

Evolutionary consequences of fertilization mode for reproductive phenology and asynchrony

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ABSTRACT: Reproductive phenology is a crucial life-history trait that is influenced by both environmental and frequency-dependent effects. The fitness benefits of any phenology strategy will depend strongly on other aspects of the life history: one of the most fundamental ways life histories can differ is fertilization mode. Despite the strong potential for fertilization mode to alter selection on phenology, explorations into how these 2 fundamental life-history traits interact are lacking. We explore theoretically how frequency-dependent effects and fertilization mode influence the evolution of asynchronous reproduction, and the evolutionary stable strategy (ESS) for a population in which individuals' mean and variance in phenology are evolvable traits. We find that when males compete for fertilizations, perfect reproductive synchrony with optimal environmental conditions is never an optimal evolutionary strategy, and asynchronous reproduction is an inevitable consequence of frequency-dependent selection. Fertilization mode qualitatively alters frequency-dependent selection on the variance in phenology, as well as the prevalence of sexual conflict over reproductive timing. Our results contrast with traditional hypotheses that have primarily considered asynchronous reproduction as an adaptive bet-hedging strategy in stochastic environments, and provide a much-needed explanation for the emerging picture of reproductive asynchrony observed in many systems.

KEY WORDS: Phenology · Fertilization mode · Reproductive synchrony · Sperm competition · Frequency-dependent selection · Evolutionary stable strategy

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INTRODUCTION

Reproductive phenology has myriad consequences for the evolution of plants and animals. The timing of reproduction determines an individual's mating opportunities (Hendry & Day 2005, Elzinga et al. 2007, Weis et al. 2014), the resource budget for mating and offspring development (Stearns 1992, Ejsmond et al. 2010), as well as the environment experienced by both mating adults and offspring (Cushing 1969, 1990, Brunet & Charlesworth 1995, Post et al. 2001, Elzinga et al. 2007). Variation in the timing of reproduction drives assortative mating, changes gene flow, and promotes local adaptation and speciation (Fisher 1958, Hendry & Day 2005, Binks et al. 2012, Weis et al. 2014).

Selection on reproductive phenology (phenology hereafter) is driven by both environmental factors and frequency-dependent effects. Obviously, there is strong selection for reproduction to coincide with environmental conditions that are conducive to mating success and offspring survival. For example, many species time mating so that subsequent offspring development coincides with seasonal resource availability (reviewed in Durant et al. 2007, Lowerre-Barbieri et al. 2011). However, when environmental conditions are unpredictable, theory predicts that within-individual variation in phenology can evolve as an adaptive bet-hedging strategy (Iwasa 1991, Iwasa & Levin 1995). Frequency-dependent effects can be more subtle and take both positive and negative forms. On one hand, per capita mate encounter rates

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and pollinator visitation rates are often positively density-dependent due to Allee effects or other mechanisms such as patch attractiveness (Allee et al. 1949, Augspurger 1981, Thomson 1981, Devaux & Lande 2010, Fagan et al. 2010). Phenology can also be influenced by positive density-dependence when highly synchronous reproduction swamps offspring predators (Augspurger 1981, Ims 1990). On the other hand, negative frequency-dependence occurs when population demographic changes force individuals to compete for a smaller fraction of available resources, mates, pollinators, or fertilizations (Fisher 1958, Birkhead & Møller 1998, Devaux & Lande 2010). While negative frequency-dependence arising from competition for mates has received attention in the context of sex-specific phenologies in hermaphrodites (particularly flowering plants) and some gonochoristic species (e.g. Bulmer 1983, Rathcke & Lacey 1985, Brunet & Charlesworth 1995, Devaux & Lande 2010), most studies of the evolution of asynchronous reproduction emphasize the counter-balancing effects of environmental variation and positive frequency-dependence.

The fitness benefits of any particular phenology strategy will depend strongly on life history. For example, wind-pollinated plants tend to have brief and highly synchronous flowering displays (sometimes on the order of 15 to 20 min) in order to minimize the amount of pollen wasted by an unpredictable pollen vector (Gregory 1973, Rabinowitz et al. 1981, Friedman & Barrett 2009). Animal-pollinated plants, on the other hand, have relatively longer displays that maximize pollen transport efficiency given the foraging behaviours and visitation rates of pollinators (Rabinowitz et al. 1981, Harder et al. 2000). One of the most fundamental ways life histories can differ is in the fertilization mode (Gross & Shine 1981, Rouse & Fitzhugh 1994, Jørgensen et al. 2011). Gametes can either be fertilized while retained inside the female (internal fertilization) or after being shed into the environment (external fertilization). While fertilization mode is almost invariably internal in terrestrial taxa (e.g. flowering plants, mammals, and birds), fertilization mode shows substantial interspecific variation in aquatic groups such as algae, fish, amphibians, and invertebrates at all taxonomic levels (e.g. amphibians: Gross & Shine 1981, Beck 1998; fish: Winemiller 1989, Winemiller & Rose 1992; sabellid worms: Rouse & Fitzhugh 1994; algae and all animal phyla: Iyer & Roughgarden 2008; scleractinian corals: Kerr et al. 2011). Fertilization mode alters selection on, and covaries with, numerous life-history traits, including gamete phenotypes, fertilization probability, mating behaviours, and the degree of parental care, all of which

will interact with phenology to determine fitness (Winemiller 1989, Winemiller & Rose 1992, Stockley et al. 1997, Beck 1998). Despite the strong potential for fertilization mode to alter selection on phenology, explorations into how these 2 fundamental life-history traits interact are lacking.

Here we use both analytic and numerical methods to investigate theoretically how fertilization mode and population density interact to influence selection on phenology. Our results highlight the fundamental importance of negative frequency-dependence arising from among-male competition for mates and fertilization in maintaining variance in the timing of reproduction, and illustrate how life-history traits such as fertilization mode alter the relative importance of environmental and frequency-dependent effects on the evolution of phenology.

MATERIALS AND METHODS

We use 2 parallel modelling approaches to study the effects of fertilization mode on the evolution of male spawning phenology. First, we use analytical methods to explore how fertilization mode and population density influence the invasibility of a population that reproduces synchronously at the environmental optimum by an asynchronous mutant. We then complement the analytical results with a numerical analysis of the evolutionary stable strategy (ESS) for a population in which individuals' mean and variance in the timing of reproduction are evolvable traits. Both analyses are based on calculating the relative fitness of a mutant compared to a resident population. The equation describing individuals' fitness has the same basic structure for all models, and has 4 components:

$$W = \int_t E(t) S(t) F(t) Q(t) dt \quad (1)$$

The first term, $E(t)$, describes the rate of egg release by females through time (t). The second term, $S(t)$, describes an individual male's proportional contribution to the total amount of sperm released by all males. The third term, $F(t)$, describes the fertilization dynamics resulting from changes in total sperm concentration. The fourth term, $Q(t)$, is a catch-all term describing the effect of seasonal changes in environmental conditions influencing density-independent offspring mortality, which we term environmental quality. This could include, for example, environmental conditions at the time of spawning, larval dispersal, or larval settlement, which influence fertil-

ization success or the susceptibility of offspring to various sources of mortality such as dispersal to inhospitable habitats or predation (Denny & Shibata 1989, Morgan & Christy 1995, Christy 2011). This fitness equation is integrated across time for each mating season to calculate an individual's total fitness. We investigate the effect of fertilization mode on the evolution of male phenology by altering the functional form of $F(t)$ to reflect biological differences in the dynamics of external versus internal fertilization.

