla but also insight into the evolution of sexual dimorphism and internal fertilization.

Despite the need to understand the patterns and consequences of variation in both male and female fertilization success, little is known

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about the fate of gametes released in aquatic environments. Historically, discussions about reproductive success in external fertilizers were based on speculation or laboratory studies (reviewed by Levitan 1995a). It has only been in the last decade that some of the practical obstacles associated with 'chasing' gametes in an aquatic medium have been overcome. Estimates of gamete concentration and fertilization have been made, but there is still no direct information on sperm competition and multiple paternity.

In contrast to most other organisms, the available evidence on external fertilizers suggests that sperm is limiting. Evidence from field experiments (Table 6.1) and natural observations of spawning (Table 6.2) demonstrate that the proportion of a female's eggs that are fertilized is often much less than 100%, and a majority of the variation in female fertilization success can be explained by male abundance, proximity, or synchrony. This somewhat different view of sexual selection has implications for the generality of Bateman's principle (Bateman 1948) and the evolution of sexual dimorphism in this presumptive ancestral reproductive strategy.

In this chapter, I offer the possibility that in externally fertilizing organisms sexual selection is intense but approximately symmetrical across sexes. This is a result of (1) sperm limitation, which results in (2), increased variation in the proportion of a female's eggs that are fertilized, and hence increased variation in female reproductive success relative to taxa with internal fertilization, and in turn results in (3), selection for enhanced fertilization success not only for males but also for females. As a consequence, sexual dimorphism in both primary and secondary sexual characteristics is reduced or absent. This hypothesis leads to the notion that anisogamy and copulation evolved because of sperm limitation rather than sperm competition, an adaptation that in this scenario benefits both males and females. In order to build these arguments, I must first define the relevant terms, review what is known about fertilization in externally fertilizing organisms and patterns of sexual dimorphism, and then attempt to place this evidence in a theoretical framework. This is not a completed project, and my goal is to stimulate interest in sexual selection on external fertilizers.

II. DEFINITIONS AND THE SCOPE OF THIS REVIEW

Free spawning is defined as the release of sperm into the environment, whereas broadcast spawning is defined as the release of both eggs and sperm into the environment. Males can free spawn, pseudocopulate (release sperm directly on females or transfer a spermatophore), or copulate (release sperm within a female's reproductive tract). Females can broadcast spawn, brood eggs on an external surface, or brood eggs

Table 6.1. Experimental evidence of variation in female fertilization success in free-spawning invertebrates. Mean and range of the percentage of eggs fertilized and a summary of the major factors influencing variation in fertilization.

	% Fertilization			
Taxa	**Mean**	**Range**	**Effect**	**Reference**
Cnidarians				
Hydrozoans				
Hydractinia echinata	41	0–91	Female fertilization decreased with male distance	Yund (1990)
Bryozoans				
Celloporella hyalina	100	100[a]	Selfing inversely related to number of conspecific male zooids	Yund and McCartney (1994)
Echinoderms				
Asteroids				
Acanthaster planci	32	0–90	Female fertilization decreased with male distance	Babcock *et al.* (1992)
Asterias forbesi	52	2–99	Female fertilization decreased with depth	Present study
Echinoids				
Clypeaster rosaceus	30	2–72	Female fertilization decreased with male distance	Levitan and Young (1995)
Diadema antillarum	23	0–99	Female fertilization increased with male density and decreased with male distance, male size not significant	Levitan (1991)
Strongylocentrotus droebachiensis	30	1–95	Female fertilization increased with male abundance, decreased with male distance and flow	Pennington (1985)
Strongylocentrotus franciscanus	18	0–82	Female fertilization increased with abundance and aggregation, decreased with flow	Levitan *et al.* (1992)
Chordates				
Ascidians				
Botryllus schlosseri	41	25–60[b]	Female fertilization increased with male density, male success decreased with male competition	Yund and McCartney (1994)

[a] Selfing hermaphrodite.

[b] Range of means across treatments.

Table 6.2. Natural observations of variation in female fertilization success in free-spawning invertebrates.

Taxa	% Fertilization		Comments	Reference
Cnidaria				
Gorgonians				
Briareum asbestinum	4	<0.01–6.5	Variation related to density	Brazeau and Lasker (1992)
Plexaura kuna	c. 20	0–100	Few male clones	Lasker *et al.* (1996)
Pseudoplexaura porosa	51	0–80[a]	Common	Lasker *et al.* (1996)
Scleractinians				
Montipora digitata	c. 30	0–75	Variation related to spawning synchrony	Oliver and Babcock (1992)
Arthropoda				
Merostomata				
Limulus polyphemus	74	0.6–100	No effect of satellite males	Loveland and Botton, in review
Echinodermata				
Asteroids				
Acanthaster planci	44	23–83	Variation related to spawning synchrony	Babcock and Mundy (1992)
Holothuroids				
Cucumaria frondosa	c. 70	45–82[b]	High density and synchrony	Hamel and Mercier (1966)
Cucumaria miniata	92	1–100	High density and synchrony	Sewell and Levitan (1992)
Actinopyga lecanora	73	67–78	Several individuals spawning	Babcock *et al.* (1992)
Bohadshia argus	57	0–96	Variation related to distance from males	Babcock *et al.* (1992)
Holothuria coluber	33	9–83	Variation related to synchrony	Babcock *et al.* (1992)

[a] Range of means across days.

[b] Range of means across multiple samples.

internally (after internal fertilization). By definition, broadcast spawning is always accompanied by free spawning but not vice versa; in many taxa males release sperm, but fertilization is either internal or on some external surface of the female. Giese and Kanatani (1987) appear to define free and broadcast spawning as above, but they sometimes use these terms interchangeably. Because holding and releasing eggs are alternative reproductive strategies with different consequences, these terms are strictly defined in this chapter. This review concentrates on broadcast spawning (leading to external fertilization) but also mentions studies in which males free spawn but females brood eggs (leading to internal fertilization). Including the latter group addresses the influence on sexual selection of release of sperm into an aquatic environment.

Sperm competition is defined as direct competition among males for a limited number of unfertilized eggs. For example, a case in which sperm from one male cannot fertilize an egg because it has already been fertilized by sperm from another male constitutes sperm competition. A case in which sperm from one male collide with more virgin eggs than that from another male is not sperm competition. The reason for drawing this distinction is that interesting differences in sexual selection arise under conditions of intense sperm competition (in which sperm are abundant) and sperm limitation (in which sperm are rare).

Arnold (1994a, p. S9) defined sexual selection as 'selection that arises from differences in mating success,' where mating success is defined as the 'number of mates that bear or sire progeny over some standardized time interval.' However, this definition of mating success does not address the issue of multiple paternity in a clutch and does not include selection that arises from differences in fertilization efficiency. For example, if five males and five females spawn synchronously, multiple paternity is likely. In addition, the selection that can influence the proportion of eggs fertilized by any one male should be included as sexual selection. Sexual selection is defined here as selection that arises from intrasexual differences in the proportion of an individual's gametes that fuse to become zygotes. This definition allows for multiple paternity and includes differences arising from mating success or fertilization efficiency. By this definition, sexual selection becomes unimportant to that sex when fecundity in that sex is no longer limited by fertilization. This definition is different from those that include mate fecundity (Arnold 1994a; Møller 1994) because it is independent of the number offspring produced – which can be influenced by natural selection – and depends simply on per-gamete success relative to others of the same sex.

I focus on dioecious marine invertebrates because hermaphroditic species (see Chapter 7) and fish (see Chapter 11) are covered elsewhere in this volume, but I refer to these other groups for comparative purposes. Detailed taxon-by-taxon coverage of the reproductive biology of free-spawning invertebrates is beyond the scope of this review but is available in the excellent set of volumes entitled *Reproduction in Marine Invertebrates*, edited by Giese, Pearse and Pearse (1975–91).

III. FACTORS INFLUENCING FERTILIZATION SUCCESS

The fertilization ecologies of internally and externally fertilizing species differ in a number of ways. Because in externally fertilizing species sperm are not deposited within the female, the probability of sperm–egg encounters can be highly variable and can depend on a variety of factors ranging from attributes of the environment to those of the population, individual, and gamete (discussed in Section III.A, B, C and D, respectively).

A. Environment

In broadcast spawners, the probability of fertilization, from either a male or a female perspective, is primarily a function of gamete concentration. In an aquatic environment, gametes can diffuse and become diluted quickly. For example, along high-wave-intensity shores, gametes diffuse so quickly that males spaced greater than 10 cm upcurrent from a female have reduced fertilization success (predicted by Denny and Shibata 1989; own unpublished data).

Under less severe conditions, such as protected coastlines, subtidal environments buffered from sea-surface conditions, or calmer weather, fertilization becomes more likely but is still constrained by the flow conditions. In the Bahamas, even under moderate-flow conditions (10 cm s^{-1}), dye particles and sperm were diluted by five orders of magnitude in only 20 s (Levitan and Young 1995). In the San Blas Islands, off the coast of Panama, under low-flow conditions (0.4–2.9 cm s^{-1}) dye particles were diluted by two orders of magnitude within 2 min of release (Lasker and Stewart 1992). Similarly, on the Great Barrier Reef, crown-of-thorns *Acanthaster planci* sea star sperm was diluted by two orders of magnitude within 1 m of release under low (2 cm s^{-1}) flow conditions (Benzie *et al.* 1994).

Several field experiments have documented a decline in the percentage of fertilized eggs with increasing water flow (Pennington 1985; Levitan *et al.* 1992; Petersen *et al.* 1992). Increased water velocity increases the rate of mixing, making gamete plumes larger and more diffuse, reducing the probability of gamete collision.

