How severe is sperm limitation in natural populations of marine free-spawners?

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Successful fertilization in marine organisms that release sperm into seawater is potentially limited by the rapid dilution of gametes; cases of severe sperm limitation have been demonstrated in nature. However, recent surveys of naturally spawning populations indicate fairly high fertilization levels in many taxa. The extreme selection exerted by sperm limitation has resulted in numerous adaptations to reduce sperm limitation and enhance fertilization. Thus, most taxa show indications of the evolutionary consequences of sperm limitation even when population level, ecological effects are minimal.

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Free-spawning marine organisms, including virtually all sessile plants and animals, as well as many sedentary and mobile animals, reproduce by releasing sperm into the surrounding seawater. In brooding organisms, fertilization occurs internally after sperm transit the water column, whereas broadcasters exhibit external fertilization following the release of both sperm and eggs into the water column. Because the release of gametes into the water column incurs potential problems not faced by copulating organisms, much recent work has focused on the processes that determine the success of fertilization in free-spawners. Initial empirical and theoretical work suggested that the potential for extreme dilution of sperm in seawater often reduces sperm concentrations to levels that limit fertilization, and hence predicted that many eggs would remain unfertilized (i.e. that sperm limitation would occur[1]). Consideration of sperm limitation has added a valuable new dimension to analyses of population dynamics[2–4] and of life history evolution[5–8] in marine free-spawners, and provides a valuable alternative hypothesis to earlier assumptions of complete egg fertilization.

Of particular ecological interest is the observation that because fertilization levels decline with distance between individuals, the degree of sperm limitation in experimental populations is negatively associated with population density and male density[2,9,10]. This relationship suggests that natural populations of marine species might exhibit low growth rates at low density owing to reproductive failure that occurs when individuals are widely spaced[2–4,9,10]. However, the fertilization consequences of low population density can be negated by large population size when eggs are fertilized by sperm from many different individuals[11].

Sperm limitation in manipulative experiments

A growing body of evidence suggests that sperm limitation in many natural populations of free-spawners might not be as severe as initially suspected. Many demonstrations of severe sperm limitation come from manipulative experiments, in which experimental organisms were deliberately isolated from conspecifics to evaluate various factors that can cause sperm limitation (e.g. distance from a sperm source[12–14], time since sperm release[15], flow regime[14], reproductive synchrony[15], population density[2,9,10], level of sperm release[16] and presence of an algal canopy[10]). Egg fertilization levels, as assayed by the direct observation of either fertilization envelopes or embryo development, vary dramatically within and among these experiments, and typically range within each experiment from almost 0 to nearly 100%. Consequently, most experiments simultaneously demonstrate the potential for both severe sperm limitation and highly successful fertilization, albeit under different ecological conditions. Thus, the degree to which these experimental demonstrations of sperm limitation are relevant to natural populations depends on the biotic and abiotic conditions under which natural spawning actually takes place[4].

Sperm limitation in field surveys

In contrast to these experimental results, a number of surveys that directly assay egg development in naturally spawning populations have demonstrated successful fertilization for much of the population (Table 1). Most surveys and experiments sample at multiple times and places, and variation among both individual samples and time- or location-specific averages can be quite substantial. Comparisons among these samples confirm that fertilization levels usually vary with density and with distance between spawning organisms[12,17–21] (but see Ref. 22), as well as with flow conditions[11]. Nevertheless, average fertilization levels (either overall, or at the time or place in which most of the population spawned) tend to be quite high (often >85%; Refs 17, 20–28). Time- or location-specific averages for peak spawns are better estimates of population-level fertilization than raw averages of all samples that include times or places in which only a few individuals spawned (averages weighted by the number of spawning individuals at each observation are an even better estimate[19]). Severe sperm limitation of a few spatially or temporally isolated individuals[12,17] indicates strong selective pressures on spawning synchrony, but has only a minor effect on population-level fertilization[19].