For simplicity, and because selection on males to maximize fertilization success is expected to be intense relative to females (Parker 1982, Birkhead & Møller 1998), we model the evolution of male phenologies only, and assume the rate of egg release, $E(t)$, is constant across generations. Consequently, while the evolution of male phenologies is influenced by the relative fitness of mutant males, female fitness is determined entirely by local sperm concentrations, $F(t)$ and environmental quality, $Q(t)$, and does not influence trait evolution in our models. In nature, environmental and frequency-dependent factors will obviously also influence the evolution of female phenologies, and genetic correlations between male and female phenologies will determine the trajectory of evolution of the population phenology as a whole (Chapman et al. 2003, Bonduriansky & Chenoweth 2009). Modelling the joint evolution of male and female phenologies would require a significant increase in model complexity and introduce multiple sources of frequency-dependent selection which would be difficult to tease apart. Instead, we choose to focus on males alone as a first step in understanding how fertilization mode might interact with frequency-dependent selection to influence the evolution of phenologies while maintaining analytic tractability and interpretability.

Fertilization modes

Fertilization mode in aquatic taxa can be either external or internal. While there is tremendous diversity in the specific biology of fertilization within these broad classifications, we focus on a comparison between 2 well-documented suites of fertilization processes associated with each: external fertilizers susceptible to polyspermy (fertilization of eggs by multiple sperm) at high sperm concentrations, and internal fertilizers that can achieve complete fertilization of eggs at low sperm concentrations. External fertilizers release both eggs and sperm into an aquatic medium, and fertilization success is deter-

mined primarily by local sperm concentrations and therefore the local density of spawning males (Levitan 1991, 2002, 2004, Marshall 2002). At low sperm concentrations, the probability of an egg being contacted by sperm is low, and few eggs are fertilized (sperm limitation). The probability of successful fertilization increases rapidly with sperm concentration but, for many species, because there is a time lag between when an egg is initially fertilized and when it becomes impermeable to subsequent sperm, egg mortality due to polyspermy can be very high at high sperm concentrations (see Franke et al. 2002, Gould & Stephano 2003, Levitan 2004, Levitan et al. 2004, Wong & Wessell 2005). Polyspermy has been documented under field conditions and in the laboratory using sperm concentrations expected to occur under field conditions in a variety of species from diverse phyla and may therefore be a common problem among externally fertilizing aquatic taxa (e.g. furoid algae: Brawley 1992, Pearson & Brawley 1996; echinoderms: Levitan 1998, Franke et al. 2002, Levitan et al. 2004; ascidians: Marshall et al. 2000, Marshall 2002; gastropods: Styan & Butler 2000 and citations therein; annelids: Kupriyanova 2006; see Gould & Stephano 2003 for a review). Consequently, the probability of successful monospermic fertilization as a function of sperm concentration for species susceptible to polyspermy is roughly bell-shaped (Millar & Anderson 2003). For generality and analytic tractability, we use an equation that gives this functional form of polyspermy-induced decreases in successful fertilization success (after Bode & Marshall 2007). We model the probability of successful fertilization for external fertilizers, $F_{ext}(S_T)$, as

$$F_{ext}(S_T) = \left(\frac{A_{ext} S_T}{2} \right)^2 e^{(2-A_{ext} S_T)} \quad (2)$$

where S_T is the total amount of sperm released by males, and A_{ext} is a positive shape parameter that determines the steepness of the curve and location of the maximum (See Table 1 for descriptions of all terms used in the models; see Appendix 1 in Bode & Marshall 2007 regarding shape parameter A_{ext}). Variation in A_{ext} can result from differences in gamete traits such as the speed and mechanism of polyspermy blocks, the size of eggs, hydrodynamic conditions, and the spatial arrangement of spawning individuals (Levitan 2002, 2004, Marshall 2002, Wong & Wessell 2005, Bode & Marshall 2007).

Internal fertilization can be achieved in several ways, including copulation, physical transfer of spermatophores, and spermcasting, whereby sperm are shed into the water column but eggs are retained in

Table 1. Key terms and parameters used in models to investigate theoretically how fertilization mode and population density interact to influence selection on phenology. ESS: evolutionary stable strategy

Term	Description
General terms	
$\mu = 0.5$	Environmental quality mean
$\sigma = 0.15$	Environmental quality standard deviation
t	Time, within season
N	Population density
A_{ext}	External fertilization curve shape parameter, determines location of maximum & steepness of curve
A_{int}	Internal fertilization curve shape parameter, determines steepness of sigmoidal function
W_p, W_m	Fitness of the population, mutant respectively
Analytic models	
e	Deviation in time from resident population strategy
d	Proportion of mutants adopting asynchronous strategy
N^*	Critical population density above which a mutant strategy will be able to invade
Numerical ESS	
m, m^*	Mean sperm release time for mutant, population respectively
v, v^*	Standard deviation sperm release time for mutant, population respectively

the female (Rouse & Fitzhugh 1994). In contrast to external fertilizers, internally fertilizing species are less likely to suffer either sperm limitation or polyspermy. Sperm limitation will still occur in the extreme case when females fail to find any mates, but otherwise, fertilization rates in internal fertilizers tend to be much higher relative to external fertilizers at similar sperm concentrations (reviewed in Pemberton et al. 2003). Polyspermy is less of a risk for internal fertilizers for several reasons. Most internal fertilizers have evolved rapid blocks to polyspermy because of high sperm concentrations resulting from direct sperm transfer into the female reproductive tract (Gould & Stephano 2003, Wong & Wessell 2005). In many groups, females can also alter the number of sperm that ultimately access their eggs (Wong & Wessell 2005). Therefore the relation between the probability of successful internal fertilization and local mate density for internal fertilizers is better described by a saturating function with a maximum fertilization probability of 1. For our numerical ESS analyses we model the functional form of this relation using a sigmoidal Holling type III equation:

$$F_{int}(S_T) = \frac{S_T^2}{(A_{int} + S_T^2)} \quad (3)$$

where A_{int} is a positive shape parameter that defines the function's steepness, and S_T is again the total sperm released by males. Variation in A_{int} could result from differences in the efficiency of males at locating potential mates, the duration of copulations or, in the case of some spermcasting species, the efficiency of filter-feeding organs at capturing sperm (Pemberton et al. 2003). For our analytic solutions,

we consider a different internal fertilization function that has a similar shape, but a more tractable analytic form:

$$f_{int}(S_T) = \frac{S_T}{(A_{int} + S_T)} \quad (4)$$

The only difference between these 2 functions is the presence of sigmoidal behaviour at very low concentrations for Eq. (2) (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m537p023_supp.pdf). For comparison, we also model constant fertilization dynamics, where fertilization success is 100% at all non-zero sperm concentrations.