Even if gametes are in sufficient concentration, fertilization may be inhibited by water movement. Shear forces on gametes released into turbulence have been predicted to cause eggs to spin at up to 100 revolutions per second (Denny *et al.* 1992). Laboratory experiments demonstrate that the shear forces experienced by gametes in highly exposed environments can disrupt sperm–egg interactions, resulting in decreased fertilization success (Epel 1991; Mead and Denny 1995).

The depth of water in which the gametes are mixed can also influence levels of fertilization (Fig. 6.1). As the volume of water decreases, the concentration of gametes increases. Some marine invertebrates move into shallow water to spawn (Giese and Kanatani 1987; Pearse 1979), wait until low tide (McEuen 1988; Sewell and Levitan 1992), or circumvent the dilution problem by releasing buoyant gamete bundles (Oliver and Willis 1987).

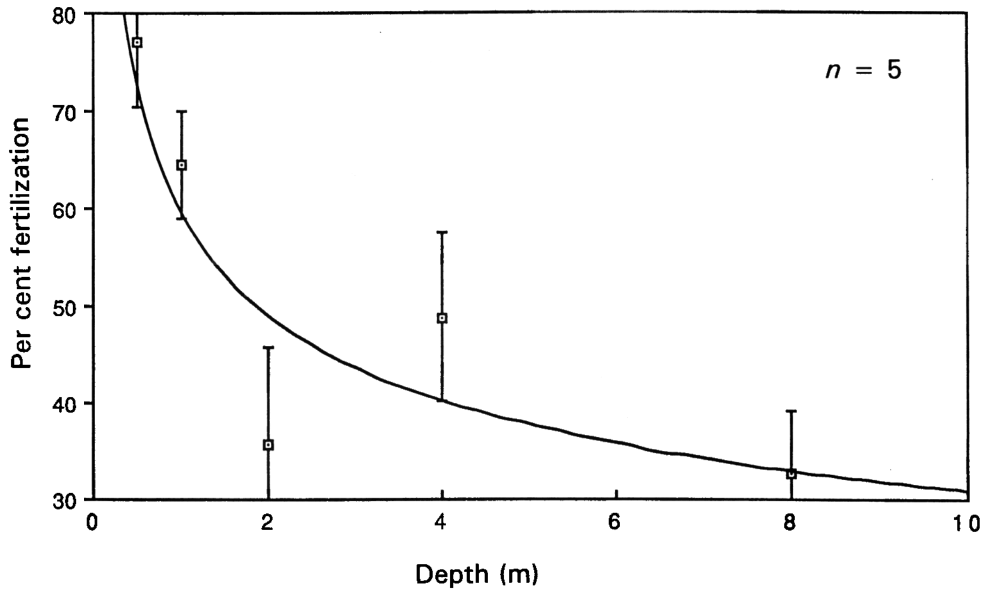

Fig. 6.1. *Female fertilization success decreases with increasing water depth in the sea star* Asterias vulgaris. *Eggs and sperm were collected in the laboratory; eggs were placed in Nitex containers, and sperm were placed in syringes. Gametes were brought to the field (sandy beach habitat, Nahant, MA, USA), and at each depth three Nitex bags were placed at the points of a triangle of 0.5 m side and suspended 15 cm off the bottom. Sperm were released into the centre of the triangle and 30 min later the containers were brought to the laboratory and examined for evidence of fertilization (mean and standard deviation reported). One replicate was conducted per day for 5 days during July 1989. Data collected by D. Levitan and S. Rumrill.*

B. Population

Gamete concentration and the probability of sperm–egg encounters are controlled not only by the rate of diffusion but also by the rate and timing of gamete release. At the population level, factors that can influence the local concentration of gametes are the distance between individuals and the abundance of individuals. There are also group behaviours such as aggregation and spawning synchrony that determine the distribution and abundance of animals that spawn simultaneously.

Most experimental studies of female fertilization success as a function of distance from a spawning male indicate that fertilization decreases to about 20% at 1 m and about 1% at 10 m (Pennington 1985; Yund 1990; Levitan 1991, 1995a; Yund and McCartney 1994; Levitan and Young 1995). Data from natural spawns also indicate that females spawning several metres from a male have very low levels of fertilization (Table 6.2). One exception to this finding is an experimental study with the large crown-of-thorns sea star in which fertilization of 6% was noted

100 m downstream of a single spawning male (Babcock *et al.* 1994). This exception may be a result of the high sperm output of this large-bodied species (Babcock *et al.* 1994) or the ability of eggs of this species to be fertilized at low sperm concentrations (Benzie and Dixon 1994).

In addition to the distance between males and females, the abundance of spawning individuals also influences the levels of fertilization. Experimental studies indicate that fertilization success increases as either the degree of aggregation or the number of spawning individuals increases. In the temperate sea urchin *Strongylocentrotus droebachiensis*, when the number of males increased from one to three, fertilization increased from around 5% to 60% 1 m from the spawning males (Pennington 1985). In the congeneric *Strongylocentrotus franciscanus*, fertilization increased by 12% as the number of males increased from two to eight in a 64-m^2 area (Levitan *et al.* 1992). In the tropical sea urchin *Diadema antillarum*, fertilization increased from 7% to 45% as the number of males increased from one to four and the experimental area decreased from 1 m^2 to 0.25 m^2 (Levitan 1991). In the brooding ascidian *Botryllus schlosseri*, an increase of up to 25% of eggs fertilized was noted when the number of free-spawning males increased from one to three colonies per experiment (Yund 1995).

Patterns of synchrony and aggregation are still poorly understood for the majority of free spawners (but see review by Giese and Kanatani 1987). In some instances synchrony appears to be high – sponges (Reiswig 1970), cnidarians (Harrison *et al.* 1984; Shlesinger and Loya 1985; Babcock *et al.* 1986; Minchin 1992; Lasker *et al.* 1996), nemerteans (Wilson 1900), polychaetes (Hornell 1894; Hargitt 1910; Schroeder and Hermans 1975; Caspers 1984; Babcock *et al.* 1992), molluscs (Gutsell 1930; Battle 1932; Wilborg 1946; Coe 1947; Babcock *et al.* 1992; Minchin 1992; Stekoll and Shirley 1993), enteropneusts (Hadfield 1975), echinoderms (Minchin 1987, 1992; McEuen 1988; Babcock *et al.* 1992; Sewell and Levitan 1992; Hamel and Mercier 1996) – whereas other observations indicate sporadic and unpredictable patterns of spawning – sponges (Reiswig 1970; Babcock *et al.* 1992), cnidarians (Shlesinger and Loya 1985; Babcock *et al.* 1992), polychaetes (Babcock *et al.* 1992), molluscs (Babcock *et al.* 1992), echinoderms (Levitan 1988; Pearse *et al.* 1988; Babcock *et al.* 1992). In the sea urchin *D. antillarum*, there was little evidence of spawning synchrony or aggregation in a systematic survey of aggregation and reproductive readiness (indicated by release of mature gametes on stimulation with KCl) in over 100 observations of natural spawning (Levitan 1988). In the north-east Pacific, individuals from several species were seen to spawn in isolation (Pearse *et al.* 1988). On the Great Barrier Reef (Babcock *et al.* 1992) a systematic survey of spawning times and number of animals seen spawning revealed a large number of isolated individuals spawning alone (Fig. 6.2A). The degree of conspecific synchrony increased during observations of multispecies spawning events (Fig. 6.2B).

Patterns of aggregation are also mixed. There are observations of

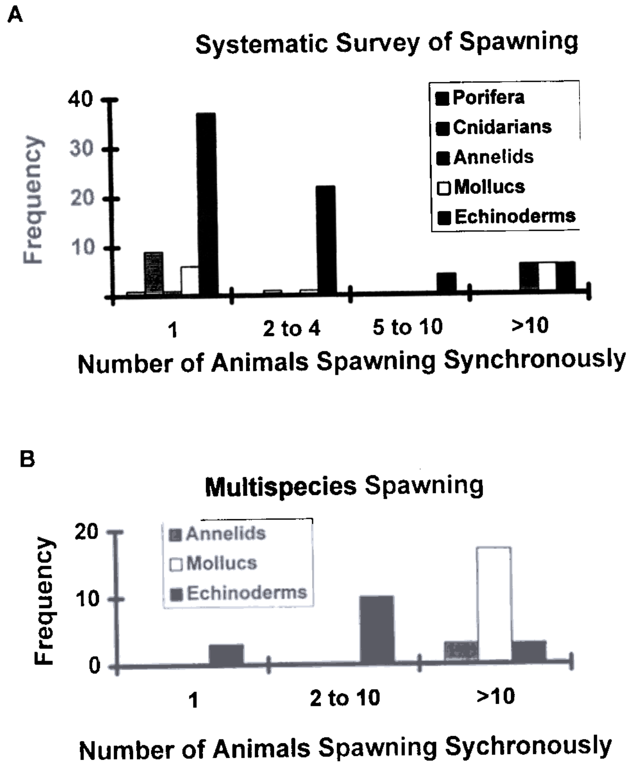

Fig. 6.2. *Frequency distribution of the number of synchronously spawning conspecifics on the Great Barrier Reef. Data from Babcock* et al. *(1992).* **A.** *Data collected during a systematic survey.* **B.** *Data collected during multispecies spawning events.*

large-group spawning (Schroeder and Hermans 1975; Pennington 1985; Giese and Kanatani 1987; Pearse and Cameron 1991; Minchin 1992), small-group spawning (Randall *et al.* 1964; Pennington 1985; Minchin 1987; Stekoll and Shirley 1993; Tominga *et al.* 1994; Unger and Lott 1994), pair spawning (Uchida and Yamada 1968; Schroeder and Hermans 1975; Run *et al.* 1988; Smiley *et al.* 1991; Tyler *et al.* 1992; Young *et al.* 1992), and isolated spawning (Randall *et al.* 1964; Pennington 1985; Minchin 1987; Levitan 1988; Pearse *et al.* 1988; Smith 1989; Pearse and Cameron 1991; Babcock *et al.* 1992).

