

# Chapter 10

## Fertilization Strategies

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### 10.1 Introduction

For marine species that live attached to hard substrata, fertilization of their gametes can present particular problems. Internal fertilizers must settle densely enough to ensure future insemination. Their risk is largely binary: proximity of conspecifics usually guarantees reproductive success, whereas isolation implies reproductive failure<sup>1</sup>. However, for the vast majority of species that broadcast gametes to the water column, fertilization success is a far more continuous, and haphazard, variable: although fertilization success can often be close to 100%, many factors cause fertilization success to fall below the potential maximum, and sometimes to zero. The fertilization imperative creates substantial selective pressure to overcome these constraints on fertilization success. This chapter will review the data, the leading hypotheses, and the controversies in this topic, focusing on unresolved issues and future directions.

Ecological and evolutionary studies of fertilization on rocky shores were pioneered by Sparck (1927) and Mortensen (1938), both of whom suggested that external fertilization success may be low due to gamete dilution. Subsequently, Thorson (1946) argued that synchronous spawning would overcome such constraints, yet it was only after the landmark study of Pennington (1985) that this topic began to attract substantial attention. Excellent early reviews were provided by Levitan and Petersen (1995) and Yund (2000). In the intervening years, theories and concepts around this topic gained more prominence, and other issues emerged, such as the importance of gamete traits and fertilizability, chemoattractants, hydrodynamics, spawning synchrony, sexual selection and compatibility—nonetheless, the primary question of whether sperm limitation or sperm competition prevails in marine organisms remains.

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<sup>1</sup>Most internal fertilizers are capable of only limited self-fertilization.

Our purpose is to review what is known about the effects of factors that positively and negatively influence fertilization success on rocky shores, and to discuss the emerging concepts and the major gaps in our understanding in this field.

## 10.2 Scope and Definition of Terms

We will focus on sessile and slow-moving (e.g. limpets, sea urchins) rocky shore organisms because their inability (or reduced ability) to aggregate and/or move to favourable sites during fertilization events imposes a strong selective pressure to develop traits and strategies that maximize fertilization success.

### 10.2.1 Definitions

*Broadcast spawning*: both male and female gametes are released and fertilization occurs externally, in the sea (some authors also designate this as free spawning, but see below).

*Spermcast mating*: male gametes are released and fertilize eggs retained by maternal individuals (also designated as free-spawning egg brooders).

*Free spawning*: considerable ambiguity has surrounded the definition of free spawning. Some authors have used this term to describe the release of sperm independently of whether the eggs are released or retained (e.g. Levitan 1998; Yund 2000; Santelices 2002), and others to describe the release of both sperm and eggs, i.e. identical to broadcasting (e.g. Pemberton et al. 2003; Bishop and Pemberton 2006). We therefore restrict ourselves to using the terms “broadcasting” and “spermcasting”, and avoid the ambiguous meaning of this term.

*Copulatory fertilization*: direct delivery of sperm to maternal individuals (by copulation or pseudo-copulation).

*Egg brooding*: retention of eggs in the maternal individual until fertilization.

## 10.3 Main Topics in Fertilization Ecology of Rocky Shore Species

In the last 20 years, well over 100 papers have been published investigating the fertilization ecology of marine organisms. We have collated many of the key papers that refer to hard substratum species, and classify these here according to the different factors that have been identified as influencing fertilization success of hard substratum species (Table 10.1).

**Table 10.1** Factors influencing fertilization success of hard substratum species (full reference list available at <http://www.ccmr.ualg.pt/maree/publications.php?pub=ch>)