All 3 fertilization functions implicitly assume that competition among males for fertilizations follows a fair raffle. Consequently, male density augments the intensity of frequency-dependence by changing each male's share of successful fertilizations.

Analytic solutions

We begin with a simple analytic model that assesses whether a purely synchronous spawning population that reproduces at the environmental optimum can ever be evolutionarily stable. The model proposes a very simple representation of frequency-dependent mating behaviour that captures the fundamentals of synchrony while remaining both analytically tractable and comparable to the more complex ESS model. We consider a population in which females release eggs to coincide with a temporally varying environment ($t' \in [0, 1]$) which exhibits a single annual maximal quality, Q , at $t = 1/2$ which we scale to unity:

$$Q(t) = 4t(1-t) \quad (5)$$

We model environmental quality as the proportion of fertilized eggs that survive to settlement.

Each individual male has R sperm resources available; an individual's strategy is defined by their choice about how to release these fixed reproductive resources through time. We consider the relative fitness of a single asynchronous mutant that invades a population with density $N - 1$ individuals that spawn synchronously at the environmental maximum. If the relative fitness of this mutant individual is greater than that of the synchronously spawning population, a purely synchronous strategy cannot be evolutionarily stable.

We model the behaviour of the mutant individual using the simplest possible description of asynchrony. Instead of releasing its entire sperm resources at the peak female spawning time (and environmental maximum), the mutant releases a small proportion, d , of its resources slightly before the maximum, at $t = 1/2 - e$, where e is the deviation in time from the resident population strategy. The following fitness relationships are all symmetrical functions of e , and thus our results are equivalent for mutants that release slightly after the maximum. The remainder $(1 - d)$ is released at the maximum, with the rest of the population. We assess the 3 different fertilization success models in turn. For each, we assess the conditions under which a small mutation ($d = 1$; $e = 1/2$) could invade a population of individuals with purely synchronous spawning strategies. We focus on identifying a critical population size N^* , above which a mutant strategy will be able to invade, because this will allow us to identify conditions under which synchronously spawning populations are unstable for all 3 fertilization modes. For this formulation of asynchronous reproduction, the integration in Eq. (1) becomes the sum of 2 terms: the fitness of each strategy at the environmental optimum, and their fitness at the slightly earlier release time (the synchronous strategy has no contribution to fitness at this earlier time, since it only reproduces at the environmental maximum).

Case 1: Constant fertilization success

In the case of constant fertilization success, the fitness of an individual with a given strategy is equal to the sum of the fertilization success of that individual's sperm across its entire release strategy. If the proportional fertilization rate of eggs is independent of

sperm density, the fitness of an individual pursuing the population (i.e. the synchronous) strategy, W_p , is equal to its share of the total sperm release at the environmental maximum:

$$W_p = \frac{1}{N-d} \quad (6)$$

Note that the total resources available to each individual, R , do not enter the fitness equation because all individuals are equally resourced.

The fitness of a mutant individual, W_m , is equal to the sum of its proportional releases at and around the environmental maximum, modified by the lower environmental quality that it experiences when spawning off the maximum:

$$W_m = \frac{(1-d)}{(N-d)} + (1-4e^2) \quad (7)$$

A mutant strategy can invade the population and perturb synchronous spawning behaviour in conditions when its relative fitness (W_m/W_p) is >1 . By expressing relative fitness as a function of the population size N (recall that N also includes the mutant), we see that the mutant will invade whenever the population is larger than:

$$N^* = d \left[\frac{4e^2 - 2}{4e^2 - 1} \right] \quad (8)$$

Invasibility is guaranteed for small values of e and d (even for quite large values such as $e = 0.4$ and $d = 0.4$) because when e is small then $N^* = 2d$. The critical population size is therefore <2 , and a mutant would be able to invade any synchronously spawning population where fertilization success is independent of sperm concentration (Fig. 1A).

Case 2: Internal fertilizers

By limiting the fertilization success when the total sperm concentration is low (i.e. when fewer individuals are spawning), internal fertilization dynamics will penalize mutant behaviour, and may thereby restore the evolutionary stability of the synchronous strategy. By modifying the fitness function with $f_{int}(S_T)$, a synchronously spawning, externally fertilizing individual has fitness:

$$W_p = \frac{1}{A_{int} + N - d} \quad (9)$$

while the fitness of the mutant strategy is:

$$W_m = \frac{(1-d)}{A_{int} + N - d} + \frac{d(1-4e^2)}{(A_{int} + d)} \quad (10)$$

From Eqs. (9) & (10), we can determine that the relative fitness of the mutant is >1 when the population is larger than:

$$N^* = d - A_{int} + \frac{(A_{int} + d)}{(1 - 4e^2)} \quad (11)$$

For small asynchronous mutations ($e, d = 1$) we can ignore quadratic terms in e and make the approximation that $N^* = 2d$. This term is always negative given the assumption of relatively small mutations, and so for internal fertilizers, the synchronous strategy is always evolutionarily unstable to small asynchronous mutations (Fig. 1B).

Case 3: External fertilizers

For external fertilizers, the fitness of the synchronous population and mutant strategies are:

$$W_p = \frac{A_{ext} \exp[2 - A_{ext}(N - d)]}{2} \quad (12)$$

and:

$$W_m = \frac{A_{ext} \exp[2 - A_{ext}d]}{2} \left[(1 - d) \exp[-A_{ext}(N - 2d)] + d(1 - 4e^2) \right] \quad (13)$$

respectively. The relative fitness of the mutant strategy is >1 when the population is larger than:

$$N^* = 2d - \frac{\ln[1 - 4e^2]}{A_{ext}} \quad (14)$$

Once again we make the approximation that $e = 1$, which allows us to approximate Eq. (14) as $N^* = 2d$.

This will be <2 (Fig. 1C), and a synchronous population can therefore always be invaded by an asynchronous mutant.

Numerical ESS analysis

Population phenologies are the cumulative result of within- and among-individual variation in reproductive timing. Phenologies in our analytic models are described entirely by the temporal deviation (d) from the environmental optimum at which mutants release a proportion (e) of their sperm resources. However, for organisms that release gametes over time, individual phenologies are perhaps more realistically described by the onset and duration (or mean and variance) of gamete release (Elzinga et al. 2007). We explored the evolutionary consequences of fertilization mode for the mean and variance in sperm release using a classic game-theoretic approach, and model the evolutionary stable strategy (ESS) for mutant males with a spawning phenology defined by a normal distribution $s(t) = N(t, m, v)$ in a resident population with spawning phenology $s^*(t) = N(t, m^*, v^*)$ (Fig. 2A). For a given population size N , the population phenology, or total amount of sperm released is:

$$s_T(t) = s(t) + (N - 1)s^*(t) \quad (15)$$

Female phenologies are again assumed to be fixed and to coincide with seasonal changes in environmental conditions. Therefore, egg availability, $E(t)$, is defined by a normal distribution $E(t) = N(t, \mu, \sigma)$, which we scale to unity. The duration of seasons is arbitrarily scaled to range between 0 and 1. The fitness of the mutant male is the product of the amount of eggs available to be fertilized, $E(t)$ (Fig. 2A), the expected fertilization success they can achieve given their fertilization mode, $F(t)$ (Fig. 2B), and the mutant's phenotype relative to the resident population (note that mutants are always modelled to invade a population with the same fertilization mode, we do not address the relative competitive ability of internal vs. external fertilization). Because spawning is temporally explicit, this product is integrated across the season (Fig. 2C,D). In the

