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MINIREVIEW

RECENT ADVANCES IN FERTILIZATION ECOLOGY OF MACROALGAE[1]

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Our understanding of natural patterns of fertilization in seaweeds has increased substantially over the last 10 years due to new approaches and methods to characterize the nature and frequency of fertilization processes *in situ*, to recognize the conditions and mechanisms enhancing fertilization success, and to anticipate population and community consequences of the patterns of natural fertilization. Successful reproduction in many species depends on a delicate juxtaposition of abiotic and biotic conditions. Important abiotic factors are those triggering gamete release (e.g. single or interacting effects of light quality and water movement) and those affecting gamete viability or concentrations (e.g. salinity effects on polyspermy blocks; gamete dilution due to water movement). Examples of important biotic components are synchronous gamete release, efficiency of polyspermy-blocking mechanisms, population density of sexually fertile thalli, interparent distances, and male-to-female ratios. Field data indicate fertilization frequencies of 70%–100% in broadcasting-type seaweeds (e.g. fucoids) and 30%–80% in brooding-type (red) algae. Red algal values are higher than previously thought and challenge presently accepted explanations for their complex life histories. Important population and community questions raised by the recent findings relate to the magnitude of gene flow and exchange occurring in many micropopulations that seemingly breed during periods of isolation, the physiological basis and population effects of male-to-male competition and sexual selection during fertilization of brooding seaweeds, and the effects of massive gamete release, especially in holocarpic seaweeds, on benthic and planktonic communities. Comparative studies in other algal groups are now needed to test the generality of the above patterns, to provide critical pieces of information still missing in our understanding of natural fertilization processes, and to elucidate the evolutionary consequences of the different modes of reproduction (e.g. brooders vs. broadcasters).

Key index words: **broadcasters; brooders; gene flow; fertilization frequency; massive gamete release; seaweeds; polyspermy blocks; sperm competition; window of opportunity**

Over the last decade an increasing number of studies considered patterns of fertilization in seaweeds from an ecological perspective. New approaches and methods yielded significant and innovative data and positioned macroalgae at the forefront of relevant biological discussions. Seaweeds are models to study mechanisms preventing polyspermy (Brawley 1991, 1992, Serrâo et al. 1999), to understand fertilization processes (e.g. Clifton 1997, Pearson et al. 1998), to evaluate sperm limitation in the sea (Levitan and Petersen 1995, Yund 2000), and to explore male-to-male competition and sexual selection (Engel et al. 1999). In addition, the new results challenge several paradigms that, until now, were accepted to explain different aspects of macroalgal reproduction. Results and patterns emerging from these studies are reviewed here. After an initial note on modes of reproduction in the sea, I discuss the nature and frequency of macroalgal fertilization, as well as some of the conditions and mechanisms enhancing successful fertilization. Finally, some anticipated consequences of the observed patterns of natural fertilization on population and community structure are highlighted.

MODES OF REPRODUCTION

For years, zoologists investigating reproductive strategies of marine invertebrates distinguished brooding from broadcasting organisms (e.g. Thorson 1950, Chia 1974, Yund 2000). In brooding organisms, fertilization occurs internally, after sperm transit the water column, whereas broadcasters exhibit external fertilization after the release of both sperm and eggs into the water column. Both kinds of organisms are considered to be free spawners because both reproduce by releasing sperm into the surrounding seawater. Consequently, brooders and broadcasters may exhibit a number of common traits. However, to shed female and male gametes into the water constitutes a striking difference with regard to fertilization dynamics and zygote dispersal compared with retention of the egg within the female in brooders. Therefore, brooders and broadcasters should differ in a number of specific aspects of their reproductive processes. For example, environmental cues for synchronous gamete release are crucial for broadcasters, whereas efficient sperm collection mechanisms are crucial for brooders.