Factor	References
Level: gamete	
Sperm	<p>Velocity, longevity</p> <p>Rothschild and Swann (1951), Vogel et al. (1982), Destombe et al. (1990), Levitan et al. (1991), Levitan (1993, 2000), Manríquez et al. (2001), Powell et al. (2001), Kupriyanova and Havenhand (2002), Johnson and Yund (2004), Levitan et al. (2004), Hodgson et al. (2007), Muhlin et al. (2008)</p> <p>Podolsky (2004)</p>
Egg	<p>Size</p> <p>Accessory structures (jelly coat, follicle cells, etc.)</p> <p>Chemotaxis, chemokinesis</p> <p>Size</p> <p>Sperm receptors</p> <p>Longevity</p> <p>General</p> <p>Lambert and Lambert (1981), Buckland-Nicks (1993), Farley and Levitan (2001), Levitan and Irvine (2001), Podolsky (2001, 2002, 2004), Villa and Patricolo (2001)</p> <p>Miller (1975, 1985), Maier and Müller (1986, review), Bolton and Havenhand (1996), Serrão et al. (1996a), Togashi et al. (1998), Jantzen et al. (2001), Marshall et al. (2002), Riffell et al. (2004)</p> <p>Vogel et al. (1982), Levitan (1993, 1996, 1998, 2002), Styan (1998), Marshall et al. (2000, 2002, 2004b), Huchette et al. (2004), Podolsky (2001, 2004), Styan et al. (2005)</p> <p>Vogel et al. (1982), Styan et al. (2005), Levitan and Ferrell (2006)</p> <p>Havenhand (1991), Benzie and Dixon (1994), Andre and Lindegarth (1995), Baker and Tyler (2001), Meidel and Yund (2001), Williams and Bentley (2002), Johnson and Yund (2004), Muhlin et al. (2008)</p>
Level: individual	
Behaviour	<p>Compatibility</p> <p>Gamete numbers, polyspermy</p> <p>Aggregation</p> <p>Synchrony, timing of gamete release<sup>a</sup></p> <p>Spawning rate</p> <p>Gaffney et al. (1993), Swanson and Vacquier (1995), Palumbi (1999), Lambert (2000), Levitan and Ferrell (2006), Levitan et al. (2007)</p> <p>Brawley (1992), Pearson and Brawley (1996), Styan (1998), Serrão et al. (1999), Berndt et al. (2002), Franke et al. (2002), Marshall et al. (2002), Levitan (2004), Lasker (2006), Levitan et al. (2007), Bode and Marshall (2007)</p> <p>Young (1988), Svane and Havenhand (1993), Coleman et al. (2001), McCarthy and Young (2004)</p> <p>Harrison et al. (1984), Pennington (1985), Babcock et al. (1986, 1992, 1994b), Brawley (1992), Hayashibara et al. (1993), Svane and Havenhand (1993), Pearson and Brawley (1996), Serrão et al. (1996b), Clifton (1997), Clifton and Clifton (1999), Coma and Lasker (1997a, b), Stewart-Savage et al. (1997), Pearson et al. (1998), Yund (1998), Brawley et al. (1999), Togashi and Cox (2001), Berndt et al. (2002), Marshall (2002), Watson et al. (2003), McCarthy and Young (2004), Levitan (1988, 2005), Levitan et al. (2004), Lasker (2006)</p> <p>Coma and Lasker (1997b)</p>

(continued)

Table 10.1 (continued)

Factor	References
Morphology	Levitan (1991), Babcock and Mundy (1992), Thomas (1994), Marshall et al. (2000), Styan and Butler (2003), Lasker (2006)
Genotype	Palumbi (1999), Levitan and Ferrell (2006), Evans and Marshall (2005), Evans et al. (2007)
Gamete delivery mode	Tenkin (1994), Bishop (1998), Pemberton et al. (2003), Phillippi et al. (2004)
Level: population	
Density, distance, competition	Pennington (1985), Grosberg (1987), Levitan (1991), Levitan et al. (1992), Babcock et al. (1994a), Yund and McCartney (1994), Yund (1995, 1998), Andre and Lindgarth (1995), Wahle and Peckham (1999), Hobday et al. (2001), Levitan (2002, 2004), Phillippi et al. (2004)
Size	Levitan (1991, 2002), Levitan et al. (1992), Gaudette et al. (2006)
Sex ratio	Serrão et al. (1999), Marshall et al. (2004b), Levitan (2004)
Level: environmental	
Topography	Pearson and Brawley (1996), Engel et al. (1999), Franke et al. (2002), Levitan (2002), Marshall et al. (2004a)
Flow	Pennington (1985), Levitan (1991, 2002), Coma and Lasker (1997b), Yund and Meidel (2003)
	Denny and Shibata (1989), Mead and Denny (1995), Denny et al. (2002), Serrão et al. (1996b), Togashi and Cox (2001), Crimaldi and Browning (2004), Gordon and Brawley (2004)
Water depth	Levitan (1995), Babcock et al. (2000)
Water quality	Greenwood and Bennett (1981), Kupriyanova and Havenhand (2005)
	Greenwood and Bennett (1981), Brawley (1992), Serrão et al. (1996a, 1999), Pechemik et al. (2007)
	Kurihara and Shirayama (2004), Kurihara et al. (2004)

