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Local Gamete Competition Explains Sex Allocation and Fertilization Strategies in the Sea

Jonathan M. Henshaw,[1],* Dustin J. Marshall,[2] Michael D. Jennions,[1] and Hanna Kokko[1]

1. Research School of Biology, Australian National University, Australian Capital Territory 0200, Australia;   2. School of Biological Sciences, Monash University, Victoria 3800, Australia

abstract: Within and across taxa, there is much variation in the mode of fertilization, that is, whether eggs and/or sperm are released or kept inside or on the surface of the parent's body. Although the evolutionary consequences of fertilization mode are far-reaching, transitions in the fertilization mode itself have largely escaped theoretical attention. Here we develop the first evolutionary model of egg retention and release, which also considers transitions between hermaphroditism and dioecy as well as egg size evolution. We provide a unifying explanation for reported associations between small body size, hermaphroditism, and egg retention in marine invertebrates that have puzzled researchers for more than 3 decades. Our model, by including sperm limitation, shows that all these patterns can arise as an evolutionary response to local competition between eggs for fertilization. This can provide a general explanation for three empirical patterns: sperm casters tend to be smaller than related broadcast spawners, hermaphroditism is disproportionately common in sperm casters, and offspring of sperm casters are larger. Local gamete competition also explains a universal sexual asymmetry: females of some species retain their gametes while males release theirs, but the opposite ("egg casting") lacks evolutionary stability and is apparently not found in nature.

Keywords: sex roles, hermaphroditism, brooding, sperm casting, broadcast spawning, mode of fertilization.

Introduction

Sexual reproduction requires that gametes find each other. Some species achieve this by releasing their gametes into the air or water for fertilization, while others keep them close to their bodies. There is surprisingly little theory to explain variation in the mode of fertilization (broadcast spawning with both eggs and sperm being released, sperm casting with release of sperm and retention of eggs, and mating with retention of both types of gametes) even

* Corresponding author; e-mail: jonathan.henshaw@anu.edu.au.

though the prevalence of the three main modes appears to differ markedly among broad taxonomic groups and between terrestrial and aquatic environments (Strathmann 1990; Bishop and Pemberton 2006). In addition, a theoretical understanding of patterns of covariation between hermaphroditism and the mode of fertilization is still lacking, despite evidence that sperm casters are more likely than broadcast spawners to be simultaneous hermaphrodites (Strathmann et al. 1984; Kupriyanova et al. 2001).

The lack of theoretical attention to the evolution of fertilization mode is unfortunate because the release or retention of gametes prior to fertilization has major implications for the evolution of other life-history traits, including many that are closely linked to sex roles. For instance, postzygotic parental care is usually only possible when adults remain close to their gametes during and after fertilization (Williams 1975; Kahn et al. 2013). Consequently, sex differences in gamete release or retention constrain which sex can provide parental care. Similarly, mate choice based on nongametic traits can occur only if adults encounter each other before fertilization. There are also macroevolutionary consequences of variation in fertilization modes. For example, population dispersal patterns are affected because zygotes resulting from the fertilization of released eggs are often carried great distances from their parents. This has flow-on effects on population genetic structure, species ranges, and rates of speciation and extinction (Scheltema 1977; Hansen 1980; Jones et al. 2009; Crampton et al. 2010).

The study of marine invertebrates is important for understanding evolutionary transitions in fertilization modes, given that the marine environment is ancestral to all animals. Present-day diversity in fertilization mode is also striking, which allows us to look for general patterns that transcend phylogenetic boundaries. Mechanisms of fertilization range from those that require adults to be in close physical proximity, such as copulation and pair spawning, to those that can operate even if adults never come into close contact,

such as when gravid females filter sperm from the open water (Bishop and Pemberton 2006). Dioecy (separate male and female individuals) and hermaphroditism are also both common (Jarne and Auld 2006), and in some species unisexual individuals even coexist with simultaneous hermaphrodites (Giese and Pearse 1974; Weeks 2012).

Reproductive diversity in marine invertebrates is not limited to variation among higher taxonomic groups. Intriguingly, even closely related species often differ in their reproductive strategies (Strathmann and Strathmann 1982). Recent phylogenetic analyses have revealed frequent transitions in reproductive behavior at all taxonomic levels (e.g., sabellid worms: Rouse and Fitzhugh 1994; asterinid sea stars: Hart et al. 1997; soft corals: McFadden et al. 2001; all animal phyla: Iyer and Roughgarden 2008; and stony corals: Kerr et al. 2011). This suggests that reproductive traits are labile over short evolutionary timescales. Crucially, the presence of diversity at lower taxonomic levels allows us to look for traits that are correlated with a particular reproductive strategy, providing us with clues as to why these strategies have evolved.

Several models consider the evolutionary consequences of fertilization mode (Shine 1978; Sargent et al. 1987; Jørgensen et al. 2011) and we are aware of one study of the coevolution of sperm release and retention with hermaphroditism and dioecy (Iyer and Roughgarden 2008). Transitions in the release or retention of eggs have, however, largely escaped theoretical attention. Here we develop the first mathematical model of the evolution of sperm casting (in which eggs are retained) and broadcast spawning (in which eggs are released). We also investigate how hermaphroditism/dioecy and egg size coevolve with fertilization mode. We provide a unifying explanation for a reported association between small body size, hermaphroditism, and egg retention in marine invertebrates that has puzzled researchers for more than 3 decades (Heath 1979; Strathmann et al. 1984). We also explain a universal sexual asymmetry: females of some species retain their gametes while males release theirs, but the opposite pattern (which we term "egg casting") apparently never occurs.

Terminology and Rationale

We can classify fertilization strategies into four modes of fertilization based on how close the gametes of each sex are to their parents at fertilization. We say gametes are retained if they are close to or inside their parent's body when fertilized. If they are far away from their parent, we say they are released. It is sometimes not possible to make a hard distinction between retained and released gametes. For instance, the eggs of some species initially adhere to the surface of their mother's body before ablating into the water column (Marshall 2002; Yund and Meidel 2003).

Broadcast spawning occurs when both sexes release their gametes into the open water (Levitan 1998). A combination of ocean currents, chemo-attractants, and gamete swimming then brings gametes together to enable fertilization (Evans et al. 2012). Sperm casting occurs when only sperm are released, while eggs are retained close to or inside their mothers' bodies (Pemberton et al. 2003). Sperm-casting species usually achieve fertilization by filtering sperm out of the water in a manner similar to filter feeding (Bishop and Pemberton 2006). Mating occurs when all adults retain their gametes until they encounter an appropriate partner. Common forms of mating include copulation (Addison and Hart 2005) and simultaneous pair or group spawning (Giese and Kanatani 1987; Kiørboe and Sabatini 1995). The fourth possibility, which we call egg casting, is that eggs are released into the water, while sperm are retained by their parents. To our knowledge, egg casting has not been observed in any animal or plant species.

To avoid confusion, we note that some authors use the term "broadcast spawning" to refer to the release of sperm, regardless of whether eggs are released or retained (e.g., Iyer and Roughgarden 2008). We apply this term only to species that release both eggs and sperm.

Three Key Relationships between Fertilization Mode, Body Size, and Reproductive Traits

Comparative analysis of reproduction in marine invertebrates has unearthed several fascinating patterns of covariation between the mode of fertilization, body size, and two key reproductive traits: egg size and simultaneous hermaphroditism.

Sperm Casters Tend to Be Smaller than Related Broadcast Spawners. In comparisons within taxa, species with smaller-bodied adults are relatively more likely to be sperm casters than broadcast spawners. Since the first review by Strathmann and Strathmann (1982; updated in Strathmann 1990), this observation has gained considerable empirical support (e.g., sabellid worms: Rouse and Fitzhugh 1994; asterinid sea stars: Hart et al. 1997; serpulid and spirorbid worms: Kupriyanova et al. 2001; and soft coral: McFadden et al. 2001). The opposite pattern appears to be rare, although in many taxa only one fertilization mode occurs. Intriguingly, the link between body size and fertilization mode appears not to apply across taxa: the smallest sperm casters of one taxon are often larger than the largest broadcast spawners of another (Strathmann and Strathmann 1982).