External fertilization in many brown and green algae is similar to that of the broadcasting invertebrates, whereas internal fertilization in red algae is much closer to a brooding process. Thus, many green and

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brown algae exhibit a pattern that is typical of the aquatic environment (Strathmann 1990), whereas the red algae approach a pattern also found in terrestrial (e.g. wind-pollinated) organisms. It is clear that a diverse array of mating systems and life histories are found within green and brown algae, and some degree of overgeneralization is acknowledged when characterizing both groups as broadcasters. However, the basic differences arising from external versus internal styles of fertilization have not been explored yet for seaweeds, and future research should elucidate whether it constitutes a basis for an important separation in mating strategies among these organisms. In the meantime, and for the purposes of this review, data on seaweeds with broadcasting versus brooding reproduction are discussed separately.

NATURAL FERTILIZATION

The nature of fertilization in the field. Experimental and observational field studies characterize sexual reproduction and subsequent fertilization of broadcasting species as a tightly synchronized and environmentally controlled process. Synchronous release of gametes by adult thalli increases the probability of gamete encounters and therefore is crucial for fertilization success. For example, populations of *Fucus ceranoides* living in estuarine conditions at the Isle of Man (Great Britain) release their gametes only during daytime high tides, and most eggs are fertilized 30 to 120 min after plants are immersed by incoming tides (Brawley 1992). In the case of *Fucus vesiculosus* living in habitats with high water motion, gamete release is restricted to calm intervals (Serrâo et al. 1996a), thereby preventing the gamete dilution predicted to occur by turbulent flow and water exchange (Pennington 1985, Denny and Shibata 1989, Levitan et al. 1992). Similarly, populations of *Fucus distichus* living in tide pools restrict gamete release to periods of very low water motion (Pearson and Brawley 1996), when pools are isolated by the low tide and gamete dilution is much reduced.

Conspecific synchrony of gamete release together with asynchronous gamete release by closely related species not only increases the probability of encounters between male and female gametes but also seems to prevent most hybridization. Working with six species of *Caulerpa*, seven species of *Halimeda*, four species of *Penicillus*, one species of *Rhipocephalus*, and four species of *Udotea* on a Caribbean coral reef, Clifton (1997) and Clifton and Clifton (1999) found that many (tens to thousand) conspecific algal thalli could become simultaneously fertile overnight. The next morning, thalli released gametes into the water column during a single and brief (5–20 min) pulse of reproductive activity. Closely related species often released gametes on the same morning but did so at different times. Such differential use of the temporal axis during the day presumably reduces the mixing of gametes, lowering the potential for hybridization.

Although such discrete and synchronous temporal patterns of gamete release appear common among broadcasting species, thereby suggesting a general importance of environmental control over gamete release, mechanisms have been identified for only a few species. Those most noteworthy are the numerous studies performed with fucoids (Brawley 1992, Pearson and Brawley 1996, 1998, Serrâo et al. 1996a,b, 1999), which identified light and decreased water movement as factors triggering gamete release. In the case of *F. vesiculosus*, which lives in habitats that are frequently stormy, adult thalli can sense reductions in water motion via boundary layer bicarbonate levels and photosynthetic metabolism (Pearson and Brawley 1996, 1998, Pearson et al. 1998). Furthermore, one signal can be modified by a second signal in some species. For example, gametes are released in *Silvetia compressa* (formerly *Pelvetia fastigiata*) after an inductive light period of 4 h. However, agitation of the experimental cultures reverses the light-induced capacity to release gametes (Pearson and Brawley 1998, Pearson et al. 1998). Similarly, in the case of *Bryopsis plumosa*, the signal for gamete release is blue light (Mine et al. 1996, Togashi et al. 1998). However, under laboratory conditions with fixed light quality, transient calm water conditions near the time of gamete release stimulated higher than predicted levels of gametangial release (Speransky et al. 2000). Therefore, at least in these species, the release stimulus determined by one signal (light) could be modified by a second signal (water motion).