<sup>a</sup>Includes key references to cues for synchronous spawning as well as effects of synchrony on fertilization success

## 10.4 Gamete Traits that Influence Fertilization Success

### 10.4.1 *In Broadcast Spawners*

A variety of both male and female gamete traits have been reported to influence the success of fertilization in laboratory experiments and in the field, particularly traits that enhance sperm:egg encounters. For eggs, these traits include cell size, the size of their accessory structures, and sperm chemoattractants. The importance of physical egg size was first highlighted by Levitan (1993), a hitherto largely unnoticed consequence of Vogel et al.'s (1982) model: larger eggs provide bigger targets for sperm and, therefore, should be fertilized more easily. Subsequent studies supported the assertion that physical size of the egg cell influenced fertilization success (e.g. Levitan and Irvine 2001), whereas others—sometimes working on the very same species—argued for an equally important role of egg accessory structures such as egg jelly or follicle cells (e.g. Podolsky 2001). Sperm availability appeared to influence selection on egg cell size, raising the debate of whether accessory structures should be selected for in preference to increasing egg size with energetically costly cytoplasm (Podolsky 2004). Sperm chemoattractants are another, probably energetically inexpensive means to increase the “effective” egg size. Under sperm-limiting conditions, chemoattractant halos around freely spawned tunicate and abalone eggs could more than double the egg target area and fertilization rates (Jantzen et al. 2001; Riffell et al. 2004). Given the prevalence of sperm chemoattractants in free-spawning marine species (Miller 1985; Maier and Müller 1986; although interestingly not in the echinoids that have been the focus of much fertilization research), this could be an important mechanism decoupling physical egg size from fertilization success. If chemoattractant production is directly linked to egg size, then this same mechanism would still result in selection for larger eggs, as modelled by Dusenbery (2000). Additionally, “fertilization efficiency” (the number of sperm required to obtain a fertilization;  $\beta/\beta_0$  in Vogel et al.'s (1982) model;  $F_e$  in Styan 1998) of eggs may vary independently of egg size: in two congeneric species of echinoderms, large eggs required significantly *more* sperm to fertilize than small eggs (Styan et al. 2005). Thus, although physical egg size may be important in some species, other traits such as chemoattractants, accessory structures and fertilization efficiency all play vital roles when sperm are limiting. As yet, there are too few data to form generalizations about which of these is most important under which circumstances, and much remains to be done in this field.

Concerning the role of sperm traits, it has long been suggested that higher sperm velocity and/or longevity increases fertilization success (Rothschild and Swann 1951; Vogel et al. 1982) but that these trade-off, likely a consequence of optimization of energetic reserves (Levitan 2000). In general, sperm start to swim following dilution upon spawning, with increasing dilution leading to increasing activity—the so-called respiratory dilution effect. In brown algae, the variable amount of mucilage released with sperm might delay activation by seawater, yet fertilization has also been reported to occur within the emersed mucilage at low tide (reviewed by Brawley et al. 1999). Whether mucilage influences longevity is not known but, following

dilution, motility of male gametes from brown and green algae has been reported for a variable (1–7 h) range of durations (e.g. Togashi et al. 1998; Clifton and Clifton 1999; also reviewed in Brawley and Johnson 1992) and to be affected by salinity when marine taxa colonize brackish habitats (Serrão et al. 1996a). For marine invertebrates, sperm longevity varies widely. Echinoderm sperm appear to be short-lived (typically, minutes to perhaps a few hours; e.g. Yund 1990; Benzie and Dixon 1994), whereas in many other taxa sperm may remain viable for many hours and even as long as a day (e.g. Havenhand 1991; Johnson and Yund 2004). This may arise due to slow sperm dilution during spawning (e.g. Meidel and Yund 2001; Marshall 2002) and/or the requirement for sperm activation by chemoattractants from the egg (e.g. tunicates, Miller 1982; Bolton and Havenhand 1996), yet extended sperm longevity has also been recorded in the absence of such factors (e.g. Havenhand 1991; Williams and Bentley 2002). Sperm swimming velocities (e.g. Serrão et al. 1996a; Kupriyanova and Havenhand 2002) are negligible relative to the magnitude of sea currents; however, sperm swimming is not irrelevant. The length scales at which sperm swim are typically close to or below the length scales of turbulent eddies and, consequently, sperm and eggs are not advected independently. Moreover, within approximately 1 mm of an egg, turbulence is negligible (Mitchell et al. 1985) and sperm swimming can play a major role. Phototactic responses of algal gametes, positive or negative, by concentrating the gametes at the surface or bottom, may lower gamete dilution (suggested in Brawley and Johnson 1992).