Simulation models of aggregation in broadcast-spawning organisms predict that fertilization success will increase in a nonlinear fashion with increased aggregation (Levitan and Young 1995). If aggregation incurs costs (e.g. the energetic cost of finding mates, or food limitation at high density) in addition to fertilization benefits, and the benefits of aggregation decrease with population size (because abundance and distribution influences fertilization success; Levitan *et al.* 1992), aggregative behaviour may not always be advantageous, even if fertilization is not maximized (Levitan and Young 1995).

One of Thorson's rules (1950) is that males often spawn first during broadcast spawning events. Sperm, along with many other environmental cues (phytoplankton, temperature, salinity, light) can trigger spawning in both males and females (reviewed by Giese and Kanatani 1987). Thorson's rule has support across many taxa: 37 species across seven phyla cited by Thorson (1950) and more recently cnidarians (Cambell 1974), priapulids (van der Land 1975), sipunculids (Rice 1975), enteropneusts (Hadfield 1975), molluscs (Pearse 1979), and echinoderms (McEuen 1988; Hendler 1991). It is not absolute because several taxa have been noted in which females spawn first – sipunculids (Rice 1975), echinoderms (Hendler 1991; Chia and Walker 1991) – and numerous studies (as cited in the preceding paragraphs) make no note of sexual differences in spawning times. Differences in spawning times and in gamete attributes may be the only instances of sexual differences commonly found among broadcast spawners. A delay in female spawning may represent active choice or simply reflect constraints on egg release (e.g. maturation; Giese and Kanatani 1987) not present in sperm. The former alternative may represent evidence for female choice in external fertilizers; females may wait until the ambient sperm concentration is acceptable before spawning. If so, research is needed into changes in the threshold of choice with spawning season, female age, gamete age, decreasing opportunity, or increasing risk of adult mortality. If the last alternative is an important constraint, then the question becomes 'why do males spawn early?' rather than 'why do females delay?' The lag time may allow males to accumulate sperm to a critical concentration before females release eggs. For example, if water movement is slight, males that spawn first may have a higher relative sperm concentration than males that delay. Obviously, males that spawn too early, like females that delay too long, risk reproductive failure. Additional studies, particularly in situations where females spawn first, may shed light on the selective pressure on sexual differences in the timing of spawning.

Multispecies spawning events are often witnessed (Babcock *et al.* 1986, 1992; Minchin 1987, 1992; Pearse *et al.* 1988; Sewell and Levitan 1992). The best-known example is on the Great Barrier Reef off Australia, where over 100 species of corals spawn in a single annual mass-spawning event (Harrison *et al.* 1984; Babcock *et al.* 1986). Most species spawn during the week following the full moon within a 2- to 3-day period. Spawning is restricted to a 4-h period starting at sunset. Although there is temporal separation among some species, at any one time numerous species spawn simultaneously (Babcock *et al.* 1986). Interestingly, in the Red Sea, species spawn at various times during the year, and interspecific overlap is small (Shlesinger and Loya 1985). Multispecies spawning may result from selection for satiation of egg/embryo predators or simply from multiple species' using the same cues for optimal spawning times for enhanced fertilization or offspring survival

(Babcock *et al.* 1986). At least on the Great Barrier Reef, it appears that the costs of species-specific spawning times outweigh those of hybridization or egg or embryo death caused by fertilization with heterospecific sperm (see Willis *et al.* in press, for heterospecific fertilization of mass-spawning reef corals).

C. *Individual behaviour*

Individuals also can influence the distribution of gametes in the environment through changes in the rate and timing of gamete release, spawning behaviour, and the amount of energy invested in reproduction. Sexual dimorphism in reproductive allocation is discussed in Section V.

The rate at which gametes are extruded from the gonopore influences the distribution of gametes in the environment. A high spawning rate increases the gamete concentration (Denny and Shibata 1989) but decreases the spatial extent of the gamete cloud. A high spawning rate should be correlated with high spawning synchrony, close male–female pairing, and intense sperm competition.

The relative concentration of sperm may be of key importance in sperm competition. Studies of reproductive success on sessile free-spawning brooding ascidians and bryozoans indicate that males that are closer to females, and hence have the opportunity to place more concentrated sperm at the female than more distant males, can outcompete more distant males for fertilizations (Yund and McCartney 1994).

Reef fish tend to spawn within seconds during tightly paired and highly synchronized spawning rushes (Robertson and Hoffman 1977; Johannes 1978; Thresher 1984) that often involve multiple males (Warner *et al.* 1975). Swarming polychaetes also spawn quickly in tight synchrony (Schroeder and Hermans 1975). Observations of benthic invertebrates indicate that, although some may spawn within seconds (echinoderms, Hendler 1991; Holland 1991), at least in some cases, individuals can spawn for intervals ranging from nearly an hour to days. Examples include sponges (Reiswig 1970; Fell 1974), enteropneusts (Hadfield 1975), molluscs (Pearse 1979), brachiopods (Chuang 1959), and echinoderms (McEuen 1988; Hendler 1991; Hamel and Mercier 1996). Measurement of spawning rate and the correlation of spawning rate with aspects of sperm limitation and competition, although neglected, might be fruitful areas of research.

Typical spawning behaviour for many broadcast-spawning fishes and invertebrates is to rise into the water column before spawning. The distance reef fish rise from the substratum into the water column is positively correlated with body size (Thresher 1984). Echinoderms typically climb onto structures, rise up on arms, or rear their entire bodies upward during gamete expulsion (McEuen 1988; Hendler 1991; Babcock *et al.* 1992; Minchin 1992). Anemones have been noted to extend their columns upward during spawning (Minchin 1992), abalone climb kelp stipes (Stekoll and Shirley 1993), and chitons can assume a vertical orientation (Pearse 1979). This behaviour is thought to increase post-zygotic survivorship by getting the gametes away from benthic filter feeders and egg predators (Robertson and Hoffman 1977; Johannes 1978), but it could also keep negatively buoyant eggs from getting trapped in the sediment before the larvae can swim. These factors are independent of fertilization. Alternatively, these behaviours could serve to facilitate gamete mixing.

I have seen two individuals of the sea urchin *D. antillarum* spawn at a leisurely rate until they bumped into each other, at which time they rapidly spawned bursts of gametes as they tried to hop on top of each other; they were the only individuals seen to spawn at that time, but they were both male. This anecdote, like many others, typifies the dilemma associated with external fertilization in many benthic invertebrates; natural selection has programmed these organisms in ways that seem adaptive – increased aggregation and spawning intensity when detecting a spawning conspecific – but nonetheless their limited mobility, perceptual ability, and opportunity promote gamete wastage and sperm limitation.

D. Gamete

The numerous factors described above determine the concentration of gametes, the rate of gamete dispersion, and the degree of mixing of gametes from different individuals. This information, although critical, is not sufficient to predict levels of fertilization. Variation in gamete performance has been noted both among species (Branham 1972; Levitan 1993) and within species (Hultin and Hagström 1956; Levitan *et al.* 1991; Benzie and Dixon 1994; Levitan 1996a) in the laboratory. Variation in gamete performance has also been documented within (Levitan 1996a) and among species (Levitan 1995b) in the field.

Variation in gamete performance is linked to variation in gamete attributes. Models that predict the degree of fertilization generally include not only gamete concentration but also a variety of gamete attributes (Rothschild and Swann 1951; Vogel *et al.* 1982; Denny and Shibata 1989), which include egg size, the receptiveness of the egg surface to sperm, sperm velocity, and sperm longevity. Egg traits that have been demonstrated to vary across taxa are buoyancy, size, the proportion of sperm–egg collisions that result in fertilizations, the size and presence of jelly coats or other structures that can capture sperm, and the presence of sperm chemoattractants. Variation has been documented in sperm traits such as velocity, longevity, behaviour, and buoyancy (Levitan 1995a).

The size of the egg target can influence the number of sperm–egg collisions. Models generally consider the target size of the egg to be cross-sectional area (Rothschild and Swann 1951; Vogel *et al.* 1982; Denny and

Shibata 1989; Levitan 1993, 1996a,b; Podolsky and Strathmann 1996). Empirical data from the laboratory indicate that, among sea urchins in the genus *Strongylocentrotus*, increased egg cross-sectional area is correlated with a decrease in the concentration of sperm needed to fertilize it (Levitan 1993). This correlation is also evident within *S. franciscanus*, where 45% of the variation among females in the amount of sperm needed to fertilize 50% of the eggs could be explained by mean egg size (Levitan 1996a). Egg size also appears to be important within a single clutch of eggs. In the sea urchins *S. franciscanus* and *Strongylocentrotus purpuratus*, larger eggs were preferentially fertilized when sperm were limiting (Levitan 1996a).

Varying egg shape could provide a mechanism to increase egg target size and sperm–egg collisions without increasing egg volume (Podolsky and Strathmann 1996), but there could be developmental constraints on egg shape. Experiments in which echinoderm eggs are artificially deformed result in abnormal cleavage patterns (Rappaport and Rappaport 1994). Fish eggs, which come in a variety of shapes, have a small restricted area for sperm attachment, the micropyle (Amanze and Iyengar 1990). Because, in some taxa, the sperm attachment site determines planes of embryonic symmetry (Schroeder and Hermans 1975), it would be interesting to determine whether deviations from a symmetrical egg shape are correlated with restrictions in the surface available for fertilization.