In the case of the 22 species of Bryopsidales investigated on a Caribbean reef by Clifton (1997) and Clifton and Clifton (1999), the nature of the finely tuned highly specific environmental control of gamete release remains unknown. Clifton and Clifton (1999) suggested that changes in temperature, light, and nutrients, as well as demographic variables, may play a role in the timing of these releases. They noticed, for example, that colder waters delayed gamete release by *Caulerpa racemosa* by about 8 $\text{min}\cdot^{\circ}\text{C}^{-1}$, whereas increasing light levels apparently initiated the process of gamete release. However, further experimental studies with these tropical species are needed to elucidate whether single or interacting factors (e.g. blue light, calm water conditions) trigger a differential response among phylogenetically related species. Certainly the assemblages of Bryopsidales described by Clifton and Clifton (1999) from Caribbean coral reefs are highly suited for such studies. Similar studies could be conducted at temperate latitudes in intertidal pools inhabited by species of *Ulva* or *Enteromorpha* as various authors (e.g. Smith 1947, Pringle 1986) described gamete release by these species at predictable times of day.

Pertinent information on similar processes in the red algae (“brooders”) is missing. However, experimental data indicate that fertilization in this group is also a rapid short-lived process and that some environmental factors (e.g. dilution effects by water movement) are of paramount importance.

Because of difficulties involved in observing red algal fertilization in the field, the available data come from laboratory experiments. In the case of *Palmaria*, spermatia attachment occurred within 5 min of delivering the male gametes into a culture of mature females (Mine and Tatewaki 1994). In the case of *Antithamnion*, the corresponding time was 10 min (Kim et al. 1996), whereas in crossing experiments with *Gracilaria* (Engel 2000) fertilization occurred within 15 min. The mean fertile life of the male gamete in *G. gracilis* is about 5 h (Destombe et al. 1990). Karyogamy after fertilization also seems to be a rapid process. Karyogamy after attachment of spermatia to the trichogyne occurred in *Palmaria* in 180 min (Mine and Tatewaki 1994), in *Aglaothamnion oosumiense* within 2–3 h (Kim and Kim 1999), and in *Callithamnion* in 5–10 h (O'Kelly and Baca 1984).

Gamete dispersal in red algae has been measured in laboratory experiments (Destombe et al. 1990) and in the field (Engel et al. 1999). Laboratory experiments suggested dispersal distances of up to 80 m. Field data, however, indicate much shorter dispersal shadows. Using two hypervariable microsatellites previously described by Wattier et al. (1997), Engel et al. (1999) identified the paternity of each cystocarp produced in a population of *G. gracilis.* Reconstruction of the parentage of the cytocarps revealed a large excess of matings at short distances (about 5 m), suggesting near-neighbor matings are frequent and that there is a strong effect of distance in fertilization success. Only 11% of the cystocarps were attributed to males living beyond that distance. On a per-female basis, male fertilization success decreased as the distance to potential mates increased.

Data on factors that might trigger and synchronize release of spermatia among brooding seaweeds are lacking; however, the short fertility of the spermatium, its short dispersal distances, and the significant effects that dilution and distance have on fertilization success all suggest that some environmental control factors also act to synchronize carpogonial maturation and spermatial release in this algal group. These factors may be as finely tuned as those already described for broadcasting seaweeds.