Egg longevity is generally longer than that of active sperm, up to several days (e.g. Havenhand 1991; Meidel and Yund 2001; Williams and Bentley 2002; also motile female gametes of green algae, Togashi et al. 1998). Again, the selective benefit of this trait seems questionable, since turbulence and advection might dilute gametes beyond the possibility of fertilization long before they become unviable (Levitan and Petersen 1995). In many cases, however, eggs may be adhesive, released under minimal turbulence (see below) and/or released in adhesive media such that they remain within a given location, thereby integrating the fluctuating sperm concentration over time as in spermcasters (e.g. tunicates, Svane and Havenhand 1993; Marshall 2002; echinoids, Thomas 1994; Meidel and Yund 2001; some furoid algae, Engelen et al. 2008). Eggs retained in this manner can obtain far higher fertilization rates than if advected freely (Svane and Havenhand 1993; Yund and Meidel 2003). Demonstrating that such behaviours are ecologically relevant requires substantial investment in fieldwork and, consequently, the extent to which similar behaviours occur in other taxa is not well understood.

#### **10.4.2 In Spermcasters**

Unlike broadcast spawners, the influence of gamete traits on fertilization success of spermcasting species is limited largely to the sperm, with the possible exception of taxa where the egg is not enclosed internally (e.g. kelps). In all other cases, spermcasters retain unfertilized eggs, and sequester sperm from the water column prior to using these for fertilizations. Perhaps unsurprisingly, therefore, extended sperm longevity has been

reported in a number of spermcasters such as ascidians (e.g. Bishop 1998; Johnson and Yund 2004) and bryozoans (e.g. Manríquez et al. 2001). Clearly, this is an important adaptation that permits sperm dispersal and dilution over considerable distances without compromising fertilization success. This contrasts with broadcasters that typically have shorter-lived and more active sperm (see above) that may require rapid fertilization before gamete dilution eradicates the possibility of further gamete encounters.

Many spermcasters are filter-feeding species with mechanisms enabling efficient utilization of dilute sperm (Bishop 1998 and references therein), thereby overcoming many issues that limit fertilization in broadcasters. Mechanisms of sperm capture are unknown (Bishop and Pemberton 2006) but sperm can be captured from extremely dilute suspensions (as low as  $10 \text{ ml}^{-1}$ ; Bishop 1998) and stored and used several weeks thereafter (Bishop and Ryland 1991). Presumably, fewer sperm are required for internal, as opposed to external, fertilization (Bishop 1998). Sperm limitation is thought to have been the selective pressure for mitotic cloning of the zygote into carpospores in red algae (reviewed in Santelices 2002). This is contradicted by the high fertilization success recorded in red algae (Kaczmarek and Dowe 1997; Engel et al. 1999), which is puzzling given that red algae are spermcasters with non-motile male gametes (spermatia), and have no known mechanisms to concentrate spermatia (although several competing spermatia have been found around trichogynes; Kaczmarek and Dowe 1997). Gamete encounters may be facilitated by extracellular projections in spermatia and release of mucilage with the gametes (reviewed by Brawley and Johnson 1992); however, more work is required to clarify the intriguing fertilization success of red algae.

### ***10.4.3 In Copulatory Fertilizers***

In comparison with broadcasters and spermcasters, processes of fertilization in copulating hard substratum taxa are poorly known. This type of internal fertilization is found primarily in crustaceans and most gastropods (limpets being an obvious exception), as well as in several lesser phyla such as flatworms. Mating behaviour and potential for selfing have been investigated in such taxa (e.g. Furman and Yule 1990), although we found no literature detailing the influence of gamete traits on fertilization success in copulatory fertilizers from hard substrata. This almost certainly arises because of the difficulties in demonstrating this (cf. fertilization is internal and, therefore, difficult to study without impacting the process itself) but also because the potential for post-copulatory manipulation of gametes by the female is so great. However, we also found no literature investigating the extent of sperm competition and sexual selection in these taxa. Given the ease with which snails, for example, can be manipulated, this is surprising. This is clearly an area where considerable progress could be made.