Although the overall pattern of high fertilization levels across multiple surveys of diverse taxa is striking, there are some notable exceptions (Table 1). Two studies have demonstrated moderately severe sperm limitation (<50% mean fertilization at times or places of peak spawning[18,29]) and two others have reported intermediate levels of sperm limitation[15,19]. A comparison of results among studies

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suggests that fertilization levels will probably vary among taxa and as a function of reproductive strategy. Highly mobile broadcasters, such as pair- and group-spawning fish, appear to have uniformly successful fertilization owing to their ability to spawn in close proximity[20,22,28]. Similarly, high fertilization levels have consistently been documented in studies of fucoid algae[23,25,26]. The lowest fertilization levels have been reported in surveys of sessile and of sedentary broadcasting invertebrates[18,29]. Although this group also includes examples of extremely successful fertilization[21,24], population-level sperm limitation will probably be more severe[4,8].

Survey results indicate that at a population level, most of the marine taxa surveyed to date are subject to only relatively low levels of sperm limitation in nature. However, individual females are often substantially more sperm limited. The high fertilization levels detected in many of these studies are unlikely to result from a bias introduced during field sampling. Most sampling protocols actually remove eggs from the water while they are still viable, and hence might underestimate true fertilization levels in nature. However, the studies conducted to date might not be an unbiased sample of all marine taxa, especially if investigators have preferentially surveyed more abundant taxa, or taxa that exhibit obvious spawning synchrony or aggregative behavior. If so, fertilization levels in asynchronously spawning, low density or non-aggregating populations might be under-reported.

The key difference between manipulative experiments and field surveys is that the latter sample natural populations when those populations are actually releasing gametes, and thus do not circumvent reproductive strategies that have evolved to promote fertilization success. By contrast, most manipulative studies strive to isolate experimental organisms from the rest of the potentially spawning population, while controlling spawning synchrony and spatial relationships within the experimental group. Although experimentation has made (and will continue to make) crucial contributions to the study of processes that affect fertilization levels, direct surveys of unmanipulated field populations provide more reliable estimates of absolute fertilization levels in nature.

Table 1. Examples of population-level fertilization in recent field surveys

Species	% eggs fertilized	Refs
Brown surgeonfish (*Acanthurus nigrofuscus*)	98.5[a]	22
Brown alga (*Fucus vesiculosus*)	95–100[a]	26
Bivalve (*Paphies australis*)	100[b]	21
Gorgonian coral (*Pseudoplexaura porosa*)	40–85[b,c]	19
Gorgonian coral (*Plexaura kuna*)	5–60[b]	18

[a]Overall fertilization range or mean.
[b]Fertilization mean or range of means when most organisms were spawning.
[c]Because fertilization levels were on average no higher in sperm addition treatments, sperm were less limiting than fertilization levels suggest.

Adaptations that enhance fertilization

Marine fertilization is often successful because organisms have evolved numerous mechanisms to prevent or to reduce sperm limitation. The occurrence of sperm limitation should exert extremely strong selective pressure on reproductive strategies to maximize the success of fertilization and hence reproduction: there is growing evidence for a multitude of such adaptive strategies. Fucoid algae release gametes only at times of low water motion[26] or when they are isolated in pools at low tide[25], in order to minimize the sperm dilution effects associated with water motion. Organisms as diverse as sea urchins, annelids and algae release sperm in viscous fluids[30], again apparently to counteract dilution effects. A number of brooding organisms with internal fertilization use feeding structures, which originally evolved for filtering phytoplankton, to extract sperm or sperm packets from seawater[31,32]. In bryozoans, the reproductive advantages of internal fertilization via a sperm collection system are so great that even species that release early stage embryos into the plankton have internal sperm/egg fusion[27]. Some ascidians store sperm[33] and can apparently accumulate dilute sperm from the water[16,32].

Mobile taxa exhibit a number of mechanisms to bring spawning individuals into close physical proximity and to reduce gamete dilution effects. These behaviors range from simple movement towards other spawning individuals[17], to the formation of mating aggregations[20,22,28] and to actual pseudo-copulation[34]. Both sessile and mobile organisms often exhibit a high degree of spawning synchrony[12,17,19] (but see Ref. 35). Extremely high levels of sperm production in some asteroids might counteract dilution effects to such an extent that successful fertilization occurs even tens of meters from a male[12,13]. Although hydrodynamic processes usually reduce fertilization efficiency, positive effects are possible when organisms inhabit surge channels that retain and mix gametes[36]. The floating gametes of many corals and the positively phototactic gametes of many green algae minimize dilution by limiting diffusion to only two, rather than three, dimensions[15].