Natural fertilization frequency. The most recent data on natural fertilization of seaweeds suggest that fertilization occurs more frequently than previously thought. Field data indicate fertilization values of 70%–100% for fucoids (Brawley 1992, Pearson and Brawley 1996, Serrâo et al. 1996a) and 30%–80% in the red algae (Kaczmarska and Dowe 1997, Engel et al. 1999). These high values are particularly significant for the red algae, because syngamy in this group was expected to be a rare event. Spermatia of red algae lack flagella. Consequently, they were expected to lack motility and to have limited dispersal capacity in space and time. In addition, sexual pheromones are unknown in the group (Searles 1980). In more recent years, however, several authors (reviewed in Broadwater et al. 1991, Brawley and Johnson 1992) described spermatia being released in mucilage strands, which may aid in their dispersal and later capture by the trichogyne, and ultrastructural studies indicated spermatia of different species have cellular projections that may modify the transport characteristics of the gamete and help it attach to the trichogyne. In 1997, Kaczmarska and Dowe reported cystocarp production and fertilization frequency in *Polysiphonia lanosa,* with values ranging from 42% to 54% in the three most fertile months. Fertilization frequency varied inversely with the age of the individual, and 54% was the value observed across all age classes. If only the youngest age class was considered, however, fertilization frequency rose to 91%. Kaczmarska and Dowe (1997) compared their data with values (29%–78%) previously obtained from a freshwater red alga *Batrachospermum boryanum* (Sheath and Hambrook 1990, Hambrook and Sheath 1991) and concluded that material fertilization success in the red algae seemed more frequent than previously thought. In addition, the cystocarps of *Polysiphonia lanosa* often exhibited trichogynes with several spermatia attached to them, which caused Kaczmarska and Dowe (1997) to question the supposed scarcity of male gametes of red algae in the field.

Recent studies of *G. gracilis* (Engel et al. 1997, 1999) added quantitative data on male performance and spermatial availability to information on fertilization in red algae. Analyzing a total of 350 cystocarps produced by 26 female and 37 male gametophytes, the ratio of males to cystocarps was found to be 0.63, indicating that a family of 10 cystocarps had approximately six different sires. On average, each male sired 5.7 cystocarps, but the range extended from 1 to 16, suggesting genetic differences in the quality and/or quantity of spermatia between males.

High frequencies of natural fertilization in red algae suggest the need for new explanations for their complex life cycle. After gamete fusion, the zygote in this algal group develops by mitosis into a diploid sporophyte (e.g. the carposporophyte), which is retained and nurtured on the female gametophyte thallus. This parasitic phase eventually produces masses of mitotically derived spores that, if settled in a favorable place, will grow into a diploid free-living sporophyte (e.g. the tetrasporophyte). Despite lacking empirical evidence from natural populations (Santelices 1990), retention and nuture of the carposporophyte was interpreted to be an adaptive response to compensate for the lack of motile gametes (Searles 1980). Fertilization processes were thought to have been inefficient in ancestral red algae in comparison with other algae with flagellated gametes. However, the available data on fertilization frequency in the red algae neither support the idea that this is an inefficient process compared with similar processes in other algal groups nor that the lack of motility of the spermatia in the water decreases their fertilization efficiency. Alternative ideas now seem necessary to explain the zygote amplification that occurs in the life history of the red algae.

Polyspermy-preventing mechanisms. Sperm limitation does not appear to be so severe in the field as once thought because of the frequency of natural fertilization revealed by recent studies (Engel et al. 1999, Yund 2000). Mechanisms to prevent polyspermy are important if sperm are not limiting to fertilization. In general, these are cellular responses preventing fertilization of an egg by more than one sperm (Jaffe 1976, Brawley 1987, 1991). Such responses are regarded as important adaptations to avoid a waste of energy and gametes, because polyspermic zygotes die soon after fertilization.

The most in-depth studies on polyspermy prevention in algae have been conducted in fucoids (Brawley 1987, 1991, 1992, Serrâo et al. 1999). Results suggest three polyspermy-preventing mechanisms, each acting at different times after fertilization. There is a fast sodium-dependent electrical block, a slow block that corresponds to cell wall formation, and an "intermediate block" (Brawley 1991) that is thought to involve enzymatic destruction of sperm receptors in the egg plasma membrane.