Hermaphroditism Is More Common in Sperm Casters. Simultaneous hermaphroditism is more common among
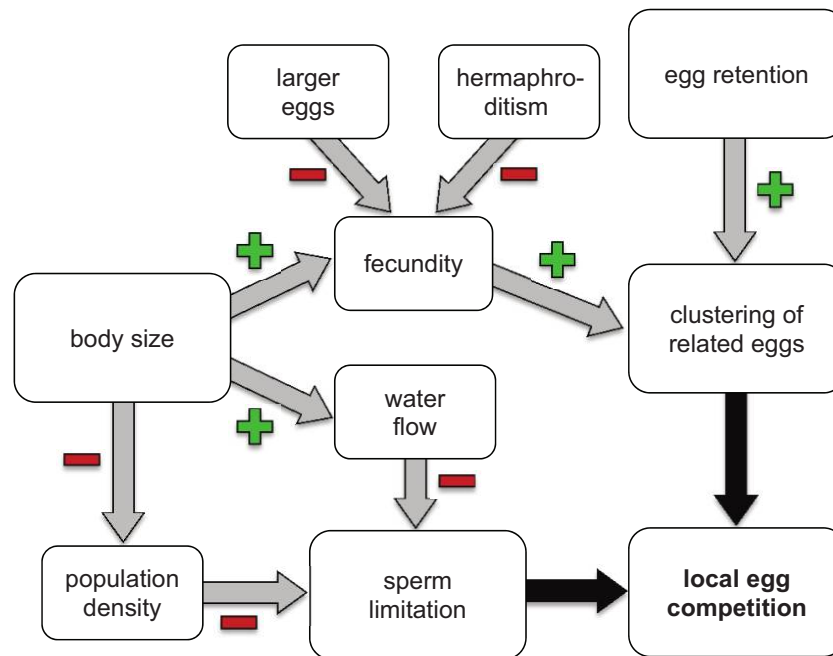
Figure 1: Processes influencing the intensity of local egg competition.

sperm casters than broadcast spawners (Heath 1979; Strathmann et al. 1984; Kupriyanova et al. 2001; Mc-Fadden et al. 2001; but see Heller 1993). It is unknown whether this association arises from independent underlying effects of body size on both traits, or whether sperm casting itself selects for simultaneous hermaphroditism.

Sperm Casters Produce Larger Offspring. On average, the offspring of sperm casters are larger than those of broadcast spawners, even after controlling for body size (e.g., sabellid worms: Rouse and Fitzhugh 1994; serpulid and spirorbid worms, Kupriyanova et al. 2001). In some instances, increased offspring size is achieved via the production of larger eggs, while in others (particularly brooders or those species with nurse eggs), offspring growth rather than egg size is responsible for large offspring.

Overview of a Model Based on Local Gamete Competition

We aim to explain the above three empirical patterns by identifying stable reproductive behavior in a model where an individual's strategy includes the option to release or retain gametes; to be male, female, or a hermaphrodite (and, in the latter case, to vary the relative allocation of resources to sperm and egg production); and to produce larger or smaller eggs. Our model explores the possibility that local competition between gametes for fertilization

provides a general explanation for these patterns, as well as why egg casting has never evolved.

In marine environments, fertilization is often limited by the availability of gametes of the opposite sex. This is true not only for sperm but also for eggs, whose fertilization success can be limited by low sperm densities under natural conditions (Levitan and Petersen 1995; Yund 2000; Marshall and Evans 2005). If sperm densities are limiting, then a high local density of eggs can cause sperm depletion, lowering the rate of egg fertilization. Consequently, eggs that are limited by sperm availability compete for access to sperm whenever they are clumped together (fig. 1). The same argument applies to sperm that are limited by access to eggs. Spatial concentration of one gamete type and low density of the other type lead to local competition among the former.

Local gamete competition (LGC) is competition between related gametes for fertilization (sensu Schärer 2009). It occurs whenever the experimental removal of some gametes increases the probability that related gametes are fertilized. LGC is a form of local resource competition (sensu West 2009) that can lead to saturating fitness curves in the competing sex.

Gametes disperse widely when they are released so, all else being equal, LGC should be less severe for released gametes than for retained gametes. Consequently, we predict that high levels of LGC select for the release of gam-

etes. We can isolate four additional factors that potentially affect the intensity of LGC:

Anisogamy. Sperm are produced in greater numbers than eggs, so they should generally experience higher LGC. This could explain the absence of egg casters: the range of ecological conditions that favor sperm release are broader than those selecting for egg release. Thus whenever the latter is favored, the former is too, resulting in broadcast spawning rather than egg casting.

Body Size. Fecundity increases with body size (Levitan 1991; Rouse and Fitzhugh 1994). If the local availability of sperm increases less than linearly with fecundity as body size increases, then larger species will suffer greater sperm limitation and higher LGC among eggs. This could occur in sperm casters if the number of sperm that females or hermaphrodites can filter out of the water increases more slowly than fecundity as body size increases. This might explain why larger species within a given taxon more often release their eggs (i.e., are broadcast spawners).

Hermaphroditism. Simultaneous hermaphroditism might reduce LGC in both sexes by dividing reproductive resources between male and female functions. If LGC is more severe for sperm casters than for broadcast spawners, then the higher prevalence of hermaphroditism in sperm casters could arise from selection to reduce LGC between retained eggs by diverting excess female reproductive capacity to male function.

Egg Size. For a fixed reproductive investment, producing fewer eggs will reduce LGC. It may also bring additional advantages such as increased survival or future fecundity of zygotes due to the resultant increase in egg size (Rius et al. 2010). When local egg competition is strong in sperm casters, larger eggs might be selected for to reduce wasteful competition between related eggs for fertilization. Larger egg size could then contribute to sperm casters producing larger offspring.

The Model

We model the effects of LGC on the evolution of fertilization mode, hermaphroditism/dioecy, and egg size in marine invertebrates across a range of body sizes. We consider only species that achieve fertilization without close contact between adults (the evolution of mating is beyond the scope of our model). In principle, any of the six combinations of broadcast spawning, sperm casting, or egg casting with hermaphroditism or dioecy could evolve. We refer to each combination as a reproductive strategy.

We assume large, well-mixed populations of sexually reproducing individuals. In dioecious populations, males and females occur at approximately equal densities (i.e., the operational sex ratio is equal to one). In hermaphroditic populations, each individual devotes the same fixed proportion r of its reproductive resources to producing sperm and the remainder $(1 - r)$ to producing eggs (model parameters are summarized in table 1). We assume that hermaphrodites are not self-fertile, a condition that holds for many species (Cohen 1990; Jarne and Auld 2006). We consider how this latter assumption might affect our predictions in "Discussion."

We assume that unisex individuals have a fixed budget M for gamete production, measured as the volume of gametes produced per unit time (Parker 2011). Hermaphrodites produce a lower volume of gametes than unisex individuals of the same size due to the cost $0 < d < 1$ of maintaining both types of gonad (Heath 1977). Each hermaphrodite thus devotes $(1 - d)rM$ resources to sperm production and $(1 - d)(1 - r)M$ to egg production. We assume that gamete budgets increase linearly with a species' average adult body size B (Hess 1993; Rouse and Fitzhugh 1994; Sewell 1994) so that $M = k_M B$ for some constant k_M.

An individual's strategy is a multidimensional trait set that comprises its egg size, reproductive strategy, and sex allocation if a hermaphrodite. These traits together determine the individual's rate of fitness gain when breeding (for simplicity we assume continuous breeding). The rate of fitness gain is equal to the product of the individual's rate of fertilization and the average fitness of the resultant zygotes.

Fitness

We compare the fitness of typical individuals in a population to that of mutants with a different strategy to determine which combinations of traits are evolutionarily stable (for full details see app. A; apps. A and B available online). We assume that any mutant with higher fitness than the population average can invade the population.