## 10.5 Gamete Mixing

### 10.5.1 *Role of Hydrodynamics*

The importance of water flow for the fertilization of broadcasters was first documented by Pennington (1985) who found reduced fertilization success of urchins induced to spawn in high flows ( $>0.2 \text{ m s}^{-1}$  versus  $<0.2 \text{ m s}^{-1}$ ), and attributed this to increased sperm dispersion and dilution. Subsequent modelling showed how advection and turbulence can result in low fertilization success (Denny 1988; Denny and Shibata 1989). This pattern of flow-mediated gamete dilution, and consequent sperm limitation, became a well-established paradigm (e.g. Levitan and Petersen 1995; Mead and Denny 1995; cf. Denny et al. 2002).

This body of literature did not, however, consider the importance of (1) variation in the probability of fertilization across time and space in a population and (2) variation in hydrodynamically cued gamete-release behaviours within a population. More recent research has focused on these issues, not least on the caveat raised by several authors (including Denny and Shibata 1989) that these models provide time-integrated, rather than instantaneous estimates of gamete concentrations. Downstream of a spawning adult, gametes have highly heterogeneous distributions in much the same way that smoke from a campfire travels in concentrated filaments. Spermcasters and broadcasting taxa that retain eggs at a given location will experience extreme variations in gamete concentration, encountering periods of no sperm, and periodically exposed to quite high sperm concentration, therefore integrating the fluctuating sperm concentrations over their retention time (e.g. Wahle and Gilbert 2002). In contrast, broadcasters will experience high spatiotemporal variation in fertilization success due to varying coincidence of sperm and egg filaments in the water column (e.g. Coma and Lasker 1997). Recent modelling has shown that turbulent structures in the flow field can cause coalescence between high-concentration filaments of freely spawned egg and sperm, enhancing fertilization rates (Crimaldi and Browning 2004). Release of gametes in viscous media (e.g. Svane and Havenhand 1993; Thomas 1994; Yund and Meidel 2003) will enhance this process and substantially raise fertilization rates above those predicted for freely spawned gametes (Crimaldi and Browning 2004), even for mild viscosity increases.

The influential paradigm of a decade ago—that flow-induced gamete dilution restricts fertilization rates in broadcast spawners—is not as pervasive as once thought, and focus is now turning to the importance of small-scale spatiotemporal variation, not least in turbulent structures, leading to significant variation in fertilization rates. This exciting development is ripe for testing with empirical data.

Flow-mediated spawning behaviour has been studied primarily in fucoid algae (reviewed by Pearson and Serrão 2006; see also Gordon and Brawley 2004 for kelp and green algae). Avoidance of spawning during high water motion periods is a conserved response superimposed on their common semilunar release patterns, resulting in high natural fertilization success (e.g. Serrão et al. 1996b). Diffusion-limited supply of dissolved inorganic carbon (DIC) for photosynthesis has been



shown to act as a signal for gamete release under favourable (i.e. calm) conditions (Pearson et al. 1998). Photoreceptors to specific blue and green light wavelengths also coordinate gamete release by some fucoid algae, and may contribute to restrict spawning to calmer intervals (Pearson et al. 2004).

Comparable information on flow-mediated spawning behaviours of marine invertebrates is limited. Several intertidal species are known to restrict spawning to periods of low tide (e.g. gastropods, Counihan et al. 2001; tunicates, Marshall 2002; anthozoans, Marshall et al. 2004). Again, this topic is in need of detailed investigations to determine the extent to which spawning behaviours have been selected for different flow regimes.

Gamete mixing of copulatory species is not influenced directly by flow environment, although by reducing densities, dislodgement due to wave action can have major impacts on fertilization success. As dislodgement risk is a product of drag and adhesion (Denny 1988), species in which the males mount the females in order to copulate face increased risk of dislodgement (Johannesson et al. 2008).