Equivalent experimental data for red algae are missing, but microscopic observations suggest equivalent polyspermy-preventing mechanisms exist in these seaweeds. Thus, although several male gametes can attach and fuse with the same trichogyne, as observed both in field collections and laboratory experiments (e.g. Cole et al. 1985, Fredericq and Hommersand 1989, West and Calumpong 1989, Hommersand and Fredericq 1990, Kim and Kim 1999), cytological studies demonstrate that the nucleus of only one of these gametes is successful in fusing with the female nucleus. Thus, only one karyogamy follows fertilization (Jaffe and Gould 1985). More recent observations using time-lapse video (Pickett-Heaps and West 1998) indicate that the fertilizing gamete is not necessarily the first one to arrive at or to fuse with the trichogyne. Using *Bostrychia* as experimental material, Pickett-Heaps and West (1998) documented that more than one spermatium can attach and fuse with the trichogyne, as also found in *Aglaothamnion* (Kim and Kim 1999). During their migration through the trichogyne, along actin microfilaments (Kim and Kim 1999), spermatial nuclei change shape and nuclei from different spermatia may pass each other (Pickett-Heaps et al. 2001). When a male nucleus reached the carpogonial base where the female nucleus lies, however, movement of any second nucleus ceased, even when it was close to the base of the trichogyne. This caused Pickett-Heaps and West (1998) to suggest the possibility of a polyspermy block or some other active means for preventing polyspermy. Reinforcing the likely need for a mechanism to prevent polyspermy, Pickett-Heaps and West (1998) also observed that when multiple spermatia attached to a trichogyne, the chances of rupture of that trichogyne increased. In such cases, all gametes involved died.

The above results would suggest that polyspermy prevention is a widespread adaptation in seaweeds with both internal and external fertilization, which is consistent with the lethal effects of fertilization of an egg by more than one sperm. Recently, however, Speransky et al. (2000) found high levels of polygamy in laboratory experiments with *Bryopsis plumosa*, although viability of polygamic zygotes was not determined. These are laboratory results, and perhaps the situation is different in the field. However, these findings stress the need to know the frequency of polyspermy in this and other taxa in nature and whether polyspermy blocks are rare or common in seaweeds. An absence of sperm phototaxis and reduced sperm motility in brackish populations of *F. vesciculosus* also reduce the likelihood of polyspermy (Serrâo et al. 1996b, 1999). Furthermore, sperm limitation may occur in the lowest salinity populations of *F. vesiculosus* in the Baltic due to a female-skewed sex ratio in these populations (Serrâo et al. 1999) that would otherwise be particularly susceptible to polyspermy due to Na^+ limitation.

The window of opportunity concept. Numerous studies performed with fucoid algae (Brawley 1992, Pearson and Brawley 1996, Serrâo et al. 1996a,b, 1999) have led to the idea that a favorable combination of several interacting factors must occur for fertilization to take place. This favorable combination of factors was named the "window of opportunity" (Serrâo et al. 1999), and it includes abiotic and biotic components. Important environmental factors are those triggering gamete release (e.g. adequate light, reduced water movement) or those reducing gamete viability or concentration (e.g. salinity, high water motion). Important biotic components are interparental distances (population density); male-to-female ratios; synchrony of gamete release, age, motility, and longevity of the gametes; and efficiency of the polyspermy block mechanisms. Although many of these factors have been tested preferentially with species living in brackish water or in turbulent intertidal environments, it is likely that the concept applies to any population persisting across a gradient of environmental conditions. Because the reproductive success of these populations appears to depend on a delicate juxtaposition of abiotic and biotic conditions, periods of sexual reproduction at extreme ends of the gradient would be shorter and more variable than in the rest of the population. In fact, Serrâo et al. (1999) predicted large annual variation in fertilization success of *F. vesiculosus* at the extremes of its most northerly population in the Baltic Sea, due to the absence of one or several factors required for synchronous release of good gametes during a reproductive season.

The window of opportunity concept is akin to the safe site concept described by Harper et al. (1965) for higher plants and to the recruitment window concept developed by Deysher and Dean (1986) for kelps. All these ideas stress that a precise combination of factor levels is required for successful completion of a biological process such as recruitment or fertilization.