Consider a mutant focal individual that produces eggs of size $\hat{m}_e$ in a population where all other individuals produce eggs of size m_e. We write $\hat{f}_{\text{female}}$ for the individual's rate of fertilization through female function (eggs fertilized per unit time) and $\hat{f}_{\text{male}}$ for its rate of fertilization through male function (sperm fertilizing per unit time). If the mutant's eggs form zygotes of average fitness $s(\hat{m}_e)$ and its sperm form zygotes of fitness $s(m_e)$, then the mutant's rate of fitness gain is given by

$$\hat{w} = \frac{1}{2}[\hat{f}_{\text{female}}s(\hat{m}_e) + \hat{f}_{\text{male}}s(m_e)].$$

Table 1: Key variables and parameters in the model

Term	Definition
The model:	
r	Sex allocation for hermaphrodites (proportion of resources allocated to male function)
M	Gamete budget (rate of gamete production for unisex individuals)
d	Cost of hermaphroditism to gamete budget
B	Body size
k_M	Scaling coefficient of gamete budget with body size
Fitness:	
m_e	Egg size (variable)
s	Zygote fitness
How does gamete release affect fertilization probability?:	
γ	Fertilization efficiency
Rates of gamete flow between regions:	
F_{nc}	Rate of water flow from a neighborhood into a fertilization cavity
F_{on}	Rate of water flow between the open water and a neighborhood
V_c/V_n	Volume of fertilization cavity/neighborhood
Gamete production and mortality:	
m_s	Sperm size (parameter)
I_e/I_s	Rate of egg/sperm production for unisex individuals
μ_c^e/μ_c^s, μ_n^e/μ_n^s, μ_o^e/μ_o^s	Mortality rates of eggs/sperm in fertilization cavities, neighborhoods, open water
μ_L	Rate of gamete loss from the fertilization arena due to currents
How does body size affect population density and pumping rate?:	
ρ	Population density
k_ρ/a_ρ	Scaling coefficient/exponent of population density with body size
k_F/a_F	Scaling coefficient/exponent of water flow into fertilization cavities with body size
How does egg size affect fertilization rates and zygote survival?:	
k_γ/a_γ	Scaling coefficient/exponent of fertilization efficiency with egg size

The factor of one-half arises because on average 50% of a zygote's genes come from each parent. Hermaphrodites trade off fertilization rates in female and male functions ($\hat{f}_{female}$ and $\hat{f}_{male}$) through their sex allocation r. For unisex individuals, one of these rates is equal to zero. Individuals that produce fewer, larger eggs will generally have lower total rates of fertilization ($\hat{f}_{female}$) but higher average zygote fitness $s(\hat{m}_e)$ due to increased offspring survival and/or fecundity (Einum and Fleming 2000; Marshall and Keough 2006; see below). Note that both $\hat{f}_{female}$ and $\hat{f}_{male}$ depend not only on the mutant individual's behavior but also on the population-wide fertilization mode and allocation of resources to sperm and eggs. This means in particular that there is feedback from overall sex allocation in the population to selection on the sex allocation of particular individuals (Shaw and Mohler 1953).

How Does Gamete Release Affect Fertilization Probability?

Gamete densities are affected by the release strategy of the parent and by that of other individuals in the population. We conceptualize this problem by dividing the fertilization arena into three regions: fertilization cavities, neighborhoods, and the open water. These regions are connected by the flow of water and gametes (fig. 2). We derive the densities of sperm and eggs assuming, for simplicity, uniform densities within each region. We are ultimately interested in gamete density differences between the regions, as these affect the fertilization rates of retained and released gametes.

A fertilization cavity is where retained gametes are stored. It might be an internal body cavity or an external area such as an indentation on the body's surface. Gametes of other individuals enter the fertilization cavity from the surrounding water by either passive water flow or active pumping (Bishop and Pemberton 2006). A neighborhood is the region of water directly surrounding a single individual where LGC between its released gametes is still possible. The open water consists of all water outside of neighborhoods that is still close enough to spawning individuals for fertilization to occur but where LGC no longer occurs. When gametes are released, they initially enter their parent's neighborhood. Water flow and active swimming then carry gametes into the open water. Currents may also sweep gametes away from the fertilization arena entirely, which we treat as a form of gamete mortality (see below).

In broadcast-spawning species, fertilization can occur both in neighborhoods and in the open water. In contrast, for both sperm casters and egg casters, fertilization only
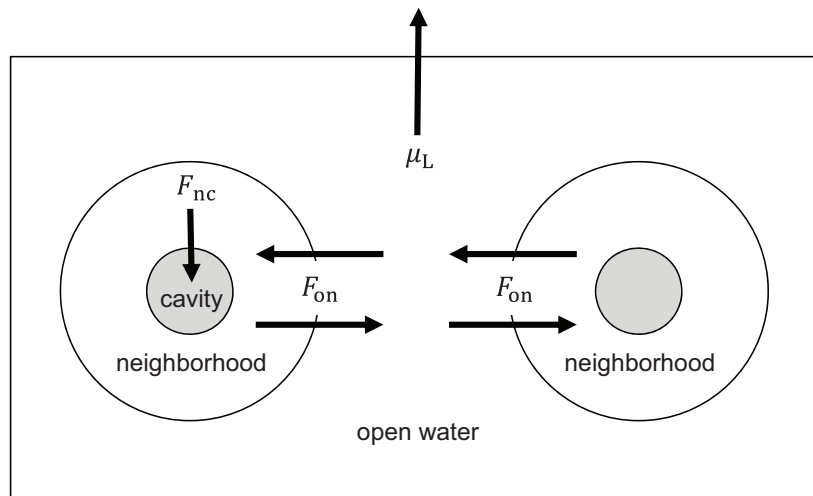
Figure 2: Flow of water and gametes among fertilization cavities, neighborhoods and the open water. On the left is a gamete-retaining individual; on the right, a gamete-releasing individual.

occurs in the fertilization cavities of gamete-retaining individuals. Thus, for released gametes to achieve fertilization, they must first be carried from their parent's neighborhood into the open water, then flow into the neighborhood of a gamete-retaining individual and finally on into its fertilization cavity.

The rate of fertilization in each of the three regions is proportional to the product of the local densities of sperm and eggs (Hutchinson and Waser 2007; Dusenbery 2009). For instance, if we write E_c and S_c for the densities of eggs and sperm in a fertilization cavity, then the rate of fertilization in the cavity is $\gamma E_c S_c$ per unit volume per unit time. The coefficient γ measures the efficiency of fertilization: higher values of γ correspond to higher fertilization rates for any fixed gamete densities. Equivalent expressions apply in the other two regions. Our next step is to derive all factors that affect sperm and egg densities in each region.

Rates of Gamete Flow between Regions

We write F_{nc} for the rate at which water is filtered through the fertilization cavity of a gamete-retaining individual (subscript nc means "from neighborhood to cavity"). Once a gamete enters a fertilization cavity, we assume that it remains there until it dies or is fertilized. Gametes enter a fertilization cavity at a rate of F_{nc} times their density in the surrounding neighborhood. For instance, if sperm occur at a density of S_n in the neighborhood of a gamete-retaining individual, then sperm flow into that individual's fertilization cavity at a rate of $F_{nc}S_n$. If the fertilization cavity has volume V_c, then this corresponds to an increase in sperm density in the cavity of $F_{nc}V_c^{-1}S_n$ per unit time.

For hermaphroditic sperm casters and egg casters, we assume that released gametes do not enter their parent's own fertilization cavity.

Unlike gamete flow into fertilization cavities, flow between neighborhoods and the open water occurs in both directions. The net rate of gamete flow is equal to the product of water flow F_{on} and the difference in gamete densities between the two regions. For instance, if S_o and S_n are the densities of sperm in the open water and a particular neighborhood respectively, then the net rate of sperm flow from the open water into the neighborhood is $F_{on}(S_o - S_n)$. This causes sperm density in the neighborhood to increase (or decrease) at a rate of $F_{on}V_n^{-1}(S_o - S_n)$, where V_n is the volume of the neighborhood.

Potential for Local Gamete Competition

We assume that released gametes interact locally within their parent's neighborhood but not once they reach the open water. This means that LGC can occur in the fertilization cavity and neighborhood of gametes' parents but not in the open water or in the neighborhoods of other individuals. Related gametes only compete for fertilization when they are clustered together and when gametes of the opposite sex are limiting (fig. 1). For individuals that retain their gametes, the availability of opposite-sex gametes is partly limited by water flow into the fertilization cavity. Consequently, high flow into fertilization cavities reduces LGC. Similarly, high flow into and out of neighborhoods reduces LGC between released gametes by spreading them out more evenly across space.

Live Fast, Die Young: Gamete Production and Mortality

Unisex individuals have a gamete budget of size M, so a pure female producing eggs of size m_e will produce $I_e = M/m_e$ eggs per unit time. Similarly, a pure male produces $I_s = M/m_s$ sperm per unit time. Unlike egg size, which evolves in our model, we treat sperm size m_s as a fixed parameter. Due to the cost d of hermaphroditism, a hermaphrodite that allocates a proportion r of its resources to male function produces $(1 - d)(1 - r)I_e$ eggs and $(1 - d)rI_s$ sperm per unit time.