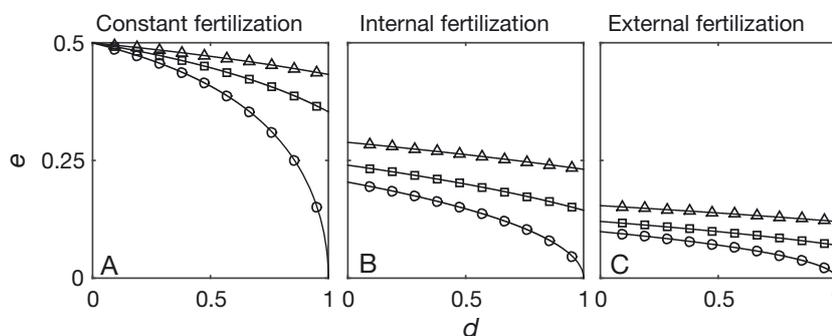


Fig. 1. Mutations that are able to invade populations that exhibit (A) no fertilization dynamics, (B) internal fertilization dynamics and (C) external fertilization dynamics, consisting of (O) 2, (□) 3, and (Δ) 5 individuals with pure synchronous spawning strategies. Combinations of deviation in time from resident population strategy (e) and the proportion of mutants adopting asynchronous strategy (d) that can successfully invade are below and to the left of the lines. Panels show model results when egg fertilizability is low (curve shape parameter values: $A_{ext} = 0.02$, $A_{int} = 10$)

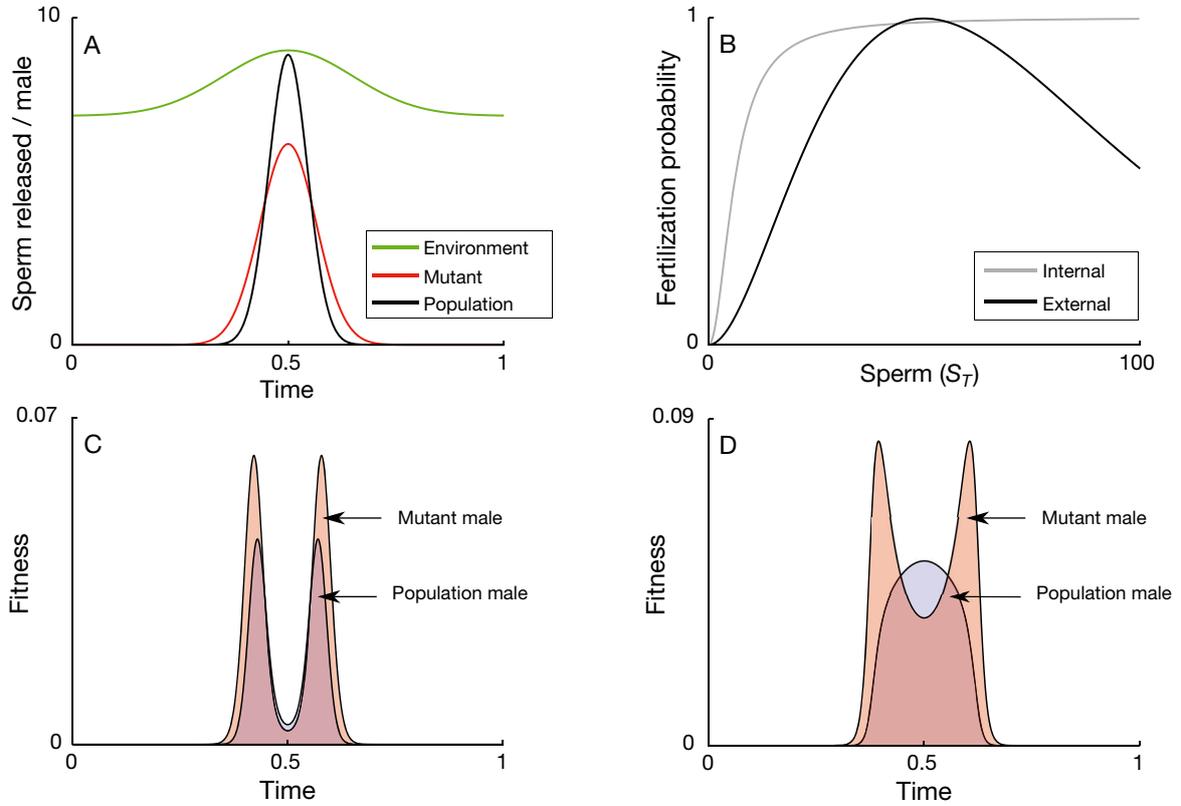


Fig. 2. Influence of negative-frequency dependence and polyspermy on the behaviour of the numerical ESS model. (A) The reproductive phenology of the population (black line) and mutant (red line), with the fluctuation in environmental quality indicated at the top of the figure ($Q(t) \in [0, 1]$). In this example, the mutant has a larger variance than the population. (B) Fertilization functions for external (Eq. 2) (black line) and internal (Eq. 3) (grey line) fertilizers. S_T = total amount of sperm released by males. Bottom panels provide an illustration of how per-male fitness (Eq. 16) is calculated for (C) external and (D) internal fertilizers through time for the population (blue curve) and mutant (red curve). In this example, male density is high enough to result in polyspermy at peak spawning, and mutants have a higher variance than the population

example given in Fig. 2C,D, both the population and mutant suffer high polyspermy during peak spawning and so are bimodal. However, the mutant has a larger variance, and therefore releases relatively more sperm than population males before and after peak spawning. This strategy allows the mutant to compete more effectively for fertilizations at this time while sacrificing competitive ability during peak spawning, and in this example, results a relative fitness greater than 1 (area under red curve exceeds area under blue curve). The same scenario is illustrated for internal fertilizers, but the population fitness curve is unimodal because internal fertilizers do not suffer from polyspermy in our models. The bimodality in the mutant fitness curve is due entirely to negative frequency-dependence resulting from competition for fertilizations. This method results in the overall fitness equation:

$$W(m, v, m^*, v^*) = \int \frac{s(t)}{s_T(t)} F(t) Q(t) dt \quad (16)$$

As in traditional game-theoretic models, the ESS represents the phenology (m^*, v^*) , such that if all males in the population employed this strategy, no mutant male with a different phenology could achieve a relative fitness > 1 (Maynard-Smith 1982). That is, if a population of males release sperm according to the ESS phenology, they cannot be invaded by any mutant with a different mean or variance sperm release rate. Formally, the ESS is defined by the value of the traits m^* and v^* that satisfy:

$$\left. \frac{\partial W(m, v, m^*, v^*)}{\partial m} \right|_{\substack{v=v^* \\ m=m^*}} = 0$$

$$\left. \frac{\partial^2 W(m, v, m^*, v^*)}{\partial m^2} \right|_{\substack{v=v^* \\ m=m^*}} < 0$$

and:

$$\left. \frac{\partial W(m, v, m^*, v^*)}{\partial v} \right|_{\substack{v=v^* \\ m=m^*}} = 0$$

$$\left. \frac{\partial^2 W(m, v, m^*, v^*)}{\partial v^2} \right|_{\substack{v=v^* \\ m=m^*}} < 0$$

The fitness function defined by Eq. (16) has no closed form solution, thus we solved for the values of m^* and v^* that satisfy the ESS conditions numerically.