SOME POPULATION AND COMMUNITY EFFECTS OF NATURAL FERTILIZATION IN SEAWEEDS

The recent data on natural fertilization of seaweeds raise important questions concerning population and community structure and organization. A first question concerns gene flow and population structure. Eggs and sperm of at least some broadcasting seaweeds are released simultaneously in calm water; the longevity of the male gamete is short, and dispersal distances seem reduced. Therefore the possibilities of self-fertilization or fertilization of gametes from spatially close and perhaps genetically related mates are high. In addition, species living in some isolated habitats, such as tide pools, tend to release their gametes mostly during low tide. Consequently, individuals in these pools may form isolated breeding and genetically related subpopulations (Pearson and Brawley 1996). Thus, gene flow among populations would largely depend on the dispersal of zygotes. However, zygotes also seem to have limited dispersal capabilities because many are negatively buoyant or phototactic and attach to the substratum within hours of fertilization (e.g. Serrâo et al. 1996b, Clifton 1997). In the red algae, limitations to dispersal and gene flow seem similar to the broadcasting seaweeds. In fact, the only field data available (*G. gracilis)* indicated (Engel et al. 1999) that only 11% of the cystocarps produced by a population of females within a 5-m^2 intertidal pool could have been sired by males living beyond the pools.

The degree of genetic relatedness between mates in any given seaweed population, the potential importance of self-fertilization in these reproductive processes, and the field conditions increasing gene flow and genetic variability are important, yet unresolved, questions in seaweeds. Fertilization processes in terrestrial plants incorporate self-incompatibility systems (Richards 1997) and systems that discriminate against pollen from neighboring relatives (Snow 1994) as mechanisms to prevent biparental inbreeding. Perhaps similar systems exist in the seaweeds.

A second question relates to the possibilities of male-to-male competition and sexual selection during fertilization of brooding (red) seaweeds. The significant intermale differences in fertilization success found by Engel et al. (1999) suggested the possibility of nonrandom mating, resulting either from female choice or from male-to-male competition. To test this idea, Engel (2000) performed fertilization experiments using single and multiple individuals as sources of spermatia. Multiple donor crosses in a controlled environment simulated the competition dynamics met in the field, whereas the comparison of multiple donor crosses with single donor crosses provided clues as to the mechanisms of nonrandom mating. Results indicated male-to-male differences in the number of cystocarps sired by different donors. In these experiments at least one male from all the sampled pools showed high fertilization performance, suggesting the absence of inherent differences in fertilization capacity between males coming from different pools. In addition, all males sired at least four cystocarps, indicating that all were capable of producing viable gametes. Therefore, differences in the number of cystocarps sired by different donors were more likely due to postadhesion (analogous to postpollination) processes than to an inability to fertilize. Engel (2000) recognized that differences in performance among male donors may be suggestive of sexual selection. However, she also recognized there is not enough evidence in seaweeds to know whether the fitness changes resulting from putative sexual selection have a genetic basis and constitute an evolutionary response (Charlesworth et al. 1987, Engel 2000). Therefore, the significant interactions found among males have been interpreted as a sign of male-to-male competition, an interpretation supported by the observations on spermatial attachment, fertilization, and differential displacement of more than one male nucleus along the trichogyne, described by Pickett-Heaps and West (1998). The crossing experiments with *G. gracilis* also indicated that for any given female gametophyte, the number of cystocarps produced increased with the number of gamete donors. Thus, the number of cystocarps produced in crosses with a single male (single donor crosses) was significantly less than when the same female thallus was exposed to the spermatia of several males (Engel et al. 1999). The number of cystocarps produced was therefore related more to number of male donors than to the total number of gametes. Because donors generally vary in quality, females sample a diversity of mates by mating many times, thereby increasing the probabilities of sampling a superior male and increasing the genetic diversity of the resulting offspring (Engel et al. 1999). Genetically diverse offspring would reduce sib competition while increasing colonization probabilities (Maynard Smith 1978).