We allow mortality rates to differ between sperm and eggs and between the three regions. We assume, however, that egg mortality is independent of egg size, partly for simplicity and partly because we are aware of no empirical study that documents the relationship between egg longevity and size. We write μ_n^e and μ_n^s for the mortality rates of eggs and sperm in a neighborhood. Retained gametes are protected from predation and the elements by their parents' bodies, so we assume that mortality in fertilization cavities is only $\alpha < 1$ times as high as in neighborhoods. This results in mortality rates of $\mu_c^e = \alpha\mu_n^e$ and $\mu_c^s = \alpha\mu_n^s$ for eggs and sperm, respectively. The loss of gametes from the open water due to water currents is an additional source of mortality μ_L, which we assume affects sperm and eggs equally. Mortality rates in the open water are then given by $\mu_o^e = \mu_n^e + \mu_L$ and $\mu_o^s = \mu_n^s + \mu_L$, respectively.

There is no correlation in our model between the strength of flow into neighborhoods and flow out of the fertilization arena (i.e., between F_{on} and μ_L). In nature there is probably a positive relationship (although the shape of such a relationship is unknown), but we argue that this modeling simplification is unlikely to affect our main conclusions, as the effect of μ_L on model predictions was minor (see "Results").

How Does Body Size Affect Population Density and Pumping Rate?

In modeling the relationships between body size, egg size, and reproductive strategy, it is important to remember that many life history traits are affected by size (Peters 1983). Larger species typically live at lower population densities (Marquet et al. 1990; White et al. 2007) and can pump water at higher rates (Riisgård 2001). This is significant because higher population densities and pumping rates reduce LGC (fig. 1), which affects the likelihood of different reproductive strategies being stable. Accordingly, to understand how LGC changes with body size, we must consider the allometry of population density and pumping rate.

We assume that population density ρ decreases with body size B according to the allometric relationship

$$\rho = k_\rho B^{a_\rho}.$$

Similarly, the rate of water flow into an individual's fertilization cavity F_{nc} increases with body size B as

$$F_{nc} = k_F B^{a_F}.$$

We consider appropriate values of the scaling exponents a_ρ and a_F in appendix B.

How Does Egg Size Affect Fertilization Rates and Zygote Survival?

Larger eggs are fertilized more easily than smaller eggs because they provide larger targets for sperm (Levitan 1993; Crean and Marshall 2008). They may also form zygotes with higher survival and fecundity (Einum and Fleming 2000; Marshall and Keough 2006). Consequently, if we want to understand how LGC shapes the evolution of egg size, we must take these factors into account.

We assume that zygote fitness s increases with egg size m_e according to the sigmoidal function (Vance 1973; Bulmer and Parker 2002; Jørgensen et al. 2011)

$$s(m_e) = \exp\left(-\frac{1}{m_e}\right).$$

This function typically produces optimal egg sizes on the order of $m_e \approx 1$ (cf. Smith and Fretwell 1974), which we take as the unit of measurement for all other volumes.

We also assume that an egg's fertilization efficiency γ increases with its size m_e. Although this relationship is likely complex, for tractability we model it using the allometric equation (Dusenbery 2011)

$$\gamma(m_e) = k_\gamma \cdot (m_e)^{a_\gamma}.$$

We consider appropriate values for the scaling exponent a_γ in appendix B.

Fertilization Rates

We now have everything needed to calculate gamete densities and fertilization rates in each of the three regions. We assume that each individual produces gametes at a constant rate over the breeding period. This allows us to approximate the fertilization dynamics by their steady state solutions, for which inflows and outflows of gametes in each region cancel out, so that gamete densities remain constant. For species in which the rate of gamete production varies greatly during a breeding period, the steady state solutions provide less accurate approximations, but we do not expect this to alter the model's main predictions.

To illustrate how to calculate fertilization rates, consider a population of dioecious sperm casters. We first calculate

the density E_c^i of eggs in a female's fertilization cavity. Since females produce eggs at a rate of I_e, the density of eggs in the cavity increases at a rate of $I_e V_c^{-1}$ due to egg production. Egg mortality reduces this density at rate of $\mu_c^e E_c^i$. Further, if S_c^f is the density of sperm in the cavity, then fertilization reduces the density of eggs at a rate of $\gamma E_c^i S_c^f$. The rate of change of egg density in the cavity with respect to time is consequently given by

$$\frac{\partial E_c^i}{\partial t} = I_e V_c^{-1} - \mu_c^e E_c^i - \gamma E_c^i S_c^f.$$

Similarly, suppose that the density of sperm in the neighborhood of a female is S_n^f. Sperm will enter her fertilization cavity at a rate of $F_{nc} S_n^f$, causing an increase in sperm density of $F_{nc} V_c^{-1} S_n^f$. Taking into account mortality and fertilization, the rate of change of sperm density in the cavity is

$$\frac{\partial S_c^f}{\partial t} = F_{nc} V_c^{-1} S_n^f - \mu_c^s S_c^f - \gamma E_c^i S_c^f.$$

Using the same approach we can calculate rates of change for sperm and egg densities in the other two regions. The steady state solutions for gamete densities are then given by setting each rate of change to zero. We solved the resulting system of nonlinear simultaneous equations numerically. Once gamete densities are known, the rate of fertilization is straightforward to calculate: for the above example, it is simply $\gamma E_c^i S_c^f$ (details of all calculations in app. A).

Which Reproductive Strategies Are Evolutionarily Stable?

The complexity of the problem precludes an analytical approach. Consequently, we used the following numerical approach to identify reproductive strategies that could not be invaded by alternative strategies. We compared the average fitness of an individual playing the population reproductive strategy to that of a specified set of mutant individuals playing a different strategy. If we found a mutant that had higher average fitness than a typical individual in the population, we concluded that its strategy could invade the population. For example, we classified a population of sperm-casting hermaphrodites as stable if it could resist invasion by pure females, pure males, and broadcast-spawning hermaphrodites (see "Discussion" for the limitations of this approach).

As egg size is a continuous variable, there is the additional issue that there is an infinite number of possible strategies. We therefore approximated the equilibrium egg size for each reproductive strategy by considering discrete egg sizes of the form $m_e = 0.05k$, with k a positive integer. We searched for egg sizes m_e^* with the property that if every individual in the population produced eggs of this size,

then mutant individuals producing neighboring egg sizes of $m_e^* \pm 0.05$ had lower fitness than the population average. We refer to such m_e^* as the stable egg size for that reproductive strategy.

We used a similar approach for sex allocation in hermaphrodites, approximating possible strategies as discrete values of the form $r = 0.1, 0.2, \ldots, 0.9$. We considered a hermaphroditic reproductive strategy to be stable if it could resist invasion by pure females, pure males, and alternative fertilization modes for at least one of these r values. Similarly, a dioecious strategy was stable if it could not be invaded by alternative fertilization modes nor by any hermaphrodite with sex allocation $r = 0.1, 0.2, \ldots, 0.9$.

We assumed that mutants differ from the population only in a single trait. For instance, we did not consider simultaneous mutations in gamete release/retention and in hermaphroditism/dioecy. Similarly, when considering traits other than egg size, we assumed that mutants produced eggs of the stable size for the population reproductive strategy.

Robustness Analysis

To demonstrate that our results hold across a wide range of parameter values (e.g., differences in the allometric scaling of population density and water flow), we ran two sets of numerical trials. In each trial, parameter values were drawn randomly from predefined ranges (details in app. B). We then determined which reproductive strategies were stable and calculated the associated egg sizes m_e^* and sex allocation r. If a hermaphroditic strategy was stable to invasion for more than one value of r, we report the average of all stable r values and associated egg sizes. The results of all trials are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.1mp91 (Henshaw et al. 2014).

Trials with Randomly Chosen Body Size. We ran 1,200 trials with body sizes chosen randomly from a range of 6 orders of magnitude (details in app. B). We then calculated correlations (Pearson's r) and associated confidence intervals between the values of each parameter and the stability of sperm casting and broadcast spawning, represented as binary variables (i.e., stable/not stable). For parameters that varied over more than 1 order of magnitude, we took the base 10 logarithm of the parameter before calculating the correlation coefficient (see table B1 in app. B, available online). The magnitudes of these correlations suggest which processes are most influential in shaping the evolution of the mode of fertilization.