Other attributes, such as jelly coats, accessory cells, or the effective range of chemoattractants, may also contribute to effective egg target size (Levitan 1995a; Podolsky and Strathmann 1996). These mechanisms have, to varying degrees, been shown to influence either levels of fertilization (jelly coats: Rothschild and Swann 1951; Podolsky 1995; follicle cells: T. Bolton and J. Havenhand, personal communication) or sperm behaviour (chemotaxis, Miller 1985) in the laboratory, but the efficiency of these potentially energetically economical solutions may be reduced under field conditions (e.g. jelly coats degrade to approximately 25% of original size in less than 1 min in moving water; own unpublished data).

Another mechanism for increasing egg target size, without increasing the level of energy investment, is to inflate eggs with water (Levitan 1993); however, developmental constraints may limit dilution (Podolsky and Strathmann 1996) and if all species dilute egg material to the same extent, it would be difficult to establish any patterns across taxa.

The ratio of predicted sperm-egg collisions to successful fertilizations varies among and within species (Vogel *et al.* 1982; Levitan 1993, 1996a), perhaps as a result of differences in properties of the egg surface (e.g. the number or distribution of sperm receptor sites) or of variation in sperm quality (e.g. inability to fertilize a particular egg or any egg).

Variation in sperm attributes may influence fertilization dynamics. Sperm morphology is correlated with function: 'In the Metazoa the primitive sperm is a small cell with a short rounded-conical head, a small and short middle piece containing a few (often four) mitochondria, and a tail consisting of a flagellum about 50 mm long' (Franzén 1987; page 34). Across taxa, 'primitive' sperm are associated with free-spawning strategies and more 'modified' sperm with pseudocopulation and copulation (reviewed by Franzén 1987). Although primitive sperm are generally similar across taxa, sperm head size does vary and is positively correlated with egg size in echinoderms (Eckelbarger *et al.* 1989). The issue of whether primitive sperm are ancestral or simply reflect convergent evolution for swimming in the sea requires attention (Rouse and Fitzhugh 1994).

Greater sperm swimming velocity should increase the rate of fertilization (Vogel *et al.* 1982; Levitan *et al.* 1991) and could be important under conditions of sperm competition (Levitan 1995a). Similarly, greater sperm longevity should increase the probability of fertilization at greater distances from males and could be important when spawning synchrony is low (Levitan 1995a). Sperm velocity varies among (Gray 1955; Levitan 1993) and within species (Levitan *et al.* 1991; Levitan 1993) of sea urchins. Sperm longevity also varies among species of sea urchins (Levitan 1993) and across taxa (Levitan 1995a; Levitan and Petersen 1995). Although no direct tests have addressed the effects of sperm longevity or velocity on fertilization success, some interesting correlations exist.

Among three congeneric species of sea urchins, *S. purpuratus*, *S. franciscanus*, and *S. droebachiensis*, there is a fivefold range in egg size, an inverse relationship between egg size and sperm velocity, and an inverse relationship between sperm velocity and sperm longevity (Levitan 1993). The inverse relationship between sperm longevity and velocity may represent a trade-off in per-spermatozoon energy allocation (Levitan 1993; Bolton and Havenhand 1996). Small eggs and fast sperm would be expected in situations of high sperm concentration and sperm competition (decreased selective pressure for attracting sperm and increased selective pressure for fast, competitive sperm). Larger eggs and longer-lived sperm would be expected in situations of low sperm concentration and sperm limitation (increased selective pressure for attracting sperm and increased selective pressure for retaining sperm viability at greater times or distances from the point of spawning). Recent empirical studies appear to confirm this prediction; *S. purpuratus* (smallest egg and fastest but shortest-lived sperm) lives in tight aggregations and is least sperm-limited, and *S. droebachiensis* (largest egg and slowest but longest-lived sperm) is more dispersed and is most sperm-limited (own unpublished data). *Strongylocentrotus franciscanus* has intermediate values of gamete attributes, aggregation, and fertilization success.

Although data are few, other groups appear to follow this pattern. The tropical reef fish *Thalassoma bifasciatum* has high levels of fertilization, often mates in groups or in pairs with streaker males (Petersen *et al.* 1992), and seems to have very short-lived sperm (*c.* 15 s). At the other extreme, the sperm of deep-sea echinoids, whose densities may be low and spawning cues rare, have been observed to swim for several days (Eckelbarger *et al.* 1989), as have sperm from cold-water Antarctic echinoderms (J. Pearse, personal communication). It is unclear whether extreme sperm longevities in the colder environments are a function of selection for longevity *per se* or simply the physiological outcome of lower temperatures.

Sperm behaviour may also influence patterns of fertilization. Fertilization-kinetics models assume that sperm move randomly (Rothschild and Swann 1951; Vogel *et al.* 1982), or that sperm swimming is negligible under natural conditions (Denny and Shibata 1989), but sperm chemotaxis (Miller 1985), variation in activity related to sperm concentration (Chia and Bickell 1983) and egg products (Epel 1978), and sperm–sperm interactions (Rothschild and Swann 1951), all of which have been observed in the laboratory, may play important roles in the sea.

Spawned materials other than the gametes themselves can influence the viscosity and dispersability of the gametes. Eggs and sperm can be released in a cloud, in stringy masses, or in clumps (McEuen 1988; Thomas 1994a,b). Eggs of different species of polychaetes disperse at different rates (Thomas 1994a). Among sea urchins, intersex and interspecific variation in dispersal rates of gametes have been observed (Thomas 1994b). Sea urchin species that live in more exposed habitats spawn more viscous materials than do shallow-water species (Thomas 1994b). Varying the susceptibility of gametes to dispersion can influence gamete concentration and sperm longevity.

The subtle influences on fertilization that gamete traits show in the laboratory reveal the potential for selection on those traits to influence reproductive success. However, determining the intensity of these selective pressures requires field tests, because environmental, population, or individual-level factors may overwhelm gamete-level factors under natural conditions.

Experiments using the sea urchin *S. franciscanus* addressed this issue. Gametes were released in a uniform manner, through a syringe, into an environment that varied substantially from day to day (flow varied from 0 to 85 cm s^{-1}) with location and sea conditions typically present off the coast of western Canada. Despite the variation in environmental conditions, gamete performance in the laboratory explained over 50% of the daily variation in field levels of fertilization (Levitan 1996a). This result shows that the influence of gamete traits on fertilization is unlikely to be swamped by other factors and that natural selection on gamete traits for enhanced fertilization success is likely to be important.

IV BROADCAST SPAWNING AND BATEMAN'S PRINCIPLE

Bateman's principle suggests that, because sperm are more numerous than eggs, sperm will compete for fertilizations and males will have highly variable reproductive success (Bateman 1948). Some males, because of circumstance or quality, will garner a high proportion of fertilizations while others will have reduced fertilization success or complete reproductive failure because most, or all, females are mated, or eggs fertilized, before they get an opportunity. By the same token, a female will, on average, have a much higher percentage of her gametes fertilized and reduced variance in fertilization success. Females will not be limited by fertilization success, and their reproductive success will be determined by the availability of resources influencing egg production or postzygotic success.

The mechanism driving Bateman's predictions is the relative concentration of eggs and sperm. Sperm are much more abundant than eggs at the point of production in almost all taxa (but see Pitnick *et al.* 1995), and when sperm are deposited within females or directly on eggs, this disparity of numbers results in sperm competition and high female fertilization success. When gametes are released into the environment, however, the distribution and abundance of conspecifics, interacting with a turbulent aquatic environment, yield a highly unpredictable distribution of egg and sperm concentrations. Although, on average, sperm will be more concentrated than eggs, sperm can be limiting, and female fertilization success is no longer assured and can be highly variable.

Gamete interactions in an aquatic environment can be described as a two-dimensional continuum, with the ratio of sperm to eggs on one axis and the absolute concentration of gametes on the other (Fig. 6.3). The sperm–egg ratio determines the degree of sperm competition or egg competition. The gamete concentration axis determines the gradient of gamete limitation and the likelihood that competitive interactions will occur at all.

From the female perspective, the difference between sperm limitation and egg competition is that, in the former, removing eggs from other females would not increase the chances of fertilization for the remaining females' eggs; sperm rarely encounter any egg. In egg competition, removing eggs from other females would increase the chances of fertilization for the remaining females' eggs; sperm numbers are significantly depleted by the number adhering to eggs. From the male perspective, egg limitation and sperm competition differ in analogous ways.

This spectrum of gamete conditions influenced by environment, population, individual and gamete considerations can vary at a number of levels among and within species, from one spawning event to another over the lifetime of an individual, and among gametes in a single clutch. At the extreme, eggs released simultaneously from a single female may drift apart, such that some eggs experience intense sperm competition while others – because of the chaotic nature of water turbulence – miss a patch of sperm entirely. Thus, in a single spawning bout, both blocks to polyspermy and sperm chemotaxis could provide useful adaptations increasing reproductive success (Levitan 1995a).