### ***10.5.2 Role of Density/Aggregation Spawning***

Gregarious and/or aggregative settlement behaviour in sessile marine species is now well documented (e.g. Burke 1986). Population density is one of the primary determinants of gamete concentrations in the water column during spawning and, hence, a key component of fertilization success in broadcast spawners. In sea urchins, fertilization success varies inversely with distance between spawning pairs (Pennington 1985), and is higher at central (rather than marginal) locations in an aggregation and in greater-density aggregations (Levitan et al. 1992). Similar results have been reported by other workers (e.g. Yund 1995; Levitan 2002a; Gaudette et al. 2006), and this general pattern has become broadly accepted. Nonetheless, there are studies that have found either no such relationship (e.g. Phillipi et al. 2004; although, interestingly, this result is for a spermcasting tunicate) or only a weak inverse relationship, with fertilization rates still comparatively high at great distances (e.g. Babcock and Mundy 1992). Moreover, aggregation size interacts with spawning synchrony to influence overall fertilization success (Gaudette et al. 2006).

### ***10.5.3 Role of Spawning Synchrony***

Spawning synchrony is key to maximizing the probability of gamete encounters in the sea, and has been shown for a wide variety of rocky shore organisms (see references in Table 10.1). Although spawning synchrony in broadcasters is expected for reproductive assurance, intriguingly it may also occur in selfing hermaphrodites (discussed in Pearson and Serrão 2006). Spawning synchrony induced by direct communication occurs in several species including soft corals (Slattery et al. 1999),

polychaetes (Watson et al. 2003) and kelps, where sperm release is induced by a pheromone secreted by the egg (Luning and Müller 1978) during calm periods, which reduces pheromone dilution (Gordon and Brawley 2004). Synchrony on broader scale may occur as a response to single or combinations of environmental signals such as lunar or tidal phases (e.g. Counihan et al. 2001; Levitan et al. 2004), hydrodynamics (e.g. Serrão et al. 1996b), temperature (e.g. Olive 1995) or availability of food such as phytoplankton (e.g. Starr et al. 1990). On a circadian scale, synchronous gamete release in many species occurs in response to light–dark or dark–light shifts (e.g. Dybern 1965; Brawley and Johnson 1992), as in the remarkable synchronous events of early morning multi-species spawning by green algae on coral reefs (Clifton 1997; Clifton and Clifton 1999), the fate of which remains totally unexplored in terms of fertilization success. Multi-species spawning synchrony (and resultant fertilization success) is, however, perhaps best known for corals (e.g. Levitan et al. 2004; Guest et al. 2005). Despite widespread correlations between spawning and various possible environmental cues, particularly with lunar cycles (for many taxa throughout the world), the physiological mechanisms behind such patterns are poorly understood (but see Pearson and Brawley 1998; Pearson et al. 2004; Guest 2008 and references therein).

## 10.6 Risk of Polyspermy and the Role of Polyspermy Blocks

Polyspermy, the fertilization of an egg by more than one sperm, is usually a lethal condition but—how often do free spawners encounter the circumstance where there are too many sperm? Although the cellular mechanisms involved in polyspermy have been studied extensively (reviewed by Gould and Stephano 2003), this question has been asked rarely and, consequently, this aspect remains unclear. An indicative answer can be inferred from the fact that polyspermy-avoidance mechanisms have been found in all free-spawning marine invertebrates and marine algae investigated to date (Brawley 1991; Gould and Stephano 2003), suggesting that polyspermy imposes a strong negative selective pressure. In situ rates of polyspermy in induced sea urchins reached 42% at high subtidal population densities (Levitan 2004) and up to 63% in tide pools (Franke et al. 2002), which may reflect the physical constraint to gamete dispersion in a tide-pool habitat. Yet, modelling also shows that at sperm concentrations where as few as 60% of eggs are fertilized, up to 11% of zygotes can still be polyspermic (C.A. Styan, unpublished simulations for urchins). So, the scant available data for invertebrates support the hypothesis that polyspermy is common, and may well be prevalent at sperm concentrations far lower than previously supposed. For broadcasting marine algae, however, natural polyspermy levels are reported to be comparatively low (usually <10%) in intertidal (Brawley 1992), tide-pool (Pearson and Brawley 1996) and subtidal (Serrão et al. 1999) habitats. Interestingly, the sodium-ion dependence of the fast polyspermy block may be compromised when marine taxa colonize ionically dilute brackish seas such as the Baltic and, in such environments, relatively high natural polyspermy

levels (10–30%) have been recorded (Serrão et al. 1999). We could find no comparable data for marine invertebrates.