Trials with Paired Body Sizes. We also ran 2,000 trials in which we compared reproductive behavior between two

fixed body sizes for each randomly generated parameter set. We did this to mimic empirical observations of closely related species, for which parameter values other than body size might be expected to be similar. In 1,000 trials we compared fixed body sizes of $B_1 = 10^2$ and $B_2 = 10^4$, and in the remaining 1,000 trials we compared body sizes of $B_1 = 10^4$ and $B_2 = 10^6$. For any given pair of body sizes, we considered that smaller body size "favored" reproductive strategy X over strategy Y whenever (*a*) only X was stable at the smaller body size B_1 and only Y was stable at the larger body size B_2; (*b*) both strategies were stable at B_1 but only Y was stable at B_2; or (*c*) only X was stable at B_1 but both strategies were stable at B_2.

Results

The model highlights the potential importance of LGC in explaining the evolution of reproduction in marine environments because it predicts all three key relationships between fertilization mode, hermaphroditism, and egg size that have been reported in marine invertebrates, as well as the absence of egg casting.

Which Reproductive Strategies Were Stable?

The results for the set of trials in which body size was chosen randomly are summarized in figure 3. All four combinations of sperm casting or broadcast spawning with hermaphroditism or dioecy were stable to invasion for at

least some parameter values. In contrast, egg casting was never stable. In most trials only one reproductive strategy was stable, while in some two or three strategies were stable. In a few trials (less than 1% overall), no reproductive strategy was stable. When multiple fertilization modes are stable for one set of parameter values, these fertilization modes represent alternative stable states (i.e., they are not mixed equilibria). We consequently do not expect transitions to occur between them if the selective environment remains constant. Rather, transitions should occur when conditions change so that the dominant fertilization mode is no longer stable.

Sperm Casters Were Smaller than Related Broadcast Spawners

Sperm becomes limiting (i.e., fertilization rates are substantially below 100%) for large sperm casters and for small broadcast spawners. This can be seen by plotting the proportion of eggs fertilized (f_{female}/I_e) for different body sizes assuming fixed choices for other parameter values (fig. 4). It is therefore logical that sperm casting declined in prevalence as body size increased, while broadcast spawning became more common (fig. 5).

A strong association between sperm casting and small body size was found in both sets of trials. Unsurprisingly, however, the signal was stronger in the trials with paired body sizes (i.e., when other parameters were held fixed). Smaller body size favored sperm casting in 1,153 of the

Sperm casting		Broadcast spawning		Number of trials	Percentage of trials
Dioecy	Herm.	Dioecy	Herm.		
		●		484	40%
●				427	36%
	●	●		213	17%
	●			28	2%
●		●		18	2%
●	●	●		18	2%
●	●			6	<1%
	●		●	3	<1%
				3	<1%
			Total	1200	100%

Figure 3: Stability of sperm casting and broadcast spawning with hermaphroditism and dioecy in trials with randomly chosen body size. Each row represents a combination of stable reproductive strategies, with stable strategies marked by a dot. Egg casting was never stable.
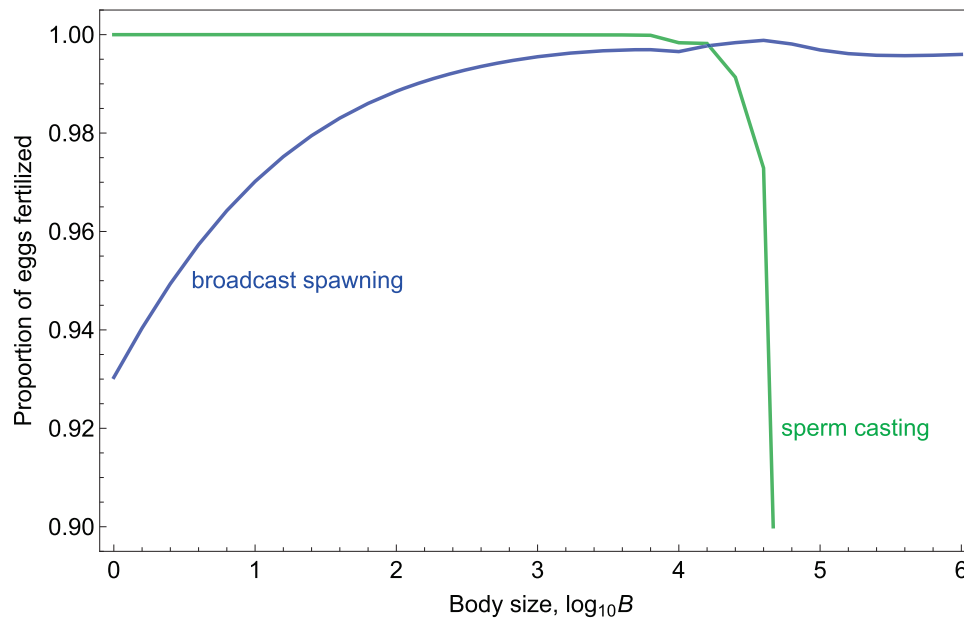
Figure 4: The expected proportion of eggs fertilized (f_{female}/I_e) increases with body size for broadcast spawners (blue) while showing the opposite relationship for sperm casters (green). The example assumes a dioecious population with fixed parameter values taken from the center of the ranges in table B1 (app. B), available online; for example, the allometric scaling of population density is assumed to follow an exponent of -0.75. The qualitative pattern remains unchanged within the range of values given in table B1. The small bumps in the curves have no biological significance as they result from the approximation techniques used.

1,258 paired trials (91.7%) in which both fertilization modes were stable for at least one of the two body sizes, while the reverse pattern occurred in only 3 trials (0.02%; binomial test, $P < .0001$). In 102 trials (8.1%), there was no trend.

Hermaphroditism Was More Common in Sperm Casters

Simultaneous hermaphroditism was far more common in sperm casters than in broadcast spawners (fig. 5). For example, in the trials with randomly chosen body sizes, hermaphroditism was stable in 268 of 713 trials where sperm casting was stable. In contrast, hermaphroditism was stable in only 3 of 736 trials in which broadcast spawning was stable ($\chi^2 = 326.8$, $P < .0001$).

Among sperm casters, the proportion of hermaphrodites increased with body size (fig. 5). This is explicable in terms of LGC because hermaphroditism allows sperm-limited females to reduce local egg competition and increase fitness by redirecting reproductive resources toward male function. Since sperm limitation increased with body size in sperm casters (fig. 4), the proportion of sperm casters that were hermaphrodites also increased with body size. Larger body size favored hermaphroditism over dioecy in 317 of 320 paired trials in which both strategies were stable for at least one body size. Sex allocation was

usually male biased. For example, in the set of trials with randomly chosen body size, hermaphroditic sperm casters allocated an average of 74% per cent of their reproductive resources to male function. We consider possible reasons for this strong male bias in the discussion.

The relative occurrence of hermaphroditism among sperm casters increased with body size. When considering both fertilization modes together, however, the proportion of hermaphrodites declined as body size increased (fig. 5). This is because sperm casting gave way to broadcast spawning as body size increased, and hermaphroditism was rare among broadcast spawners.

Sperm Casters Made Larger Eggs

Another evolutionary response to local egg competition was to increase egg size. When eggs competed locally for fertilization, females responded by producing fewer, larger eggs to increase the probability of each egg being fertilized. Although this still resulted in fewer fertilized eggs in total, this was offset by the increased fitness of each resulting zygote due to its greater size. The net outcome was greater overall fitness (fig. 6).