Because sperm are more abundant than eggs, sperm competition

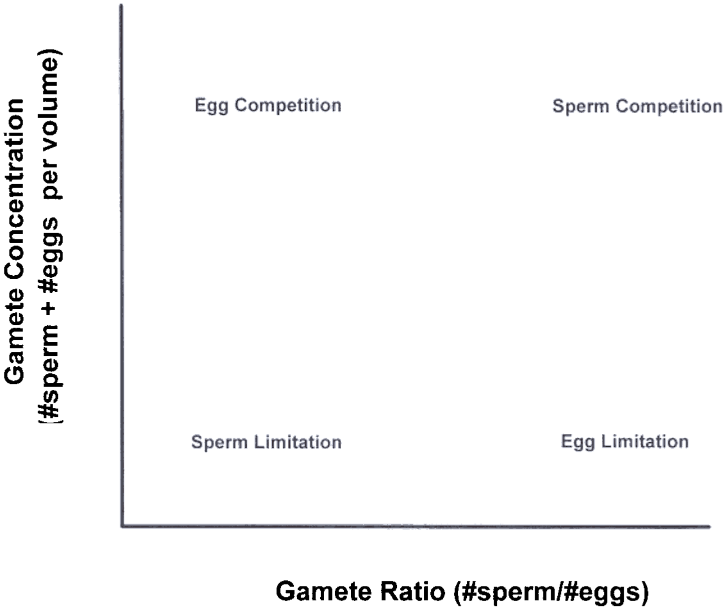

Fig. 6.3. *Gradient of relative and absolute gamete concentrations. There is a need for data from which to create a contour plot of the frequency distribution of absolute and relative gamete concentration during natural spawning events. These data will provide information on the intensity and symmetry of sexual selection in externally fertilizing species.*

should be more common than egg competition, but aspects of spawning behaviour and the nature of spawned materials may influence the relative dispersal of eggs and sperm. For example, if large numbers of eggs tend to remain clumped on or near the spawning female (McEuen 1988; Smith 1989; Thomas 1994a,b) and wisps of sperm occasionally pass by, then egg competition (certainly within a female and potentially among females) could occur. Once gametes have dispersed away from the spawning adults and gamete concentrations become exponentially reduced, then gamete competition will diminish and gamete interactions become rare.

Whether the present lack of field evidence for egg competition in broadcast spawners is due to our investigative biases or the general lack of information on gamete competition in broadcast spawners, or simply reflects the reality that eggs do not compete has yet to be determined. Laboratory studies on sea urchins have documented that, in a vial, larger eggs are preferentially fertilized over smaller eggs when sperm are limiting, so egg competition may exert a strong selective influence on egg size (Levitan 1996a). An important step in assessing gamete competition in broadcast spawners will be construction of a frequency distribution of gamete distributions on the gradients illustrated in Fig. 6.3.

There is very little information on how variability in fertilization success in males compares with that in females. Because each zygote is the product of one sperm and one egg, the average number of zygotes produced will be identical across sexes. What is less obvious is the distribution of fertilizations among individual males and females.

The key to determining the distribution of fertilization among sexes is the use of genetic markers to estimate parentage. In broadcast spawners the problem of identifying parentage is much more difficult because, in many cases, neither the male nor the female parent is known. In such cases, determining parentage by exclusion is not a very efficient mechanism because a marker must be absent in all the potential parents of one sex before it can be used to exclude parents of the other. The use of rare markers for inclusion or statistical clustering of highly polymorphic markers is preferable (Levitan and Grosberg 1993). Although such parentage assignments have been made in broadcast spawners in controlled experiments in the laboratory (Levitan and Grosberg 1993), the only field test has involved egg-laying horseshoe crabs (Brockmann *et al.* 1994; as discussed in Section V).

In situations or taxa where maternity can be observed with confidence, the problem of assigning paternity is more tractable. Genetic markers have been successfully used to determine paternity in free-spawning brooding ascidians (Grosberg 1991; Yund and McCartney 1994; Yund 1995) and bryozoans (Yund and McCartney 1994). Only one of these studies (Grosberg 1991) used a natural population and, in that case, the dispersal of a rare allele from a focal sperm source was investigated rather than comparisons of paternity among males. In Grosberg's study, the density of animals was high enough that variation in female fertilization success caused by sperm limitation was assumed to be negligible (R. K. Grosberg, personal communication). In the other ascidian studies (Yund and McCartney 1994; Yund 1995), variation in both male and female fertilization was noted, and the distribution was attributed to both body size (sperm production) and positional effects (male–female distance). In these experimental studies, however, the positions of individuals were assigned and isolated from natural populations, so the overall levels of natural variation have yet to be determined. In the bryozoan study (Yund and McCartney 1994), variation in fertilization success was confounded by the animals' ability to self-fertilize.

V SEXUAL SELECTION AND SEXUAL DIMORPHISM

The notion that sperm and egg competition should be viewed as a continuum has been expressed in another way by Arnold (1994b). He suggests that the intensity of sexual selection can be expressed by the steepness of the slope between mating success and fecundity and that

Bateman's experiments highlight one pair of slopes (linear for males and single-mate saturation for females) out of a range of possibilities in which sexual selection can be intense for either males or females. One appealing aspect of this approach is that it provides a mechanism for comparing the shape of the sexual-selection relationship between sexes and matching these differences with patterns of sexual dimorphism. Sexual selection can be intense, but if the curves are similar across sexes then sexual dimorphism in, for example, energy allocation or body size may not evolve. Arnold (1994b) predicted a curve of diminishing returns in functionally male plants for which mate distance and pollination success are related. Because mate distance seems to be critically important in broadcast spawners (see Section III.B above), a similar curve for diminishing returns seems appropriate for both male and female spawners and has been observed in experimental studies (Levitan 1991). If the curves are similar over the range in mating success typically experienced in nature, then a reduction in sexual dimorphism is predicted. This would be the case if sperm limitation is common.

Plots of reproductive success as a function of investment in gametes and as a function of mating success provide a tool for understanding the relationship between gamete interactions, investment, and sexual dimorphism (Fig. 6.4). Equal investment in gametes across sexes suggests that the return on reproductive investment is similar across sexes, because of either ubiquitous sperm limitation or intense sperm competition (Levitan and Petersen 1995). In both cases a linear return on investment is predicted for both sexes; if twice as many eggs (or sperm) are produced, then twice as many zygotes should be produced relative to other individuals (Fig. 6.4a,b). If sperm competition or limitation is less important, then diminishing returns on investment are predicted for males but not for females because sperm typically greatly outnumber eggs (Charnov 1982; Petersen 1991).

The distinction between sperm competition and sperm limitation can be illuminated by the relationship between mating success and reproductive success (Fig. 6.4c,d). Sperm limitation results in increased offspring production with increased mating success for both males and females equally. For example, if a spawning male encounters double the number of spawning females, he doubles the total number of zygotes produced (e.g. 10% of eggs fertilized from twice as many eggs). Similarly, if a female encounters double the number of spawning males, she doubles the chances that sperm will fertilize her eggs. Males and females gain equally from increases in mating success, provided that sperm are limiting and competition is absent. Sperm competition results in sexual asymmetries in fecundity gains with increasing mating success. When all of a female's eggs are fertilized, then female fecundity is at a maximum, but a male's fecundity will continue to increase with mating success until all his sperm form zygotes (an unlikely event).

Sperm competition should result in sexual dimorphism in nongonadal traits (e.g. body size), as male–male competition and female choice

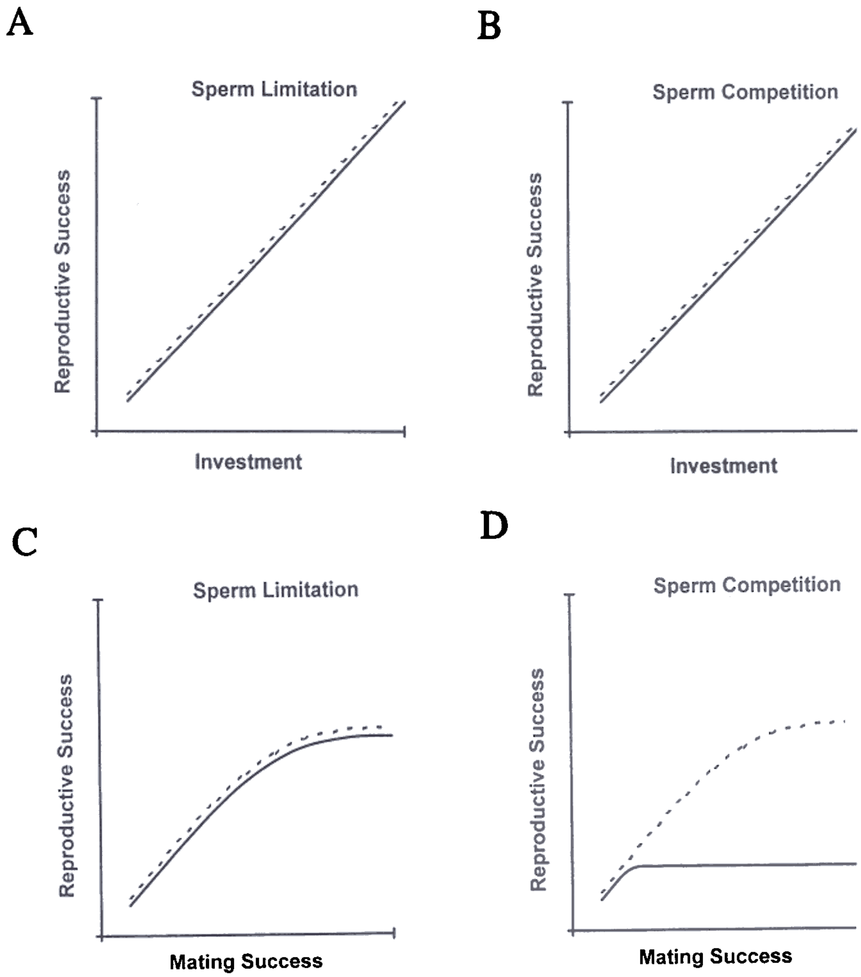

Fig. 6.4. *Reproductive success as a function of gamete investment (A and B) and mating success (C and D). Females are represented by the solid line and males by the dotted line. Under conditions of either sperm limitation or sperm competition, a linear relationship between gamete investment and reproductive success is predicted. In contrast, when reproductive success is a function of mating success ('the number of mates that bear or sire progeny over some standardized time interval', Arnold 1994a, p. S9) the response curves are predicted to be identical when sperm are limiting (C) but to differ when sperm compete in the same water mass for virgin eggs (D).*

become increasingly important. In contrast, sperm limitation should result in reduced sexual dimorphism, as sexual selection is equally intense across sexes.