Other attributes of gametes appear to have evolved in response to the selective pressures of sperm limitation. For example, larger eggs might have evolved to increase the target area for sperm[5,8] (but see Ref. 6), and sperm chemotaxis presumably evolved to facilitate sperm/egg contact across short distances[37] (on the order of egg diameters). Increased sperm longevity might have evolved to facilitate fertilization between widely spaced individuals[38]. In some solitary ascidians, sperm longevity is maximized by releasing sperm in an immotile state and then inducing motility only upon contact with egg exudates[39]. Recent evidence indicates that sea urchin eggs have a much longer inherent longevity (1–3 weeks)[40] than the 8–12 hours previously reported[10], thus potentially permitting fertilization to occur at a low rate over a long timespan.

Are there sometimes too many sperm?

There is growing evidence that most marine organisms possess sophisticated mechanisms to cope with a problem that is the antithesis of sperm limitation: eggs often encounter too many sperm. The fusion of more than one sperm with an egg results in polyspermy, which is lethal to the embryos of most taxa. Diverse mechanisms to prevent polyspermy are ubiquitous in three kingdoms and almost every marine phylum[41], suggesting that multiple sperm/egg contacts must be a common feature of fertilization in the marine realm[12,23]. Unfortunately, information on the actual incidence of polyspermy in nature is limited (but see Refs 23,25).

Many taxa have two separate polyspermy blocks that operate on different time scales (seconds and minutes, respectively)[41]. In fish, sperm penetrate the egg through a single channel (the micropyle), which is blocked after one sperm enters[41]. However, sperm concentrations in nature can be so high that even the fastest polyspermy-preventing mechanisms are not 100% effective, as evidenced by the presence of polyspermic eggs in field survey samples[23,25]. When environmental conditions inhibit polyspermy blocks, reproductive failure, owing to a high incidence of polyspermy, might be severe enough to limit population distributions[23]. Nevertheless, the existence of polyspermy-preventing mechanisms is consistent with some level of sperm limitation, because variation in sperm concentration can result in multiple sperm/egg contacts for some eggs, although others remain unfertilized[1,8,9]. Revised fertilization models can incorporate potential reproductive losses from both polyspermy and sperm limitation[7].

In addition to potentially contacting too many conspecific sperm, marine organisms face a second problem related to surplus non-conspecific sperm. Accidental contact with sperm from non-conspecifics, which is likely to result in a non-viable embryo after sperm/egg fusion, is common enough to have resulted in the evolution of species-specific gamete recognition systems[42]. The potential for contact with gametes both from closely related and from distantly related taxa is high when diverse species spawn in response to a common environmental cue[17]: gametic incompatibility systems appear to reduce congeneric hybridization in joint spawns[21].

Ecological versus evolutionary consequences

Some level of sperm limitation occurs in nature. However, in most of the taxa surveyed to date, severe sperm limitation mainly seems to affect individuals that are located on the periphery of a population or that release gametes out of synchrony with other members of the population[12,17,19]. At a population level, the degree of sperm limitation reported in most surveyed taxa is unlikely to represent a major limiting step in population growth (but see Refs 18,29). The 0–20% losses reported in most taxa during fertilization (and even the 90–95% losses reported for the most extreme cases) are several orders of magnitude lower than most estimates of larval mortality. Comparisons between larval and recruit densities[43] suggest that larval survival is generally on the order of only 10^{-4} to 10^{-7}. All reproductive losses impact population dynamics in recruitment-limited taxa, thus even relatively low levels of sperm limitation could have appreciable population-level consequences and should be incorporated in models of population dynamics. However, for most of the free-spawning taxa surveyed to date, the demographic consequences of sperm limitation are probably less than those of larval mortality, and are more comparable to mortality during post-settlement and adult stages of the life cycle.