Since sperm casters suffered higher local egg competition than broadcast spawners, they produced larger eggs on average. The difference in egg size between the two
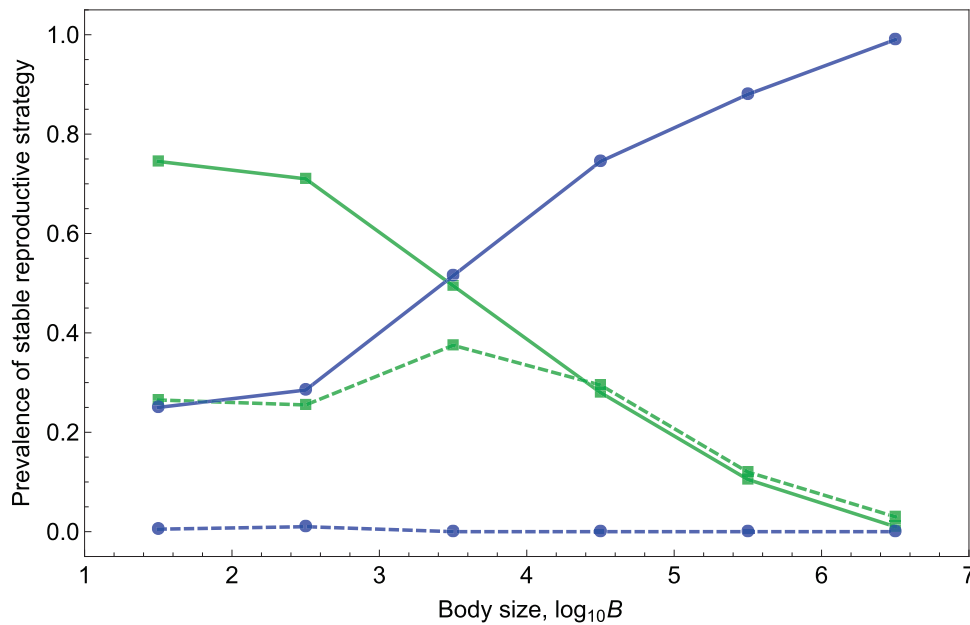
Figure 5: Prevalence of stable sperm casting (green squares) and broadcast spawning (blue circles) with dioecy (solid lines) and hermaphroditism (dashed lines) as body size varies. Shown as the proportion of 1,200 trials with randomly chosen body size in which each reproductive strategy was stable, with body sizes grouped by order of magnitude. Proportions add up to more than one because several reproductive strategies can be alternative stable states for the same parameter values.

fertilization modes was, however, only pronounced at body sizes for which both sperm casting and broadcast spawning were evolutionarily stable. This is because these were the largest body sizes for which sperm casting was still stable and therefore corresponded to the conditions of severe sperm limitation that most strongly favored increased egg size. Across trials with randomly chosen body size in which both sperm casting and broadcast spawning were stable, the eggs of sperm casters were 22.5% larger than those of broadcast spawners ($t[331.6] = 6.2$, $P < 10^{-8}$). In contrast, egg size did not differ significantly between sperm casters and broadcast spawners when only one mode was stable ($t[807.3] = -1.3$, $P = .19$).

Body Size Was the Most Important Parameter, but Other Factors Mattered Too

Body size was the parameter that most strongly influenced the evolution of fertilization mode. Body size was highly negatively correlated with the stability of sperm casting but highly positively correlated with that of broadcast spawning (fig. 7). In contrast, high rates of water flow into neighborhoods and fertilization cavities (high F_{on}, k_F, a_F, and low V_n) favored sperm casting over broadcast spawning, as they reduced sperm limitation in the fertilization cavity. For the same reason, sperm casters fared relatively better under high population densities (high k_ρ and a_ρ)

and when sperm were more numerous due to a high anisogamy ratio (low m_s) or low sperm mortality (low μ_n^s).

Since gamete mortality was highest in the open water, broadcast spawners were more dependent on the speed of fertilization than were sperm casters. Consequently, broadcast spawners did relatively better when fertilization was more efficient (high k_γ). Other parameters, including the rate of water flow away from the fertilization arena (μ_L) and the rate of egg mortality (μ_n^e), had relatively minor effects on the evolution of fertilization mode.

Discussion

Our model of egg retention and release and its coevolution with hermaphroditism/dioecy highlights the importance of local gamete competition in determining the stability of the six possible reproductive strategies. Body size and gamete release strategy interact to influence the intensity of LGC. Sperm casters experience sperm limitation and intense local egg competition at large body sizes, while broadcast spawners suffer sperm limitation at smaller body sizes.

Why does the effect of body size on sperm limitation differ between these two modes of fertilization? Among broadcast spawners, greater sperm production more than offsets the decline in population density at large body sizes. Consequently, our model predicts higher sperm densities
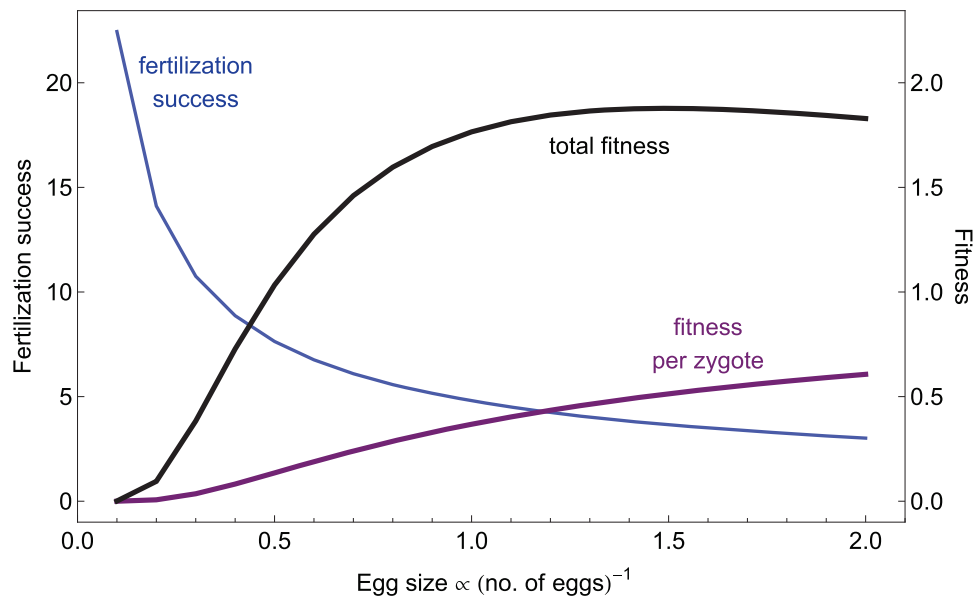
Figure 6: Total fertilization success (blue), fitness of individual zygotes (purple), and total fitness (black) as egg size increases while the number of eggs decreases. Shown for a mutant female in a population of dioecious sperm casters with body size $B = 10^5$. All other parameters are taken from the center of the ranges in table B1 (app. B), available online.

in the open water for larger species, which leads to a greater proportion of released eggs being fertilized. For retained eggs, in contrast, sperm availability does not keep pace with egg production as body size increases. Here lower population densities combine with less than isometric scaling of water flow into sperm casters' fertilization cavities as body size increases. Although larger body size also produces better flow from the neighborhood into the fertilization cavity, sperm casters will eventually become sperm limited as body size increases, because they cannot improve the flow from the open water into a neighborhood. As a consequence, larger sperm casters suffer greater LGC between eggs for fertilization.

Explaining Key Relationships between Fertilization Mode and Reproductive Traits

The effect of body size on sperm limitation and LGC in our model offers a basis to understand three well-established empirical observations in marine invertebrates and one universal pattern across all taxa. First, sperm-casting species of marine invertebrates are typically smaller than their broadcast-spawning relatives (Strathmann and Strathmann 1982; Rouse and Fitzhugh 1994). Our model suggests that sperm limitation lowers the reproductive success of large sperm casters and small broadcast spawners. This results in an association between small body size and sperm casting.

Second, sperm casters are more likely to be hermaph-

rodites (Strathmann and Strathmann 1982; Kupriyanova et al. 2001). Our model shows that when the flow of sperm into the fertilization cavity is too low to ensure fertilization of all eggs, sperm casters experience diminishing fitness returns to investment in eggs. In contrast, sperm release ensures that fitness returns to investment in sperm remain approximately linear. Consequently, sperm-limited females are selected to redirect some of their reproductive budget toward the male function, leading to simultaneous hermaphroditism. This sexual asymmetry in fitness returns does not occur in broadcast spawners: fitness gain curves remain roughly linear for both male and female reproduction when both eggs and sperm are released. In our model, hermaphroditism is rare in broadcast spawners because the negligible advantage it provides over dioecy in reducing LGC is insufficient to overcome the cost of not specializing in producing only one type of gamete.