Polyspermy risk may result in sexual conflict, in which traits that increase male reproductive success will simultaneously decrease female reproductive success. The scenario through which this arises is simple: in sperm-limiting conditions, adaptations that maximize fertilizations are selectively beneficial for both males and females. Once sperm are no longer limiting, however, these adaptations have a high cost for females (high sperm concentrations increase polyspermy) and, therefore, mechanisms that reduce fertilizations are selected for, whereas in males sperm are selected for even faster swimming, binding, and egg penetration. This conflict between male and female function has been suggested as a driver of rapid evolution of gamete recognition proteins in sea urchins (e.g. Vacquier 1998) and, indeed, sexual conflict theory predicts this form of variation in sperm:egg binding compatibility in broadcasting marine species (e.g. Gavrillets 2000). Available empirical data support this hypothesis (Levitan and Ferrell 2006) but much remains to be done in this field.

## 10.7 Fertilization Compatibility

Intraspecific variability in fertilization success appears to be common in hard substratum taxa (e.g. urchins, Palumbi 1999; Levitan and Ferrell 2006; Evans et al. 2007; mussels, Beaumont et al. 2004; oysters, Gaffney et al. 1993; polychaetes, Kupriyanova and Havenhand 2002; abalone, Havenhand and others, unpublished data). As outlined above, the theoretical basis for this is well established; however, the consequences of variable fertilization probability *after* sperm:egg encounter have been largely overlooked in rocky shores taxa (but see Levitan and Ferrell 2006). Variable compatibility will reduce the effective population size, restricting reproductive success and intra-population gene flow, with cascading consequences for population dynamics. Again, the extent, nature and causes of variability in fertilization compatibility have yet to be explored in the vast majority of hard substratum taxa.

A second consequence of variable gamete compatibility is mediating hybridization in synchronous broadcast spawning of closely related species. This may be aggravated by chemical interference due to the often non-specific nature of pheromones (e.g. Maier and Müller 1986; Bolton and Havenhand 1996). Yet, subtle (i.e. minutes) species spawning asynchronies have been reported (Clifton and Clifton 1999) and at least a 2-h shift in spawning peak time appears sufficient to avoid hybridization (Levitan et al. 2004). Several recently diverged rocky shore species appear to have undergone incomplete reproductive isolation and still hybridize occasionally (e.g. brown algae, Coyer et al. 2002; Engel et al. 2005; sea urchins, Levitan 2002b; bivalves, Bierne et al. 2002; Beaumont et al. 2004; corals, Vollmer and Palumbi 2002; Levitan et al. 2004). Speciation/hybridization processes trade-off under sperm-limiting conditions: specialization of gamete recognition proteins reduces risk of hybridization but may simultaneously reduce success of intraspecific fertilizations. Consequently, pre-zygotic

hybridization barriers may be more likely to evolve under sperm competition (e.g. in high-density populations; Levitan 2002b).

## 10.8 Conclusions

Rocky shore taxa show many convergent adaptations to increase fertilization probabilities, yet the debate as to whether sperm limit, or compete for, external fertilizations (e.g. Levitan and Petersen 1995; Yund 2000) is still active. We conclude that both sperm limitation and sperm competition play essential roles in driving the ecology and evolution of fertilization in rocky shore species. We have described multiple reported adaptations to avoid sperm limitation, thereby highlighting that this is an important selective factor. Nonetheless, it is difficult to demonstrate naturally occurring sperm limitation: populations that have not evolved adaptations to overcome sperm limitation are less likely to persist and be observed. Conversely, it is equally apparent that adaptations to avoid polyspermy are diverse and common, suggesting that hydrodynamic conditions, perhaps in combination with adaptations to avoid sperm limitation, can often lead to sperm competition. It is the balance between these competing selective pressures that has created the patterns we see today in rocky substratum taxa. Understanding how these patterns evolve will require a detailed understanding of the micro- to meso-scale variation in fertilization success, both in space and time. This presents exciting prospects for the coming decade.

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