RESULTS

There are 3 principal findings of our models. First, our analytic model demonstrates that completely synchronous spawning by males at the environmental optimum is never an ESS due to negative frequency-dependence in male reproductive success (Fig. 1). Second, negative frequency-dependence due to among-male competition for fertilizations drives the evolution of spawning away from the environmental optimum through increases in male ESS variance (v^*). Third, fertilization mode qualitatively alters the relation between male ESS variance (v^*) and population density (N), as well as the prevalence of sexual conflict over the timing of reproduction (Fig. 3) (See Table 2 for a summary of numerical ESS results).

Effects of fertilization mode and population size

Fertilization mode and the associated relation between local sperm concentration and fertilization success strongly influenced v^* , but had no effect on the ESS mean release time (m^*). m^* was always predicted to coincide with the peak in female spawning ($\mu = 0.5$), which was at the midpoint of the season in our model. Except at high population densities (N), internal fertilizers are predicted to have a higher ESS variance than external fertilizers (Fig. 3A,B). As N increases, v^* for internal fertilizers asymptotically approaches the expected ESS for males with constant

Table 2. Numerical ESS model predictions. Key to symbols: (\uparrow) high variance; ($\uparrow\uparrow$) very high variance; (\downarrow) low variance; (+) indicates sexual conflict is predicted to occur; (–) sexual conflict is not predicted. N : density; v^* : ESS male sperm release time variance

Mode	N	Process	Egg fertilizability	
			Low	High
External	High	v^* Conflict	\uparrow (Int > Ext.)	\uparrow (Int < Ext.)
	Low	v^* Conflict	\downarrow	\uparrow
Internal	High	v^*	\uparrow	$\uparrow\uparrow$
		Conflict	–	+
	Low	v^* Conflict	\downarrow +	\downarrow +

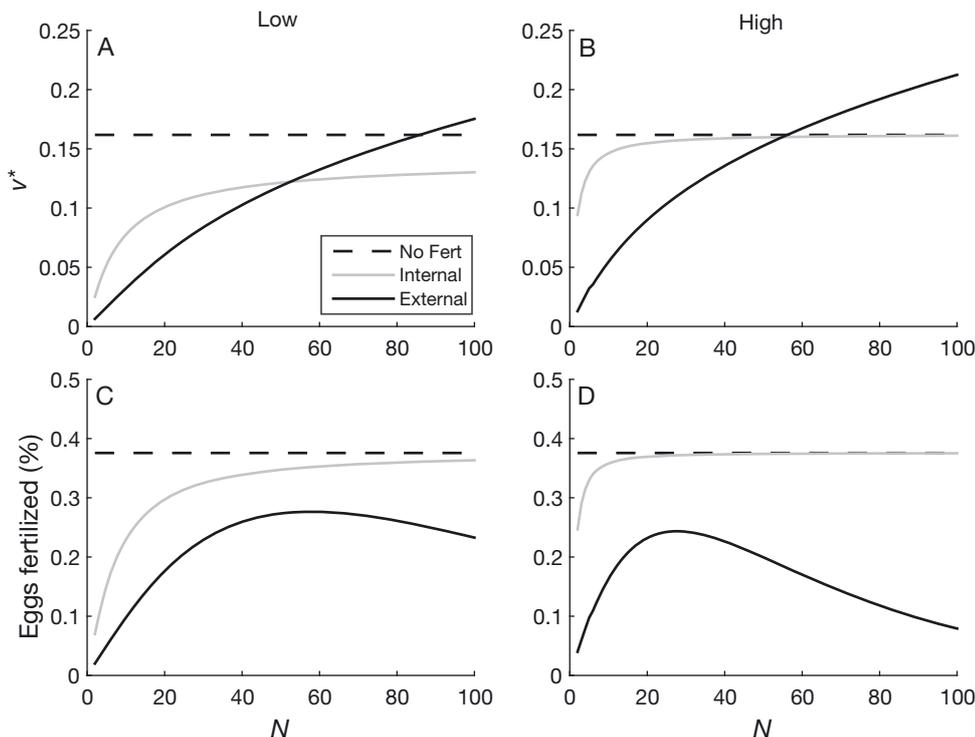


Fig. 3. Male sperm release time variance (v^*) when egg fertilizability is (A) low ($A_{ext} = 0.02$, $A_{int} = 10$) and (B) high ($A_{ext} = 0.04$, $A_{int} = 2$), and female fitness with (C) low and (D) high egg fertilizability, as a function of population density (N) for external (black) and internal (grey) fertilizers, with constant fertilization dynamics (dashed line)

fertilization dynamics. This is because fertilization success for internal fertilizers asymptotes at 1 with increasing N (Figs. 2A & 4A,B). For external fertilizers at high population sizes, decreasing fertilization success at peak spawning times due to polyspermy (Fig. 4C,D) result in v^* that exceeds those of either internal fertilizers or males with constant fertilization success (Fig. 3A,B).

Female fitness and sexual conflict

Our numerical ESS results suggest that for externally fertilizing species, the male ESS will result in decreased female fitness across most population densities we explored. Specifically, the relation between female fitness (the proportion of eggs fertilized) and population size is convex, with a maximum at intermediate population densities (Fig. 3C,D). At lower densities, v^* is small relative to σ , which simultaneously prevents females from acquiring fertilizations during adjacent periods of high environmental quality, and inflicts fitness losses due to polyspermy during peak spawning times (Fig. 4C,D). At high densities, v^* is large and, although the proportion of eggs lost to polyspermy is high throughout the middle of the season (Fig. 4C,D), females cannot achieve equivalent fitness due to decreases in environmental quality on the shoulders of the reproductive season.

In contrast to external fertilizers, our model suggests that the strength of sexual conflict over the timing of reproduction in internally fertilizing species

will decrease rapidly with increasing population density. The relation between N and both v^* and female fitness is a saturating function (Fig. 3B,D). Thus, as population density increases, the difference between female realized fitness and their maximum possible fitness decreases asymptotically.

Effects of traits influencing egg fertilization

Our results for both v^* and female fitness do not change qualitatively with the value of A_{ext} or A_{int} . Changes in traits or conditions that increase the likelihood of mate encounters, sperm and egg contact, or egg fertilizability (larger A values) always increase v^* as well as the steepness of the relations between v^* and N (Fig. 3A,B), and between v^* and female fitness (Fig. 3C,D; Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m537p023_supp.pdf).

Increases in egg fertilizability (larger A_{ext}) shift the location of the female fitness maximum to lower population densities, and increases the steepness of the fitness surface (Fig. 3C,D). This results in an accompanying shift in the population densities where males and females are not in conflict, but also decreases the range of population densities where sexual conflict is lowest. For internal fertilizers, higher mate encounter rates, or sperm filtering efficiency (higher A_{int}) decrease the strength of sexual conflict at lower population densities, but do not qualitatively alter this relation, or the value female fitness asymptotically approaches with increasing N (Fig. 3C,D).