Third, the offspring of sperm-casting marine invertebrates are larger than those of broadcast spawners (Rouse and Fitzhugh 1994; Kupriyanova et al. 2001). Our model predicts this pattern, at least to the extent that the larger offspring are a result of larger eggs (Roff 2002). Our model shows that greater egg size can result from a selective pressure to ameliorate LGC: when sperm is limiting, female sperm casters are selected to produce fewer, larger eggs. This ensures that a greater proportion of eggs are fertilized, while increasing the fitness of resulting zygotes.
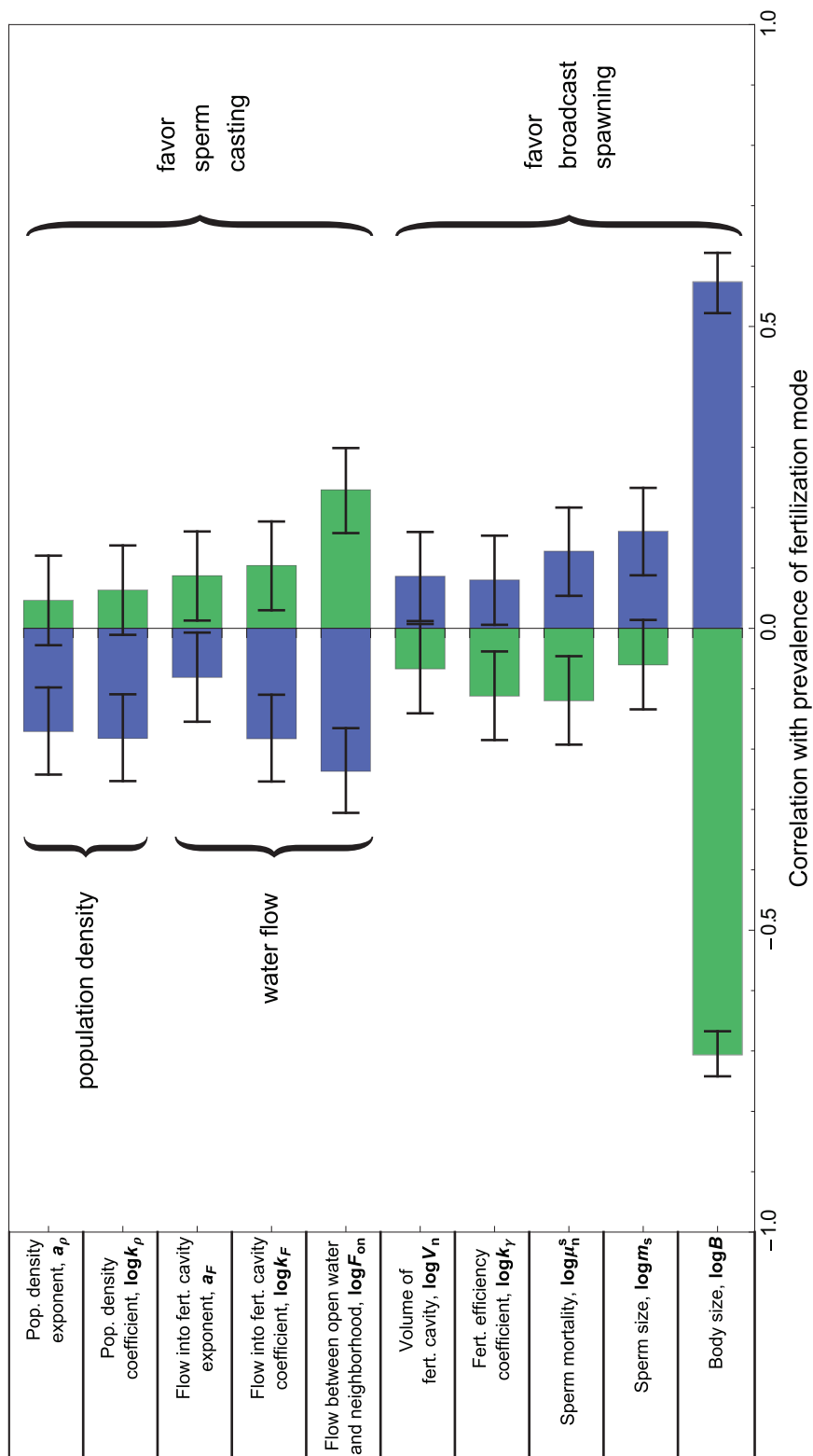
Fourth, there are no documented cases of egg casting

Figure 7: Correlation of selected parameters with the prevalence of stable sperm casting (green) and broadcast spawning (blue) in trials with randomly chosen body size, shown with 99% confidence intervals. Positive correlations indicate that the prevalence of a fertilization mode was associated with larger values of the parameter. Only parameters that were significantly correlated with at least one fertilization mode are shown.

in nature. In our model, retained sperm consistently suffered from higher LGC than retained eggs. Consequently, parameter values that selected for egg release always also selected for sperm release.

New Predictions

Our model gives rise to two new predictions that can be tested empirically. First, we predict a subtle and interesting relationship between body size, fertilization mode, and hermaphroditism. Smaller body sizes are associated with sperm casting, and sperm casting is associated with hermaphroditism. Consequently, smaller species are more likely to be both sperm casters and hermaphroditic in our model. However, among sperm casters themselves, hermaphroditism is predicted to be more common at larger body sizes. This is because hermaphroditism evolves to ameliorate sperm limitation, which increases with body size in sperm casters.

Second, we predict that hermaphroditic sperm casters will bias sex allocation toward male function to reduce local competition between eggs. This occurs because when eggs are retained and fertilization rates are low, LGC is more intense among eggs than among sperm (where it may even be absent). As a result, we might expect male-biased allocation to be more common in sperm casters than in broadcast spawners (in which LGC is low for both eggs and sperm). As a caveat, we discuss below how our model might exaggerate the strength of male bias. We have, however, built another model (not shown) that confirms that any level of male-biased allocation can arise given very general assumptions that lead to sperm limitation in the fertilization cavity. Additional factors not considered in our model, such as self-fertilization and polyspermy, might select against greater allocation of resources to male function (e.g., Bode and Marshall 2007).

Empirical evidence of a link between sperm casting and male-biased sex allocation is equivocal, although this may be due to the small number of studies (review: Schärer 2009). We note also that there is still much debate about how to measure reproductive investment. This makes it challenging to determine the extent, or even if, male-biased allocation occurs (Hayward and Gillooly 2011). Since absolute sex allocation is difficult to measure, future studies could aim to compare relative allocation between sperm casters and broadcast spawners.

Model Limitations: Numerical Evaluation of Evolutionary Stability

We treated a reproductive strategy as stable if it could resist invasion by any mutant that differed from the population in a single trait. For instance, a population of dioecious sperm casters was considered stable if it resisted invasion both by hermaphrodites and by broadcast spawners. Similarly, an egg size was stable if it could resist invasion by mutants producing slightly smaller or larger eggs. These are types of local stability (Otto and Day 2007).

Considering only local stability leaves open the possibility that populations could be invaded by mutations that simultaneously affect multiple characters or by mutations of large effect. Indeed, in cases where sperm casting and broadcast spawning were both locally stable, a pleiotropic mutation for egg release and small egg size could often invade a population of sperm casters. This did not, however, occur when only one reproductive strategy was stable: in such cases stability was global.

Mixed equilibria, in which more than one reproductive strategy is simultaneously stable in a population, are another interesting possibility. For instance, hermaphrodites coexisting with pure males is rare but widespread in animals (Weeks 2012). Mixed fertilization modes are also known to occur. For example, Barazandeh et al. (2013) recently observed both mating (which our model does not consider) and sperm casting in the barnacle *Pollicipes polymerus*. It is possible that the few trials in our model in which no single reproductive strategy was stable represent cases where the parameter values lead to mixed equilibria.

Last, to keep computations manageable, we tested whether hermaphrodites with a given sex allocation r could be invaded by pure males or pure females, but we did not examine stability against any other sex allocation values. Our model may therefore exaggerate the strength of male-biased sex allocation in sperm casters. For the same reason, it may also predict stable hermaphroditism for a wider range of parameters than it would under a more restricted definition of stability. We do not expect these issues to affect the key qualitative predictions of the model.

How Does Self-Fertilization Affect Our Predictions?

Our model assumes that hermaphrodites require allosperm, yet some marine invertebrate species appear to self-fertilize (Jarne and Auld 2006). As it provides an additional mechanism to increase the fertilization rate of eggs (Jarne and Charlesworth 1993), introducing selfing into our model would reduce local egg competition in hermaphrodites. This could affect our predictions in two main ways.

First, higher fertilization rates due to selfing would allow hermaphroditism to persist at a wider range of body sizes than our model currently predicts and correspondingly reduce the range of body sizes over which dioecy is stable. This should not, however, affect our qualitative predictions that hermaphroditism is more common in sperm casters

than broadcast spawners and that among sperm casters, hermaphroditism is associated with larger body size.

Second, since selfing ensures that most eggs are fertilized, female fitness curves should saturate more slowly in species that self. In contrast, male fitness may saturate more quickly, because sperm that are produced for self-fertilization experience strong local competition (Schärer 2009). Consequently, allowing selfing in our model could reduce or eliminate male-biased sex allocation in hermaphroditic sperm casters. This would not affect our predictions for species that are obligate outcrossers.