Descriptions of massive gamete release by different kinds of broadcasting seaweeds suggest the process should have important, yet unaddressed, community effects in the natural habitats where these processes occur. In places with an abundance of holocarpic species, as in the Bryopsidales on the Caribbean coral reefs studied by Clifton (1997), there seems to be periodic supply of substrate for colonization due to seaweed reproduction. There, 3% to 5% of the population typically became simultaneously fertile (several hundred to thousand of conspecific algal thalli) on any given day (Clifton and Clifton 1999). These siphonous algae released their entire cytoplasm as gametes and died. The empty thalli often disintegrated within hours due to the combined effects of water motion and consumption by grazers. Thus, episodes of sexual reproduction influence community structure on reefs because algal density and percentage cover drop quickly during periods of peak reproduction (Clifton and Clifton 1999). The effects of these reproduction-derived changes in abundance on species interactions and community organization remain largely unexplored in these and other habitats. Equally unexplored are the trophic inputs into the planktonic system and into filter-feeder communities as a consequence of massive gamete release, which can often be detected with the naked eye, because water visibility may be reduced significantly (Clifton 1997). Although such "clouds" may disperse within 10–15 min, they imply a massive input of cellular material, much of which may not survive to become successfully established zygotes. The effects of these reproductive episodes on the dynamics of planktonic communities and on the growth of filter feeders has seemingly gone unstudied until now, both in tropical and temperate habitats. Gamete production and release by seaweeds appears to be a significant, predictable, and highly energetic food resource, with potentially important effects on the organization and dynamics of those communities.

CONCLUSIONS

The previous pages attest to the numerous significant advances made in fertilization ecology of seaweeds over the last decade. Recent work has revealed that fertilization success, and some of the controlling factors, are somewhat similar in the brooding and broadcasting types of fertilization. However, more studies are needed to elucidate whether what appears to be an important difference in mating styles (e.g. brooders vs. broadcasters) has had evolutionary consequences in the seaweeds. To determine whether the patterns discussed above are indeed general to other algal groups, comparative studies on other algae using similar approaches and methods are needed. In particular, more information is required to evaluate whether the high frequency of natural fertilization and the mechanisms preventing polyspermy, as described above, are general to most seaweeds. Future empirical studies conducted under varied environmental conditions and with different taxa will provide critical insight into the multifactorial control of fertilization and direct theoretical development of the window of opportunity concept. Population biology experiments together with physiological studies would probably help to explain the outcome of male-to-male competition during fertilization. Interdisciplinary approaches also seem necessary to understand the pattern of small temporal separation of gamete release among related species, as well as the community consequences of massive gamete release.

Studies over the last decade have also highlighted critical pieces of missing information. The following information is particularly needed: (1) the mechanisms, functions, and responses that determine synchrony of fertilization in the red algae; (2) how often fertilization occurs in habitats characterized by intense water movement; (3) the dispersal capabilities of zygotes in the field; and (4) the mechanisms preventing fertilization among genetically related mates, as well as those preventing hybridization among phylogenetically related species. Field and laboratory studies have shown that in some populations hybridization may occur. Therefore, information on the frequency and population consequences of these events in nature is also needed.

Overall, the recent studies on fertilization ecology of seaweeds have helped to outline a more holistic and integrated view of fertilization processes in seaweeds. They have stressed the multifactorial effects of the abiotic environment on gamete maturation and release. In addition, they demonstrate the need to combine populational and cytological parameters to understand fertilization processes in these organisms. Male-to-female ratios, the degree of spatial association between potential partners, and the local effects of associated vegetation on water velocity and gamete dilution now appear as important as the cellular physiology of the gametes or the effects of the abiotic environment on the control of gamete maturation and release. Successful fertilization seems to depend on a delicate juxtaposition of many factors.

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