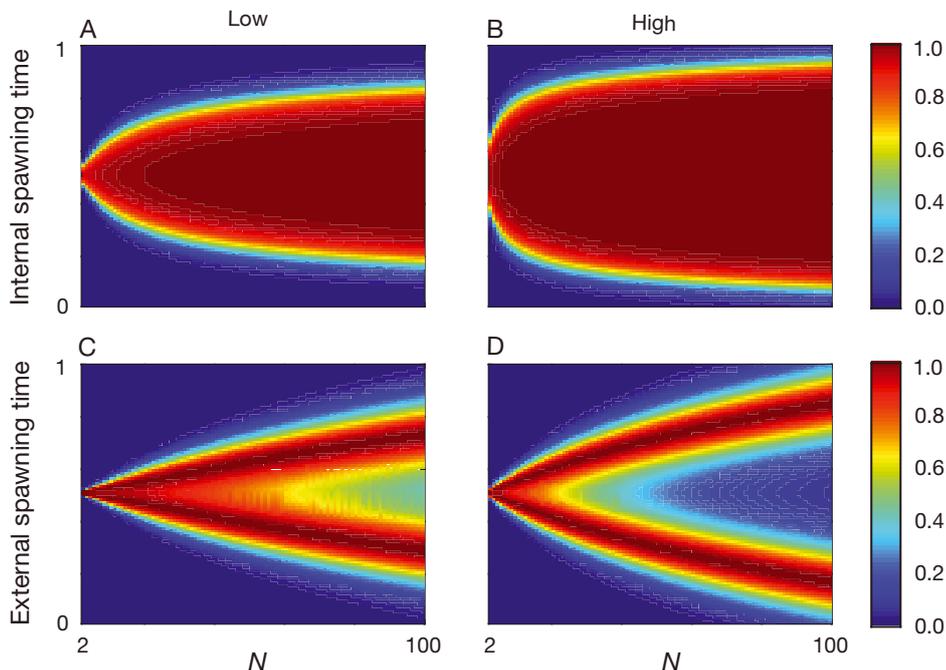


Fig. 4. Probability of successful monospermic fertilization through the reproductive season as a function of population density (N) for (A,B) internal and (C,D) external fertilizers. (A,C): low egg fertilizability ($A_{ext} = 0.02$, $A_{int} = 10$); (B,D): high egg fertilizability ($A_{ext} = 0.04$, $A_{int} = 2$). The y-axis represents the reproductive season through time and is scaled arbitrarily to range between 0 and 1. The colour scale indicates the probability of successful fertilization

DISCUSSION

Evolution of reproductive asynchrony

We found that completely synchronous reproduction by males when environmental conditions are most conducive to offspring survival is never an optimal strategy due to frequency-dependent selection. Specifically, negative frequency-dependent selection on reproductive timing due to among-male competition for fertilizations counterbalanced environmental variation to maintain within- and among-individual variance in phenologies in our models. A corollary of this finding is that asynchrony is an inevitable consequence of frequency-dependent selection when males compete for fertilizations. This result is conceptually similar to predictions from a long history of theoretical models of niche evolution (Roughgarden 1972), and the evolution of continuous traits along environmental gradients (e.g. Lande 1976). In these models, intraspecific competition for resources creates frequency-dependent selection on the trait of interest, while in our model among-male competition for fertilizations drives frequency-dependence. Likewise, the study of flowering phenologies in angiosperms has long acknowledged the potential influence of frequency-dependent processes, such as patch attractiveness, pollinator competition, and seed predation, as well as their interaction with environmental conditions to influence the evolution of phenological variance (e.g. Augspurger 1981, Rabino-witz et al. 1981, Thomson 1981, early literature reviewed in Rathcke & Lacey 1985, Elzinga et al. 2007, Devaux & Lande 2010). The importance of frequency-dependent selection has even been recognized in the evolution of gamete recognition proteins in externally fertilizing marine species (Levitan & Ferrell 2006, Panhuis et al. 2006), but has yet to be thoroughly explored in the context of reproductive phenologies. A fundamental consequence of anisogamy is that sperm from different males compete numerically to fertilize eggs (Parker 1982, Birkhead & Møller 1998) and therefore negative frequency-dependence due to among-male competition is likely to be a general mechanism maintaining variance in male reproductive timing.

Despite the potential importance of negative-frequency-dependent selection on reproductive phenology, the longstanding view of reproduction in aquatic systems is that it must be highly synchronous and coincident with favourable environmental conditions (see seminal papers by Thorson 1936, 1946, 1950). Similarly, early fisheries models predicted that

spawning should evolve to synchronize offspring larval development with favourable environmental conditions (Cushing 1969, 1990, Lowerre-Barbieri et al. 2011). These ideas have remained influential. For example, mass spawning of coral species on the Great Barrier Reef has often been described as synchronous (Harrison et al. 1984, Babcock et al. 1986), as has the reproduction of many marine algae species (Clifton 1997). Synchronous reproduction in crabs and reef fish coincident with diel, lunar, and tidal cycles has been proposed as an adaptive strategy to avoid predation (Morgan & Christy 1995, Christy 2011). Studies of spawning time in many commercially important fish species have documented annual peaks in reproductive activity as measured by spawning stock biomass, and synchronized diel periodicity of spawning behaviours (Lowerre-Barbieri et al. 2011). However, many species thought to have highly synchronous reproduction exhibit greater among- and within-individual variance in phenology than initially thought, and don't necessarily time reproduction to coincide with optimal environmental conditions. Many corals that participate in mass spawning also spawn during multiple periods each year, each lasting up to several months (Baird et al. 2009). Some species of marine polychaetes have been shown to predominantly spawn when temperatures are sub-optimal for fertilization success (Lewis et al. 2002, 2003). Weak reproductive synchrony has been documented in a variety of taxa, including sea urchins (Levitan 1988) and intertidal ascidians (Marshall 2002); as well as in several crab species across a gradient of seasonal resource fluctuation intensity and larval predation by planktivorous fish (Morgan et al. 2011). Likewise, many fisheries species and tropical reef fish are batch spawners that exhibit high individual and population level variance in spawning time and duration, and individuals often skip spawning events (Robertson 1990, Robertson et al. 1990, Sadovy 1996, Lowerre-Barbieri et al. 2011). These studies suggest that reproduction in aquatic systems may be less synchronous than previously thought.