LGC versus Alternative Explanations

The application of the model's predictions to the natural world rests on two key assumptions: first, LGC is more severe for retained gametes than released gametes; and second, sperm limitation is common enough under natural conditions for local competition between eggs to have adaptive consequences.

Evidence for sperm limitation and local egg competition has been found in some marine invertebrates but not others (Levitan and Petersen 1995; Yund 2000; Marshall and Evans 2005). One way to test the strength of LGC empirically would be to experimentally reduce the number of gametes from some individuals and then measure whether the individuals' remaining gametes are more likely to be fertilized.

Making precise predictions regarding the current severity of a problem such as LGC is however inherently difficult, because we predict selection to shift reproductive strategies in a direction that ameliorates this problem. In other words, all else being equal, LGC may be more severe at certain body sizes (fig. 4), but all else is not equal if this leads to the absence of certain combinations of body size and reproductive strategy. Although it will remain difficult to predict which species should presently suffer most from LGC, it is noteworthy that even in species with consistently high fertilization rates, complex adaptations to reduce sperm limitation hint at its past importance (Yund 2000). This suggests that LGC has been a significant selective force in the evolution of reproductive behavior in marine invertebrates.

Earlier attempts to explain the links between small body size, sperm casting, and hermaphroditism met with limited success. Some argue that larger species release eggs because a female's ability to produce eggs increases more quickly with body size than her capacity to retain them (Heath 1977; Strathmann and Strathmann 1982). This could also select for simultaneous hermaphroditism in sperm casters if females divert excess reproductive capacity into male reproduction (Heath 1979; Schärer 2009). Although this hypothesis has found support in some species (Beekey and

Hornbach 2004; Gil et al. 2011), evidence for this type of developmental constraint remains weak (Schärer 2009; references in Sewell 1994) and seems unlikely to account for the association between body size and fertilization mode in most taxa.

We suggest that our model has two advantages over previous explanations. First, it unites the observed associations between small body size, sperm casting, and hermaphroditism in a common explanatory framework, rather than explaining each observation separately. Second, it provides a plausible account for the empirical variability of these patterns. Although sperm casters are smaller on average than closely related broadcast spawners, the association between sperm casting and small body size does not appear to hold across taxa, and in many taxa only one fertilization mode is present (Strathmann and Strathmann 1982). Our model suggests that this might reflect differences in population density and flow environment among taxa. In taxa where population densities are generally high, sperm casting is predicted to remain stable at larger body sizes than in taxa with low population densities. Similarly, taxa that can maintain high flow rates into the fertilization cavity (e.g., those with highly developed pumps) will permit sperm casting at larger body sizes. In both cases the intensity of LGC is lower.

Interestingly, sperm casting is the predominant mode of reproduction in colonial marine invertebrates (Strathmann and Strathmann 1982), despite large colony size (the analogue of body size in unitary organisms). Colonial organisms may be less likely to be limited by flow rates into the fertilization cavity because when colony size increases due to the asexual addition of a new module, a new fertilization cavity is also added. Colony growth therefore does not compromise fertilization rate and sperm casting can remain stable.

Analogous Problems in Other Taxa

We have focused on the evolution of sperm casting and broadcast spawning in marine invertebrates. To what extent are analogous problems faced by other taxa? For highly motile organisms, it is probably more efficient to search for mates than to rely on dispersal of gametes. Accordingly, mating is the dominant mode of fertilization in land animals (Strathmann 1990; but see Zizzari et al. 2009) and highly motile marine animals. Motility is also likely fundamental to land animals' preference for dioecy (Puurtinen and Kaitala 2002; Eppley and Jesson 2008).

The most obvious comparison is with plants. Since plants do not move to mate, their challenges to ensure fertilization appear comparable to those of sessile marine animals (Pemberton et al. 2004). In terrestrial environments, sexual reproduction occurs exclusively via pollen

casting (the analogue of sperm casting), although pollen transfer is often via an animal vector (Niklas 1997), a mechanism which is curiously absent in the sea (Strathmann 1990). Even in aquatic environments, higher plants appear never to release their ovules, although some green algae do broadcast spawn (Clifton 1997). The absence of broadcast spawning in higher plants is puzzling given that water-pollinated plants not only face a similar fertilization environment to marine animals but in many cases also have motile sperm (Rosenstiel et al. 2012).

Models of the evolution and maintenance of fertilization modes in plants and in nonmarine environments could highlight general features that apply to all sexually reproducing organisms and elucidate differences in selection between environments and taxonomic groups that have as yet escaped theoretical attention. Further studies might also shed light on sex differences in the evolution of parental care, mate choice, and morphology, all of which are fundamentally linked to a species' mode of fertilization. The model we have presented here offers a foundation on which to build tailored models to better explore these wider possibilities.

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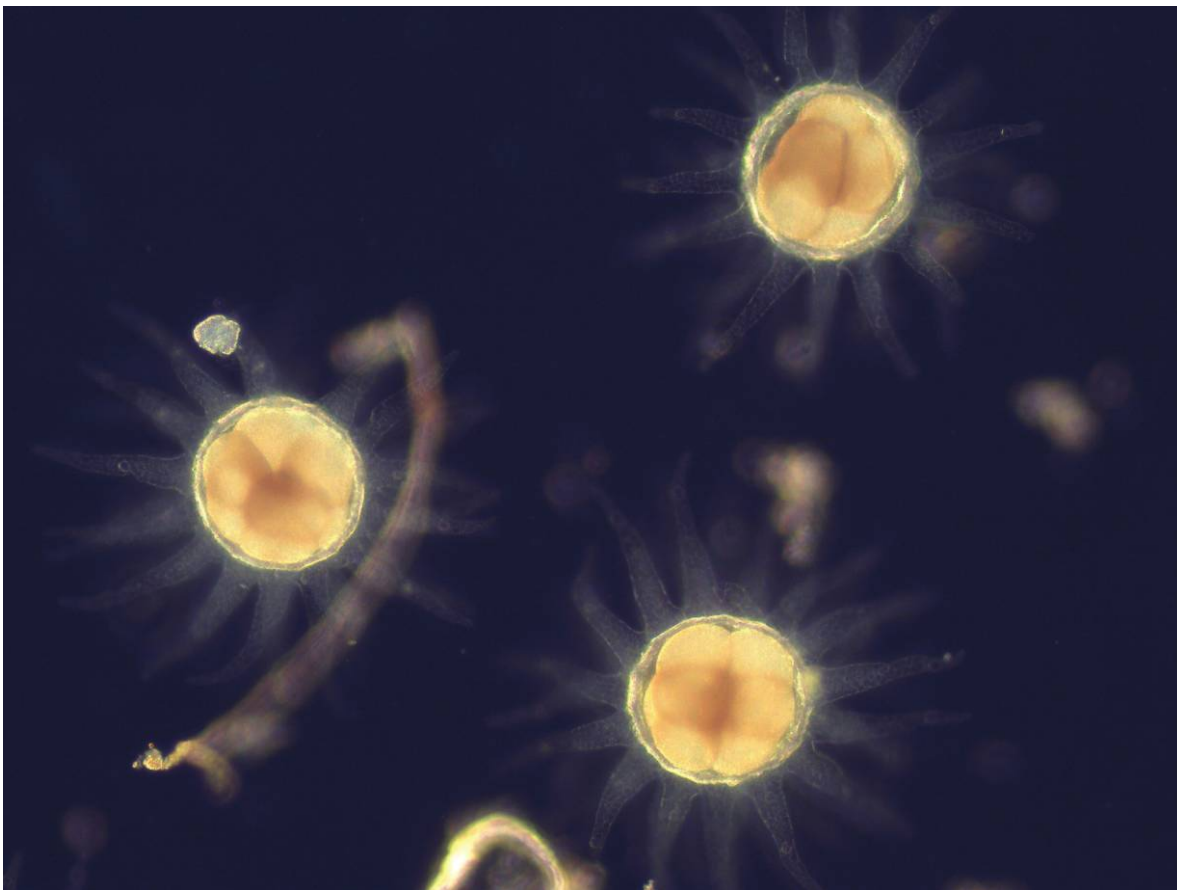
Developing embryos of the ascidian *Ciona intestinalis*, a broadcast-spawning hermaphrodite. Note the fingerlike projections on the surface of the eggs to maximize the probability of being contacted by sperm. Credit: Amy Hooper.