Populations in which the density has been reduced, to levels lower than have consistently occurred during evolutionary history (through disease, direct human exploitation, or community and habitat changes associated with human activities), are likely to be substantially more sperm limited. Many commercially over-exploited taxa are recruitment-limited or display positive density-dependent population dynamics[3,4,44] (but see Ref. 45). Consequently, the effect of sperm limitation at low population density has been incorporated into fisheries models[3]. Although the various ecological factors that determine the dynamics of exploited populations are rarely completely understood, sperm limitation is suspected to play a role in some cases[4,44].

Even in the absence of substantial population-level ecological consequences in many taxa, sperm limitation that affects individuals should exert a strong selective force on reproductive systems and should lead to the evolution of reproductive strategies that will reduce its impact. However, when evaluating the evolutionary consequences of fertilization dynamics, it is important to simultaneously consider the possible effects of multiple fertilization phenomena. In particular, high egg fertilization levels with frequent multiple sperm contacts per egg, suggest that the evolutionary dynamics of many marine systems, as in virtually all terrestrial systems, will be affected by sperm competition (competition among males for access to eggs). An assessment of the relative selective pressures of sperm competition versus sperm limitation is crucial to analyses of the evolution of reproductive systems in marine organisms[5,8,16]. Sperm competition has been empirically demonstrated in a handful of free-spawning invertebrates (horseshoe crabs, ascidians and bryozoans)[9,46] and is widely anticipated in fish systems[47]. Thus, the taxonomic distribution will probably be quite broad. Any species that has a mating system in which multiple males release sperm simultaneously and that possesses mechanisms to prevent polyspermy is potentially subject to sperm competition. Given the large number of taxa that meet these two criteria, sperm competition appears likely to be a potent evolutionary force in marine free-spawners, in spite of the occurrence of some degree of sperm limitation[1,8,9].

Prospects

To date, results suggest a number of directions for future work in the field of marine fertilization ecology. First, there is a need to assess the magnitude of sperm limitation in more natural populations via techniques that avoid the biases of some past studies. For example, future surveys should encompass the total period of egg viability to prevent systematically underestimating fertilization levels. Surveys should include a treatment in which sperm are added to an aliquot of collected eggs to test whether sperm addition actually increases the observed fertilization level[18,19] (analogous to pollen addition experiments used to test for pollen limitation in terrestrial plants), instead of inferring sperm limitation from the extent to which egg fertilization levels fall below 100%. The successful development of an aliquot of fertilized eggs should be monitored as a check for post-fertilization developmental failures that might be caused by polyspermy[7,23,25].

Second, we need to continue to assess patterns of severity of sperm limitation among different taxa, reproductive strategies and habitats. Current data suggest that fish[20,22,28], brooders (that can concentrate sperm from the water column)[32] and algae (that spawn at times of low water movement)[26] are substantially less sperm-limited than many sessile and sedentary broadcasters[8]. But what about brooders that lack efficient sperm collection mechanisms? Does the extremely low fertilization level estimated for one brooding coral[48] indicate that these taxa are even more susceptible to sperm limitation? Efforts should also be made to survey more rare and asynchronously spawning taxa.

Third, basic information on spawning patterns and proximal cues for gamete release is crucial for many taxa. Except for basic seasonal patterns, little is known about natural spawning patterns in many taxa, even in some of the best understood experimental systems (e.g. echinoids) (but see Ref. 35). In order to accurately extrapolate fertilization levels in nature from models and from experimental results, we need more detailed information on: the degree of spawning synchrony in populations; the number of spawns participated in by each individual; the portion of each individual's gametes released in each spawn; and the hydrodynamic conditions at the time of spawning.

Sperm limitation continues to represent a valuable alternative hypothesis to the uncritical assumption of complete egg fertilization. Although populations of some taxa appear likely to be sperm limited, the extreme selective pressure exerted by sperm limitation might have led reproductive systems to evolve so that sperm limitation is not severe in many free-spawners. However, even for taxa that lack substantial population-level ecological effects, sperm limitation acting on individuals will probably be an important factor in life history evolution.

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