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

Philip O. Yund

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.

**Sperm limitation in field surveys**

In contrast to these experimental demonstrations of 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.

**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, time since sperm release, low regime, reproductive synchrony, population density), level of sperm release and presence of an algal canopy. 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. In contrast to these experimental demonstrations of sperm limitation, many natural populations are likely to exhibit low fertilization levels, as assayed by the direct observation of either fertilization envelopes or embryo development, albeit with a minor effect on population-level fertilization. In contrast to these experimental demonstrations of severe sperm limitation and highly successful fertilization, albeit under different ecological conditions.

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

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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. Similarly, high fertilization levels have consistently been documented in studies of luscoid algae. The lowest fertilization levels have been reported in surveys of sessile and of sedentary broadcasting marine invertebrates. Although this group also includes examples of extremely successful fertilization, population-level sperm limitation will probably be more severe.

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.

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 that most marine organisms have evolved numerous mechanisms to prevent or to minimize the sperm dilution effects associated with water motion. Many taxa exhibit a number of strategies that facilitate fertilization between widely spaced individuals. For example, larger eggs might have evolved to increase motility only upon contact with egg exudates. In bryozoans, the reproductive advantages of internal fertilization via a sperm packet collection system are so great that even species that release early stage embryos into the plankton have internal sperm/egg fusion. Some ascidians store sperm and can apparently accommodate dilute sperm from the water. 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, to the formation of mating aggregations, and to actual pseudo-copulation. Both sessile and mobile organisms often exhibit a high degree of spawning synchrony (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 (but see Ref. 36). Although hydrodynamic processes usually reduce fertilization efficiency, positive effects are possible when organisms inhabit surge channels that retain sperm/egg contact over short distances (but see Refs 23,25). Increased sperm longevity might have evolved to facilitate fertilization between widely spaced individuals. In some solitary ascidians, sperm longevity is maximized by releasing sperm in an immobile state and then inducing motility only upon contact with egg exudates. Recent evidence indicates that sea urchin eggs have a much longer inherent longevity (1–3 weeks) than the 8–12 hours previously reported. 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. For example, larger eggs might have evolved to increase motility only upon contact with egg exudates. In bryozoans, the reproductive advantages of internal fertilization via a sperm packet collection system are so great that even species that release early stage embryos into the plankton have internal sperm/egg fusion. Some ascidians store sperm and can apparently accommodate dilute sperm from the water.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>% eggs fertilized</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown surgeonfish (Acanthura nigrofuscus)</td>
<td>98.5–100%</td>
<td>22</td>
</tr>
<tr>
<td>Brown algae (Fucus vesiculosus)</td>
<td>95–100%</td>
<td>26</td>
</tr>
<tr>
<td>Bivalve (Paphies australis)</td>
<td>100%</td>
<td>21</td>
</tr>
<tr>
<td>Gorgonian coral (Pseudopleura porcella)</td>
<td>40–85%</td>
<td>19</td>
</tr>
<tr>
<td>Gorgonian coral (Pleurosia kula)</td>
<td>5–60%</td>
<td>18</td>
</tr>
</tbody>
</table>

*Overall fertilization range or mean.*

*Fertilization mean or range of means when most organisms were spawning.*

*Because fertilization levels were on average no higher in sperm addition treatments, sperm were less limiting than fertilization levels suggest.*
presence of polyspermic eggs in field survey samples. When environmental conditions inhibit polyspermy blocks, reproductive failure, owing to a high incidence of polyspermy, might be severe enough to limit population distributions. Nevertheless, the existence of polyspermmy-preventing mechanisms is consistent with some level of sperm limitation, because variation in sperm concentration can result in multiple sperm/egg contacts for some taxa. Revised fertilization models can incorporate potential reproductive losses from both polyspermy and sperm limitation.

In addition to potentially contacting too many conspecific sperm, marine organisms face a second problem related to surplus non-conspecific sperm. Accidental contact with gametes 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. 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; gametic incompatibility systems appear to reduce congeneric hybridization in joint spawns.

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. At a population level, the degree of sperm limitation reported in most surveyed taxa is likely to underestimate the true extent of sperm limitation and is probably less than those of larval mortality. Comparisons between larval and recruit densities suggest that larval survival is generally on the order of only 10^-4 to 10^-7.

All reproductive losses impact population dynamics in relation to the taxon, 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 those consistently observed 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. Consequently, the effect of sperm limitation at low population density has been incorporated into fisheries models. 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.

Even in fish populations, the 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 should be undertaken. Revised fertilization models can incorporate potential reproductive losses from both polyspermy and sperm limitation.

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 reconsider 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 (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.

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, brooders that can concentrate sperm from the water column and algae (that spawn at times of low water movement) are substantially less sperm-limited than many sessile and sedentary broadcasters. But what about brooders that lack efficient sperm collection mechanisms? Does the extremely low fertilization level estimated for one brooding coral 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) in order to accurately extrapolate fertilization levels in nature from models and from experimental results, we need more detailed information on the degree of sperm competition 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...
REFERENCES