However, because the intensity of sexual selection decreases to zero when reproductive success is no longer limited by fertilization, and

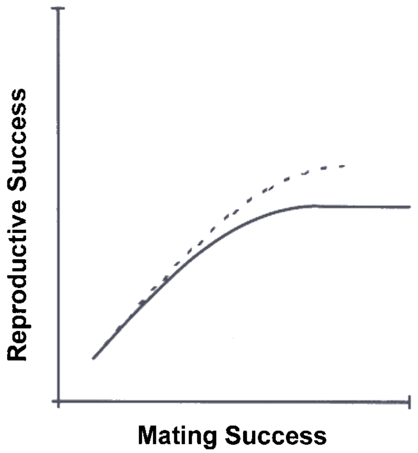

Fig. 6.5. *Reproductive success as a function of potential mating success. Females are represented by the solid line and males by the dotted line. If the actual range of mating success is below the threshold at which the male and female curves diverge, then sperm is limiting, the sexes experience equally intense sexual selection, and sexual dimorphism should be reduced. If the actual range in mating success is above the threshold at which male and female curves diverge, then sperm is not limiting, sperm compete, sexual selection is more intense for males than for females, and sexual dimorphism should be enhanced. If the range in mating success spans the threshold, intermediate levels of sperm competition and sexual dimorphism are predicted.*

because males produce many more gametes than females do, it is unlikely that sexual selection will be equally intense over the entire range in potential mating success. In other words, the level of mating success needed to ensure that 100% of a female's eggs are fertilized should be much lower than the level of mating success needed to ensure that 100% of a male's sperm fertilize eggs. The important criterion is how the relationship between potential mating success and reproductive success relates to the actual range in mating success realized in nature. If the actual range in mating success is below the threshold at which the intensity of male and female sexual selection diverge, then sexual dimorphism should be lower than in situations in which the range in mating success is above this threshold (Fig. 6.5).

These graphical models (Fig. 6.4a,b) predict that, if either sperm competition or sperm limitation is the dominant selective regime in broadcast spawners, then the two sexes' investments in gametes should be identical. This prediction is consistent with available data. Sexual dimorphism in gonadal indices appears to be absent in broadcast spawners. Gonadal indices should be used with caution if there is an allometric relationship between body size and gonad size. However, because sexual dimorphism in body size is rare or absent in broadcast spawners (Table 6.3, p. 197), comparisons of gonadal indices between sexes within a species should be less problematic. Among the echinoderms, which generally broadcast spawn, no difference in gonadal indices were noted in any class (Table 6.4, p. 200). Because eggs and sperm have different functions, it is not surprising that the composition of gonads differs between the sexes in the asteroids and echinoids examined (Table 6.5, p. 202). Males have higher ash and protein components, females have higher lipid levels, and carbohydrate levels seem equivalent across sexes. Among the free-spawning mollusc classes, gonadal indices appear to be similar in species tested in the Polyplacophora (Pearse 1979) and Pelecypoda (Sastry 1979; Newell and Bayne 1980; Choi *et al.* 1993). In one case, males had higher gonadal indices in one out of two populations of mussels (Newell *et al.* 1982). These data, which indicate equal investment in gametes in the two sexes, cannot be used to differentiate between sperm limitation and sperm competition but can be used as evidence that noncompetitive pair spawning, with high levels of female fertilization, is uncommon in these taxa.

The graphical models (Fig. 6.4c,d) also predict that, if sperm limitation is the dominant selective regime in broadcast spawners, then reductions in sexual dimorphism in nongonadal traits such as body size should be evident. Alternately, if sperm competition is common in broadcast spawners, then sexual dimorphism in nongonadal traits should be evident as male competition and female choice become divergent selective forces. The evidence matches the hypothesis that sperm limitation is the common selective environment in broadcast spawners. A correlation between external fertilization and reduced sexual dimorphism has often been stated without presenting data or a citation (e.g. Parker 1984; Strathmann 1990). A glance at Table 6.3 may indicate why – the pattern is striking. When both eggs and sperm are released, sexual dimorphism of any kind is overwhelmingly absent. In groups where males free spawn but females brood eggs, sexual dimorphism is also reduced and restricted to anatomical modifications associated with brooding. Size dimorphisms are common when fertilization is internal.

Perhaps most convincing are taxa that generally have one mode of reproduction with exceptions. In the Echiura, most free spawn, and no sexual dimorphism has been noted, but in the family Bonellidae, size dimorphism is extreme (males are dwarf) and fertilization is internal. In the polychaetes, although free spawning is common, species that copulate can have dwarf males that have been described as ‘no more than a swimming penis’ (Schroeder and Hermans 1975). Echinoderms typically free spawn, but the protandric sea cucumber *Leptosynapta clarki* has internal fertilization and small males (Sewell 1994), and concentricycloid males tend to be smaller and to have anatomical modifications for pseudocopulation (Rowe *et al.* 1991). Gastropod molluscs generally have internal fertilization, but the archaeogastropods tend to free spawn and to have reduced sexual dimorphism (Webber 1977).

Potential exceptions to this correlation between mode of reproduction and sexual dimorphism include a few species of pelecypods with slight shell differences, a few species of brittle stars (echinoderms), the males of which

Table 6.3. Patterns of gamete release and nongametic sexual dimorphism in invertebrates. In some cases, differences in the anatomy or colour of the reproductive structures were noted. These instances are reported as 'no external dimorphism'. The bottom of the table reports a summary of these patterns.

Taxa	Male	Female	Sexual dimorphism	Reference
			None	Fell (1974)
			None	Cambell (1974)
			All hermaphrodites	Pianka (1974)
Platyhelminthes				
Turbellaria	Copulate	Brood	Dwarf males in dioecious species	Henley (1974)
Gnathostomulida	Copulate	Brood	All hermaphrodites	Sterrer (1974)
Nemertinea	Free spawn/ pseudocopulate	Broadcast/brood	Males smaller in some species that pseudocopulate	Riser (1974)
Nematoda	Copulate	Brood	Yes, in dioecious species	Hope (1974)
Rotifera	Copulate	Brood	Males smaller in dioecious species	Thane (1974)
Gastrotricha	Copulate	Brood	All hermaphrodites	Hummon (1974)
Kinorhyncha	Copulation (assumed)	Brood	Some morphological differences	Higgins (1974)
Entoprocta	Free spawn	Brood	No consistent evidence for dimorphism	Mariscal (1975)
Tardigrada	Copulate/ pseudocopulate	Brood	Males often smaller	Pollock (1975)
Priapulida	Free spawn	Broadcast	No external dimorphism	van der Land (1975)
Sipuncula	Free spawn	Broadcast	None	Rice (1975)
Pogonophora	Spermatophore	Brood	Males can be smaller	Southward (1975)
Echiura	Free spawn/ copulate	Broadcast/brood	In family Bonellidae fertilization is internal with dwarf males; in other groups fertilization is external, with no size dimorphism	Gould-Somero (1975)
Annelida				
Polychaeta	Free spawn/ copulate	Broadcast/brood	Species that copulate often have dwarf males; otherwise no dimorphism	Schroeder and Hermans (1975)
Clitellata	Copulate	Brood	All hermaphrodites	Lasserre (1975)
Phoronida	Free spawn	Broadcast/brood	?	Zimmer (1991)
Bryozoa	Free spawn	Broadcast/brood	All hermaphrodites	Reed (1991)
Brachiopoda				
Articulata	Free spawn	Broadcast/brood	None (except brood chambers) majority no dimorphism	Long and Strickler (1991)

Continued

Table 6.3. Continued

Taxa	Male	Female	Sexual dimorphism	Reference
Mollusca				
Aplacophora	Free spawn	Assumed broadcast	None in dioecious species	Hadfield (1979)
Monoplacophora	Free spawn	Broadcast	None	Gonor (1979)
Polyplacophora	Free spawn	Broadcast	No external dimorphism	Pearse (1979)
Pelecypoda	Free spawn	Broadcast/brood	Rare shell differences, vast majority no external dimorphism	Sastry (1979)
Gastropoda	Most copulate/few free spawn	Most brood/few broadcast	Archaeogastropods tend to free spawn and to have little dimorphism; the other groups tend to copulate and to have size dimorphisms	Beeman (1977), Berry (1977), Webber (1977)
ıopoda	Free spawn	Broadcast	No external dimorphism	McFadien-Carter (1979)
Cephalopoda	Copulate	Brood	Size dimorphisms noted	Haven (1977), Arnold and Williams-Arnold (1977), Wells and Wells (1977), Charniaux-Cotton *et al.* (1992)
Arthopoda				
Crustacea	Copulate	Brood	Size and appendage dimorphisms	Giese and Kanatani (1987, 1992)
	Copulate, spermatophore	Brood	Primary and secondary sexual characters commonly dimorphic	Giese and Kanatani (1987), Gillot *et al.* (1992)
Merostomata	Free spawn (close pairing)	Broadcast	Males smaller and appendage dimorphism	Giese and Kanatani (1987)
Pycnogonida	Free spawn (close pairing)	Brood		Giese and Kanatani (1987)
Echinodermata				
Asteroida	Free spawn (pairing rarely)	Broadcast/brood	None (except brood pouches)	Chia and Walker (1991)
Ophiuroida	Free spawn (pairing noted)	Broadcast/brood	Some males smaller in rare pairing species	Hendler (1991)
Echinoidea	Free spawn (pairing rarely)	Most broadcast/some brood	None (except brood pouches)	Pearse and Cameron (1991)