In fact, our understanding of reproductive synchrony in natural populations of aquatic species is extremely limited, especially for external fertilizers. This is because relatively few studies report both the individual and population level data necessary to quantify it. Direct observation of individual reproduction is sometimes possible for internally fertilizing coastal species (e.g. Christy 1978), as well as for brooding fish species with established nests (Robertson 1990, Robertson et al. 1990, Sadovy 1996, Low-

erre-Barbieri et al. 2011). However, quantifying reproductive synchrony can be technically difficult for many external fertilizing species. Reproductive synchrony is highly scale-dependent: synchrony only matters at the temporal and spatial scales at which gametes, or reproductively active individuals, interact. For example, individual spawning events in many sea urchin populations take place over one to several hours, but sperm released from individual males dilutes to ineffective concentrations within seconds of being released (Levitan 1988, 1998, Lotterhos & Levitan 2011). This rapid dilution of gametes during advection in externally fertilizing species means reproductive synchrony only matters at small spatial scales. *In situ* fertilization success declines sharply with the distance to nearest spawning males in several sea urchin species, and is effectively zero when mates are >1.5 m away (Levitan 1998, 2002). Few studies have managed to measure synchrony at the temporal or spatial scales that matter to the organisms of interest. In a notable exception, Levitan et al. (2011) documented spawning times for individual colonies in populations of 3 *Montastraea* coral species. Population phenologies lasted ~60 min for all 3 species, but each colony only released gametes for ~1 min. Gamete ageing influences within-individual variation in these species — sperm are most effective at fertilizing eggs 30 min after spawning, and die 60 to 90 min later — but the scale of this variation does not equalize fertilization probabilities for colonies spawning at different times (Levitan et al. 2004). Thus, the precise timing of reproduction with environmental cues does not necessarily result in synchronous reproduction; to detect reproductive asynchrony, the timing of reproduction must be measured on the temporal scale at which competition for fertilization takes place.

Previous explanations for asynchronous reproduction have traditionally invoked stochastic variation in environmental conditions (Iwasa 1991, Iwasa & Levin 1995, Post et al. 2001, Durant et al. 2007, Morgan et al. 2011). In effect, unpredictable environmental conditions represent both changing cues for reproduction and a moving target for selection on individual phenology (Durant et al. 2007, Christy 2011, Morgan et al. 2011). Previous theory has emphasized that in temporally unpredictable environments, within-individual variance in phenology is an adaptive bet-hedging strategy (Iwasa 1991, Iwasa & Levin 1995). Both bet-hedging and among-male competition for fertilizations could create selection for increased within-individual variance that would push spawning away from the environmental optimum. How-

ever, it is unclear what the evolutionary consequences of feedback between these processes would be. While both are likely to influence the evolution of phenologies simultaneously, our results suggest that among-male competition for mates and fertilizations may act as an important counterbalance to environmental and biotic sources of positive frequency-dependence, and provides a mechanistic link between other life-history traits such as fertilization mode and the evolution of phenology.

Effects of fertilization mode and population density

The effect of population density on our model predictions of phenological variance was mediated by fertilization mode. External fertilizers were predicted to have lower ESS variance than internal fertilizers at lower population densities, but higher variance at high population densities (Fig. 3A,B). These predictions reflect the fact that phenologies in externally fertilizing males are influenced by selection caused by polyspermy in our model. Males must release sperm synchronously enough to ensure high fertilization success, but if too many males release sperm too synchronously, high local sperm concentrations destroy a large proportion of eggs via polyspermy. Paradoxically, egg mortality due to polyspermy is greatest when environmental conditions are most conducive to offspring survival; peak sperm concentrations occur at the environmental optimum, and egg mortality is therefore highest at this time. At higher densities, increased polyspermy causes the distribution of monospermic fertilizations through time to become increasingly bimodal (Fig. 4C,D), resulting in stronger selection for higher variance in male phenologies. However, this does not result in reproductive isolation or speciation in our numerical ESS model because males' ESS mean release time (m^*) remains at the environmental optimum.

At low densities, our model predicts that internal fertilizers will have a higher ESS variance than external fertilizers because of negative frequency-dependence caused by among-male competition for fertilizations. Because internal fertilizers can achieve higher fertilization success at lower densities relative to external fertilizers (Fig. 4A,B; Pemberton et al. 2003), the fitness benefits of outcompeting rival males for fertilizations outweigh the costs of releasing sperm during less favourable environmental conditions. Consequently, internal fertilizers respond more strongly to negative frequency-dependence than external fertilizers at lower densities. Because

internal fertilizers generally do not experience egg mortality due to polyspermy (Gould & Stephano 2003, Wong & Wessell 2005), at higher densities the ESS variance for internal fertilizers becomes increasingly constrained by environmental conditions, and asymptotically approaches the value obtained under constant fertilization dynamics. Thus an unanticipated prediction from our model is that, except at very low population densities, internally fertilizing species should more closely track seasonal fluctuations in environmental conditions than externally fertilizing species.

Our numerical ESS predictions are consistent with observed spawning phenologies in many aquatic taxa. For externally fertilizing species susceptible to polyspermy, males are predicted to release sperm more synchronously under sperm-limiting conditions (e.g. low male densities, rapid sperm advection), than under conditions that result in polyspermy (e.g. high densities, aggregated spatial distribution, slow sperm advection). Given the attention that sperm limitation has received as an explanation for synchronous reproduction in external fertilizers, our prediction that polyspermy should create selection for high variances that can exceed even seasonal environmental fluctuations seems somewhat counterintuitive (Thorson 1950, Levitan 1993, Yund 2000). However, this prediction is consistent with observed spawning phenologies in marine taxa that experience high population densities, or that aggregate during mating. For example, many aggregating sea urchin species spawn sporadically during each lunar month (Levitan 1988), and populations of the gregarious sessile serpulid polychaete *Galeolaria caespitosa*, which can reach densities of thousands per square meter, spawn continuously during the year (Kupriyanova 2006). Although polyspermy is less important among fishes, many externally fertilizing species that aggregate for mating exhibit similar patterns of asynchronous reproduction (Robertson 1990, Robertson et al. 1990, Sadovy 1996, Lowerre-Barbieri et al. 2011). The prediction that external fertilizers will have a lower ESS variance than internal fertilizers at lower population densities is also consistent with spawning patterns in a variety of taxa. Many internally fertilizing freshwater fish species (e.g. many species of the Cyprinodontiformes) are characterized by small population sizes and opportunistic spawning throughout the year (Winemiller 1989, Gonçalves et al. 2011). Likewise, spermcasting is a common mode of internal fertilization among marine invertebrates from diverse phyla, and males of these species generally release sperm slowly and sporadi-

cally over long periods of time (Pemberton et al. 2003).

There have been relatively few studies to explicitly test our models' predictions in aquatic taxa. For externally fertilizing species, Marshall & Bolton (2007) showed in a flume experiment that slower sperm release rates resulted in higher fertilization success of multiple downstream batches of eggs in the marine tube worm *Galeolaria caespitosa*, but they did not perform sperm competitive trials. Conversely, Levitan (2005) demonstrated in the sea urchin *Strongylocentrotus franciscanus* that under realistic field conditions males releasing sperm a longer time interval before females enjoy a competitive advantage for fertilization success over other males, but this study did not directly manipulate the duration of sperm release. Among internal fertilizers, there is some experimental evidence from shallow water crab species that supports our models' predictions, albeit through plastic behavioural responses rather than trait evolution. Several studies have demonstrated that male crabs increase the duration of mating behaviours in the presence of male competitors (e.g. Jivoff 1997, Rondeau & Sainte-Marie 2001). Kim et al. (2010) indirectly augmented the strength of among-male competition for mates in a food-supplementation experiment while documenting reproductive phenologies in both sexes for a population of fiddler crabs *Uca terpsichores*. They found that well-fed males increased both the intensity and duration of mating displays, while female mating phenologies remained unchanged. Thus, male phenological variances in this species may increase with the intensity of among-male competition independently of the timing of female receptivity, a result that is consistent with our prediction that male reproductive phenologies in internal fertilizers should reflect a balance between among-male competition and environmental conditions. For both externally and internally fertilizing species, our model predictions pose a question that has been largely overlooked in aquatic taxa: How are the temporal distributions of male investment in reproduction influenced by the intensity of among-male competition?