Table 6.3. Continued

Taxa	Male	Female	Sexual dimorphism	Reference
Holothuroidea	Free spawn (pairing rarely)	Broadcast/brood	None (except brood pouches)	Smiley *et al.* (1991)
Crinoidea	Free spawn	Broadcast/brood	None (except brood pouches)	Holland (1991)
Concentricycloidea	Pseudo-copulate (assumed)	Brood (assumed)	Males often smaller	Rowe *et al.* (1991)
Chaetognatha	Pseudo-copulate	Brood	All hermaphrodites	Reeve and Cosper (1975)
Hemichordata				
Enteropneusta	Free spawn	Broadcast	None	Hadfield (1975)
Pterobrancha	Free spawn	?	None	Hadfield (1975)
Chordata				
Tunicata	Free spawn	Broadcast/brood	All hermaphrodites	Berrill (1975)
Acrania	Free spawn	Broadcast	None	Wickstead (1975)

Summary of sexual dimorphism and reproductive mode

	Sexual dimorphism		
Reproductive mode	Absent	Rare	Common
Free spawning and brood	2	1	5[a]
Free spawning and broadcast	20	2	1
Pseudocopulation and brood	0	0	
Copulation and brood	0	0	

[a] Only dimorphism is the presence of brood chambers.

are often smaller, and horseshoe crabs (arthropods), the males of which are generally smaller. Size dimorphism in brittle stars appears to be associated with male–female pairing. Observations of pairing appear to be associated with dwarf males, although there are few data (Hendler 1991). When males pair and attach to females, the likelihood of sperm limitation decreases and sexual dimorphism would be more likely (i.e. the sexes will differ in the costs and benefits of increased gamete production).

Horseshoe crabs characteristically spawn while clasped in pairs. This behaviour results in relatively high female fertilization success (R. Loveland and M. Botton, unpublished data; Table 6.1) and increases the possibility of male–male competition. Competition and multiple paternity among male horseshoe crabs are common (Brockmann *et al.* 1994). Male–female pairs climb up the shore and spawn in the presence of satellite males that, on average, sire 40% of progeny (Brockmann *et al.* 1994), an average higher than documented for fish competition. The high rate of satellite-male success is correlated with the position of the satellite male. Satellite males in the optimal position (anterior margin of

Table 6.4. Gonadal indices by sex in echinoderms. Publications prior to 1987 compiled by Lawrence and Lane (1982) and Lawrence (1987). Gonadal index is the gonadal wet weight divided by the body wet weight. Because authors often multiply this value by various constants, comparisons of indices across taxa may not be appropriate.

Taxa	Male	Female	Reference
Asteroidea			
Acanthaster planci	12	17	Conand (1985)
Asterias amurensis	14	17	Kim (1968)
Asterias rubens	17	24	Kowalski (1955); von Bismark (1959), Jangoux and Vloebergh (1973)
Asterias vulgaris	5	10	Lowe (1978)
Astropecten latespinosus	35	35	Nojima (1979)
Astrotole scabra	19	19	Town (1980)
Echinaster echinophorus	22	12	Ferguson (1974)
Echinaster sp.	30	12	Ferguson (1975)
Echinaster type I	11.8	17.5	Scheibling and Lawrence (1982)
Echinaster type II	25	27.7	Scheibling and Lawrence (1982)
Leptasterias hexactis	19	5	Menge (1975)
Leptasterias pusilla	270	300	Smith (1971)
Luidia clathrata	No difference	(6)	Lawrence (1973)
Oreaster hedemanni	3.8	3.4	Rao (1965)
Oreaster reticulatus	8	16	Scheibling (1979)
Patiriella gunnii	No difference	(13.2)	Byrne (1992)
Patiriella calcar	No difference	(12.5)	Byrne (1992)
Patiriella exigua	4.1	8.6	Byrne (1992)
Patiriella pseudoexigua	9.5	12.5	Chen and Chen (1992)
Pisaster giganteus	5	3	Farmanfarmaian *et al.* (1958)
Pisaster brevispinus	8	6	Farmanfarmaian *et al.* (1958)
Pisaster ochraceus	12	17	Farmanfarmaian *et al.* (1958)
Solaster stimpsoni	28	18	Engstrom (1974)
Mean	25.6	26.6	
Standard error	11.3	12.5	
Echinoidea			
Diadema setosum	30	40	Kobayashi and Nakamura (1967)
Echinarachius parma	11	15	Cocanour and Allen (1967)
Echinocardium cordatum	0.06	0.11	Moore (1936)
Echinometra lucunter	22	40	McPherson (1969)
Echinus esculentus	2	1.5	Moore (1934)
Eucidaris tribuloides	10.5	9.5	McPherson (1968a,b)

Table 6.4. Continued

Taxa	Male	Female	Reference
Evechinus chloroticus	11.8	2	Dix (1970)
Heliocidaris erythrogramma	9.9	9.1	Lawrence and Byrne (1994)
Heliocidaris tuberculata	13.2	13.0	O'Conner *et al.* (1976), Lawrence and Byrne (1994)
Hygrosoma petersii	32.3	31.8	Ahlfield (1977)
Lytechinus variegatus	1.6	1.8	Moore *et al.* (1963), Moore and McPherson (1965)
Meoma ventricosa	0.53	0.58	Chesher (1969)
Mespilia globulus	0.40	0.61	Kobayashi (1967)
Moira atropos	0.4	0.6	Moore and Lopez (1966)
Paracentrotus lividis	8.9	9.1	Byrne (1990)
Strongylocentrotus franciscanus	8	8	Bennett and Giese (1955)
Strongylocentrotus nudus	30	30	Fuji (1960a)
Strongylocentrotus intermedius	27.6	29.2	Fuji (1960a,b)
Strongylocentrotus purpuratus	20.8	19.8	Bennett and Giese (1955), Giese *et al.* (1958)
Tripneustes gratilla	14.5	15.5	O'Conner *et al.* (1976)
Tripneustes ventricosus	1.2	1.2	Moore *et al.* (1963)
Mean	12.2	13.4	
Standard error	2.4	2.9	
Holothuroidea			
Actinopyga echinites	6.1	7.8	Conand (1982)
Aslia lefevrei	17.5	18.0	Costelloe (1985)
Cucumaria lubrica	52	35	Engstrom (1974)
Holothuria mexicana	10	15	Engstrom (1980)
Holothuria scabra	0.1	0.35	Krishnan (1967)
Holothuria floridana	9	12	Engstrom (1980)
Microthele fuscogilva	0.8	2.4	Conand (1981)
Microthele nobilis	2.9	5	Conand (1981)
Stichopus japonicus	12	18	Choe (1962)
Thelenota ananas		1.6	Conand (1981)
Mean	11.2	11.5	
Standard error	4.9	3.4	
Ophiuroidea			
Amphioplus abditus	0.5	0.5	Hendler (1973)
Amphioplus sepultus	0.3	0.2	Hendler (1973)
Bathypectinura heros	10.3	9.0	Ahlfield (1977)
Ophiomusium lymani	6.4	6.7	Ahlfield (1977)
Ophiomusium spinigerum	13.9	11.0	Ahlfield (1977)
Mean	6.3	5.5	
Standard error	2.7	2.2	

Table 6.5. Proximate composition (per cent dry weight) of gonads in sea stars and sea urchins.

			Soluble				Insoluble				
	Ash		Carbohydrate		Lipid		Protein		Protein		
Species	M	F	M	F	M	F	M	F	M	F	Reference
	8.9	4.0	1.0	1.2	20.9	25.9	28.0	25.4	41.2	43.5	McClintock *et al.* (1995)
Tosia parva	18.9	5.3	0.5	0.5	17.6	54.7	19.3	19.2	43.7	20.3	McClintock *et al.* (1995)
Echinoids											
Heliocidaris erythrogramma	9	4	11	8	26	50	37	29	11	9	Lawrence and Byrne (1994)
Heliocidaris tuberculata	9	8	11	12	22	27	42	45	2	9	Lawrence and Byrne (1994)
Mean	11.5	5.3	5.9	5.4	21.6	39.4	31.6	29.6	24.5	20.4	

satellite male underneath anterior margin of clasping male) average 49% of sired progeny, compared with only 7% for males in other positions (Brockmann *et al.* 1994). The greater success of satellite horseshoe crabs than of fish may be a result of morphological or behavioural constraints that prevent the clasping male from sequestering the female or her eggs during their protracted spawning bouts.

Although sexual dimorphism may evolve from reproductive constraints other than sexual selection, the combined empirical evidence of sperm limitation in general (Tables 6.1 and 6.3), the evidence that both male and female fertilization success increases with the number of spawning animals (mating success) (Levitan 1991; Levitan *et al.* 1992; Yund and McCartney 1994; Yund 1995), and the reduced sexual dimorphism in both gonadal (Table 6.3) and nongonadal (Table 6.4) traits suggest that sexual selection is intense, but similar across sexes, in external fertilizers and that the mechanism driving sexual selection is mutual fertilization limitation rather than sperm competition.

VI SPERM LIMITATION, SELECTION ON EGG SIZE, AND THE EVOLUTION OF ANISOGAMY

Parker *et al.* (1972) developed a model for the evolution of anisogamy based on sperm competition. They assumed that, in free-spawning organisms, 'sperm competition is rampant because all ejaculates must compete in the same external medium for fusions with ova' (Parker 1984, p. 6).

Shortly after Parker's (1984) review was published, Pennington (1985) published the first *in situ* experiment and measurement of external fertilization, demonstrating the potential for sperm limitation. Since then, numerous studies have been conducted, and all have demonstrated some degree of sperm limitation (Tables 6.1 and 6.2; review by Levitan 1995a). If ubiquitous sperm limitation in external fertilizers results in reduced sexual dimorphism, and external fertilization is an ancestral trait, how did the original morphological sexual dimorphism, anisogamy, evolve from an isogamous ancestor?

Incorporating the emerging information on external fertilization into the Parker *et al.* model requires two considerations (Levitan 1996a). First, sperm–sperm interactions (sperm competition for fertilization) are likely to be low, so although sperm may still compete in the Darwinian sense (males with more fertilizations will have greater fitness), racing, battling, or preventing fertilizations by other sperm and the notion of female choice may have reduced importance compared with sperm limitation.

Second, because sperm are limiting, selection for enhanced fertilization can act on females as well as on males (Levitan 1996a). This departure from Bateman's principle and the evidence that egg size influences the proportion of eggs fertilized (Levitan 1993, 1996a) suggest that selection for fewer, larger eggs is a function not only of postzygotic success, as argued by Parker *et al.* (1972), but also of enhanced fertilization success (Levitan 1993, 1996a,b).

The notion that fertilization rate can influence selection on gamete size is not a recent one. Kalmus (1932) and Scudo (1967) presented models for how gamete encounter rate can result in selection for anisogamy using group-selection arguments. Schuster and Sigmund (1982) developed a model indicating that collisions between gametes become more likely as size asymmetries increase.

Because females produce eggs, the effect of selection on egg size must be viewed from the maternal perspective. Optimal egg size is the one that maximizes maternal fitness, by balancing the number and fitness offspring (Vance 1973; Smith and Fretwell 1974). When sperm are limiting, fertilization success is an important component of egg fitness (Levitan 1993, 1996a,b).

A model for optimal egg size that incorporates both pre- and postzygotic factors has been constructed for free-spawning echinoids (Levitan 1996a,b). In echinoids, size at metamorphosis tends to be similar across taxa. In the three *Strongylocentrotus* species mentioned earlier (*S. purpuratus*, *S. franciscanus*, and *S. droebachiensis*), although there is a fivefold difference in egg volume (Emlet *et al.* 1987), size at settlement for all three species is 0.20 mm (Emlet *et al.* 1987; Sinervo and McEdward 1988). This pattern suggests that selection for variation in egg size is likely to occur either pre- or post-zygotically but before settlement, during the larval, planktonic phase.

In the model, egg number is estimated to be the inverse of egg volume, and the total amount of egg material is assumed to be constant. The proportion of eggs fertilized (ϕ_∞) is estimated by a fertilization-kinetics model (Vogel *et al.* 1982) which incorporates the sperm–egg collision rate (b_O, mm^3 s^{-1}; the product of egg cross-sectional area and sperm velocity), egg (E_O, eggs ml^{-1}) and sperm (S_O, sperm ml^{-1}) concentration, the sperm–egg contact time (t) and a fertilization constant (b; mm^3 s^{-1}), which, when divided by the collision rate, provides the proportion of sperm–egg collisions that result in fertilization.

$$\phi_\infty = 1 - \exp(-bS_O/b_OE_O(1 - e^{-b_OE_Ot})). \quad (1)$$

The number of settling individuals (N_s) is calculated from the number of fertilized eggs (N_e), the instantaneous mortality rate (m), and the development time in the plankton (dt), where development time is a function of egg size (Vance 1973).

$$N_s = N_e e^{(-dtm)}. \quad (2)$$

The average empirical estimate of the daily planktonic mortality rate for the *Strongylocentrotus* species is 0.1615 day^{-1} (range = 0.06–0.27; Rumrill 1990). The relationship between development time and egg size is calculated to be: time (days) = 18.987 (egg volume[mm^3])$^{-0.1156}$ (Levitan 1996b).

Predictions of the egg size that maximizes parental fitness vary as a function of ambient sperm concentration and planktonic mortality (Fig. 6.6). This model predicts how sperm limitation results in selection for larger eggs than would be predicted by models that incorporate postzygotic survivorship alone.

The implication for the evolution of anisogamy is that conditions of sperm limitation resulted in selection for numerous smaller sperm that had an increased probability of finding an egg in a diffuse medium. Sperm limitation, along with factors associated with postzygotic survivorship, influenced selection on females for enlarged eggs. This modification of Parker *et al.*'s 1972 model assumes that sperm limitation, rather than sperm competition, along with selection for postzygotic success, was the mechanism driving the evolution of anisogamy (Levitan 1996a).

Taken at face value, and on the assumption that isogamy and external fertilization are the ancestral state, this result implies a modification in the sequence of events resulting in the evolution of sexual dimorphism and sexual selection. Protists that became colonial and larger began to experience increased selective pressure for increased zygote size to reduce the risks associated with growth to maturity (Parker *et al.* 1972; Knowlton 1974). Once the advantages of large zygote size became established, fertilization limitation would select for increased sperm numbers (at a cost of reduced size) and egg size (to a size larger than predicted solely by postfertilization survivorship), enhancing collision frequency and resulting in anisogamy. In addition, fertilization limitation would also select for behavioural modifications for increased aggregation and synchrony and for the maintenance of reduced sexual dimorphism with equal investment in gonads. Close-pair spawning, pseudocopulation, and copu-

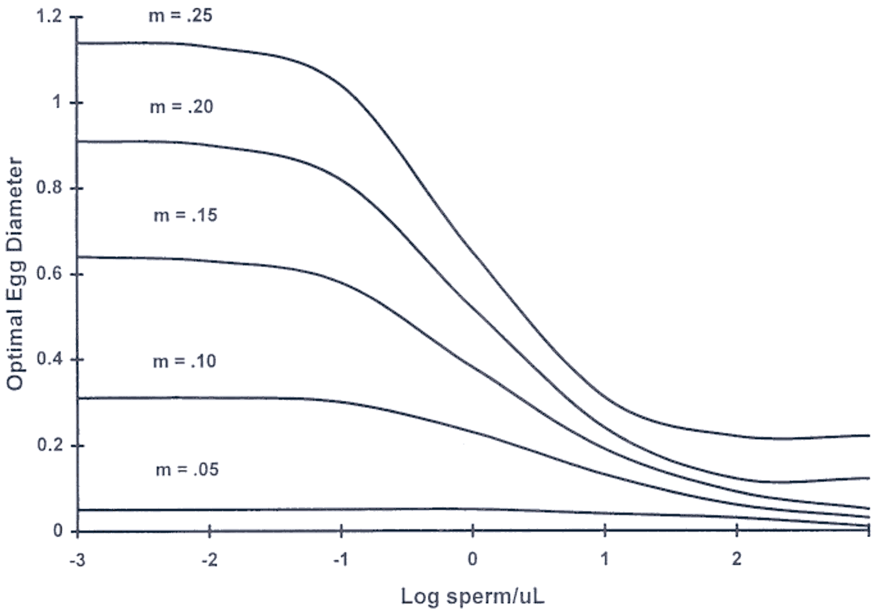

Fig. 6.6. *The optimal egg size that maximizes maternal fitness is predicted to be a function of sperm concentration and the daily larval mortality rate (m) in free-spawning echinoids. See text for model. The total amount of egg material is 1 ml, egg concentration is 0.01 μl^{-1}, sperm–egg interaction time is 600 s, sperm velocity is 0.130 mm s^{-1} (Levitan 1993), b_0 is 0.0000952 $mm^3 s^{-1}$ (Levitan 1993). The lines represent egg sizes that maximize the number of settling offspring for a given sperm mortality rate and sperm concentration. Figure from Levitan (1996a).*

lation evolved as escapes, at least at first, from sperm limitation (rather than from sperm competition; Parker 1984). With the evolution of internal fertilization and brooding of postzygotic stages by females, two changes in the selective environment occurred. First, variation in female fertilization success drastically decreased, whereas male fertilization success remained highly variable (or increased in variability because single males could more easily monopolize females), setting the stage for sexual asymmetries in the intensity of sexual selection and male–male competition (including its special case, sperm competition). Second, females began holding and controlling the fate of the offspring, setting the stage for female choice. Sexual dimorphism then becomes a prominent feature of internally fertilizing taxa.

In this scenario, internal fertilization is selectively advantageous to both males and females. Males benefit because the average success of males increases, and males best at copulation gain greatly. Females also benefit greatly because fertilization ceases to be a limiting factor, and choice becomes an option. Because significant anatomical change in females is associated with internal fertilization, it seems reasonable to assume that, for internal fertilization to evolve, it must benefit females.

Alternately, if sperm competition drove selection for internal fertilization, it is not clear how reducing sperm competition would benefit females (Knowlton and Greenwell 1984).

The sperm-limitation hypothesis implies not that sperm competition is absent among broadcast spawners but that it has reduced importance and may be balanced by egg competition. Choosing among this hypothesis, the more traditional view of the effect of sperm competition on sexual dimorphism, and some 'middle ground' will require much more new information on the distribution, abundance, and parentage of gametes in the sea (e.g. Figs 6.3 and 6.4), as well as accurate phylogenies to establish which traits are ancestral to others. Given such a wide array of taxa, environments, and strategies, studies of gamete interactions in external fertilizers have great potential. With the advent of molecular markers and DNA-amplification techniques, this potential can now be fulfilled.

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