Female fitness and sexual conflict

Our numerical ESS suggests there may be qualitative differences in the prevalence of sexual conflict over spawning phenology in external versus internal fertilizers. These results are only suggestive because female phenologies were not allowed to evolve in our

models. Thus, while the evolution of male phenologies could result in decreased female fitness in our models, female phenologies were not allowed evolve in ways that could decrease male fitness, or limit the parameter space explored by males. It is nevertheless interesting that for external fertilizers in our numerical ESS model, the male ESS variance will maximize female fertilization success at intermediate population densities (Fig. 3C,D; maximum at $N \cong 58$, and $N \cong 25$ for low and high A_{ext} values respectively), but result in decreased female fitness at both low and high population densities. This apparent conflict is a consequence of female fitness being influenced simultaneously by environmental conditions and egg mortality due to polyspermy. Even at relatively low densities, males are predicted to release sperm over a short period of time, resulting in sperm concentrations that cause some polyspermy during the middle of the season (Fig. 4C,D). Counterintuitively, so long as females can still obtain monospermic fertilizations when environmental conditions are relatively good, they enjoy higher total fertilization success at intermediate densities where non-trivial levels of polyspermy occur (Figs. 3C,D & 4C,D). At high densities, females are 'squeezed' between severe egg mortality due to polyspermy during the middle of the season and decreasing environmental quality on the shoulders of the season, and female fitness begins to decline.

Sexual conflict in external fertilizers is strongly density-dependent and has generally been considered in the context of balancing sperm limitation and polyspermy (Levitan 2004 2005, Bode & Marshall 2007). At low densities, local sperm concentrations limit fertilization and both sexes have been predicted to evolve traits that increase fertilization rates (Levitan 1998, 2005, Levitan & Ferrell 2006). At high densities, males experience intense competition for fertilizations, while females experience selection to decrease fertilization rates in order to avoid polyspermy (Franke et al. 2002, Levitan 2002, 2004, Bode & Marshall 2007). For example, polyspermy-mediated sexual conflict has been shown to result in strong frequency-dependent selection on gamete traits influencing fertilization such as egg size and gamete compatibility proteins (Levitan & Ferrell 2006, Panhuis et al. 2006). More recently, Bode & Marshall (2007) showed theoretically that at low densities where sperm is limiting, competition should cause males to release less sperm at any given time than would result in complete fertilization of females' eggs. Our results support the idea that external fertilizers experience sexual conflict at most population

densities (Bode & Marshall 2007), but suggest that polyspermy-mediated conflict can happen at both low and high densities. The nature of this conflict, however, depends strongly on whether phenologies are constrained by environmental conditions. If phenologies are not constrained by environmental conditions, female fitness will increase with population density despite higher rates of polyspermy. This prediction is in direct contrast to previous models of sexual conflict in external fertilizers but congruent with empirical studies which have documented non-trivial levels of polyspermy, even under sperm-limited conditions (Franke et al. 2002, Marshall 2002, Levitan 2004). Although sex-specific phenologies were not possible in our models, the prevalence of sexual conflict over reproductive timing suggests that this is a likely evolutionary outcome for this group, an expectation that is consistent with observed differences in male and female spawning behaviours in many externally fertilizing marine invertebrates (Levitan 2005, Lotterhos & Levitan 2011).

For internal fertilizers, the male ESS variance will result in lower female fitness only at low population densities (Fig. 3B,D). At low densities, competition for fertilizations causes males to release sperm over time such that local sperm concentrations are never high enough to maximize female fertilization success. Our model predicts that males and females will not be in conflict over the timing of reproduction at high densities, when competition among males for fertilizations is strongest, and sexual conflict over a variety of other traits is well documented (Parker 1982, reviewed in Chapman et al. 2003). While there are many classic examples of sexual conflict in internal fertilizers, very few studies have considered conflict over the timing of reproduction. It would be interesting to see if, as our model suggests, there is indeed little conflict over the timing of reproduction in internally fertilizing species that experience strong sexual conflict and selection on traits affecting pre- and post-copulatory mate choice.

Effects of traits influencing egg fertilization

The results for male ESS variance were robust to changes in the relation between fertilization success and sperm concentration (A_{ext} , A_{int}), and so may be generally applicable to a variety of species and environmental conditions. Interestingly, our model predicts an evolutionary association between egg phenotype and phenology, particularly for externally fertilizing species. Traits such as egg size, the density

of sperm receptor sites on the egg surface, and gamete compatibility proteins can all interact with population density to influence the likelihood of monospermic fertilization (Levitan 2002, 2004, Levitan & Ferrell 2006). Trait values that increase the likelihood of egg fertilization increase male sensitivity to negative frequency-dependent selection on the variance in phenology due to polyspermy and competition for fertilizations and alter the conditions under which males and females are predicted to be in sexual conflict (Fig. 3C,D). Thus, our model predicts that species with larger, more fertilizable eggs should reproduce more asynchronously than species with smaller, less fertilizable eggs.

For internal fertilizers, in addition to gamete traits, traits that increase male efficiency at locating and copulating with mates, or filtering sperm, influence phenology primarily through negative frequency-dependence due to among-male competition for fertilization. As with external fertilizers, trait values that increase the likelihood of egg fertilization increase male sensitivity to negative frequency-dependent selection, resulting in larger variances. However, because internal fertilizers do not suffer the same effects of polyspermy, this effect is most visible at low population densities. When fertilization probabilities are relatively low (e.g. low densities, small eggs, inefficient mate searching), male phenologies should have relatively low variances (but higher than predicted for external fertilizers). Under conditions resulting in high fertilization probabilities (e.g. high densities, large eggs, efficient mate location), selection should favour male phenologies with variance of similar magnitude to prevailing environmental fluctuations (Fig. 3A,B).

CONCLUSIONS

Our analysis expands on traditional hypotheses regarding the evolution of asynchronous reproduction to recognize the importance of negative frequency-dependent selection due to competition among males for fertilizations. We show that when males compete for fertilizations, perfect reproductive synchrony with optimal environmental conditions is never an optimal evolutionary strategy, and asynchronous reproduction is an inevitable consequence of frequency-dependent selection. In addition, our models show that important life-history traits, such as fertilization mode, can alter species sensitivity to this frequency-dependence and qualitatively alter selection on within- and among-individual variance

in phenologies. Our model predictions are broadly consistent with observed phenologies in many aquatic taxa. However, more detailed studies that adequately measure variation in both individual and population phenologies at temporal and spatial scales relevant for gamete interactions are needed against which to test our model predictions.

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