Evolution of Anisogamy in Organisms with Parthenogenetic Gametes

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Abstract: The two sexes are defined by the sizes of the gametes they produce, anisogamy being the state with two differing gamete sizes (hence, females and males). The origin of this divergence has received much research interest, both theoretically and empirically. The gamete dynamics (GD) theory is a widely accepted theoretical explanation for anisogamy, and green algae have been an important empirical testing ground for the theory. However, some green and brown algae produce parthenogenetic gametes (gametes that can develop without fusing with another gamete), in contrast to an assumption in GD theory that unfused gametes do not develop. Here, we construct a GD model accounting for parthenogenetic gametes. We find that under conditions of panmixia and highly efficient fertilization (i.e., conditions of classical GD models from 1972 onward), the results remain largely unaltered by parthenogametes. However, under gamete-limited conditions anisogamy evolves less easily in the new model, and a novel result emerges: whereas previous models typically predict the evolution of either anisogamy or small isogamy, the current model shows that large isogamy can evolve when parthenogenetic gametes evolve under conditions of inefficient fertilization. Our analyses uncover unexplored complications relating to sex ratios under this relatively uncharted gametic system. We discuss limitations these complications impose on our models and suggest avenues for future research. We compare model results to algae with parthenogenetic gametes in nature.

Keywords: anisogamy, isogamy, female, male, parthenogenesis, algae.

Introduction

The evolution of anisogamy is of fundamental importance in evolutionary biology: it creates the male and female sexes and underlies the phenomena of sexual selection and sexual conflict (Darwin 1871; Bateman 1948; Parker et al. 1972; Togashi and Cox 2011; Parker 2014; Lehtonen et al. 2016). A plausible adaptive explanation originates from the biophysics of syngamy under broadcast spawning, involving the gamete size-number trade-off and the zygote fitness-mass relationship. Each parent has a limited energy budget for gamete production and zygote viability relates positively to zygote size, which can generate disruptive selection between parents that increase gamete size and those that increase number. Under such assumptions and depending on the form of the relation between zygote size and fitness, anisogamy can arise from isogamy if (i) there is competition for fertilizations among the gametes of different parents (gamete competition; Parker et al. 1972; Lehtonen and Kokko 2011; Parker 2011) or if (ii) fertilization is inefficient, so that a significant proportion of gametes from all parents remain unfused (gamete limitation; Levitan 1996; Lehtonen and Kokko 2011). Both gamete competition and gamete limitation form credible selective forces contributing to the evolution of anisogamy (Lehtonen and Kokko 2011), although unless gamete competition is very weak, it is the stronger selective force even if gamete limitation is very severe (Parker and Lehtonen 2014).

Focus on anisogamy evolution under the above-described assumptions, termed the gamete dynamics (GD) theory (Lehtonen and Parker 2019), has expanded continuously since publication of articles by Parker et al. (1972) and Knowlton (1974), especially in the past decade (e.g., see the review by Lessells et al. [2009], the monograph edited by Togashi and Cox [2011], and articles by Togashi et al. [2012], Parker and Lehtonen [2014], Lehtonen et al. [2016], Hanschen et al. [2018], da Silva [2018], and da Silva and Drysdale [2018]). By now, GD theory forms a

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powerful and cogent rationale for anisogamy, with increasing supporting evidence.

An important aspect of the theory is understanding how changes in the basic GD assumptions affects its robustness. For instance, most GD models assume that both mating types broadcast their gametes and that synangy is external. Anisogamy then involves two symmetric alternative equilibria: either mating type can become the small gamete producer (male) or the large gamete producer (female). Recently, it has been shown that if ancestral isogamy evolved under some early form of internal fertilization (as is possible in the volvocine algae, the main study group for empirical support of GD theory), the principle difference is that anisogamy then involves just one asymmetric equilibrium: the mating type that retains its gametes becomes female (Lehtonen and Parker 2019).

Another basic GD assumption is that gametes must fuse to form zygotes before continuing development. However, parthenogenetic gametes occur in some organisms (e.g., some green and brown algae). A parthenogenetic gamete (i.e., a parthenogamete) can develop without fusing with a partner gamete if it fails to find one—in other words, parthenogenetic development seems to be a backup strategy that is used primarily under conditions of inefficient fertilization. Algal life cycles involving parthenogenetic gametes can be quite complex, and an example is shown in figure 1. The diploid stage in haploplanktonic green algae with parthenogenetic cycles often has thick cell walls that may aid survival through severe environmental conditions (e.g., drying in summer low tides in shallow water and low winter water temperature in deep water) and can vary considerably in length, as does the degree of cellularity of the sporophyte (e.g., unicellular with a giant cell in the genus *Bryopsis* and multicellular in the genus *Ulva*; van den Hoek et al. 1995). Note that GD selection for anisogamy can take place only across the sexual pathway, where gametes of different mating types combine to create a zygote, and the best strategy for gamete size is dependent on the size of the partner gamete. When gametes reproduce asexually, selection acts to optimize gamete size following the Smith-Fretwell (1974) principle. Evidence suggests that only those gametes that fail to fuse sexually enter the parthenogenetic pathway (Togashi et al. 1999), suggesting that there are costs associated with parthenogenesis.

In the present article, we examine how gamete parthenogenesis affects GD predictions and review reproduction in ulvophycean marine green algae in light of our results.

Models

To model the effect of parthenogenetic gametes on the evolution of anisogamy, we use a life-cycle form for an organism with parthenogenetic gametes and broadcast spawning that includes just one asexual pathway, the parthenosporophyte pathway (fig. 1). Our model is novel in that it includes parallel asexual and sexual reproductive cycles (parthenogenetic gametes and gametic fusion), but its basic structure resembles the models of Bulmer and Parker (2002), as modified by Lehtonen and Kokko (2011) and Lehtonen and Parker (2019) to permit group structure and gamete limitation. The parthenosporophyte pathway (fig. 1) is the only asexual pathway present in some species, and in others the probability that a second asexual pathway (the parthenogametophyte pathway, in which gametes develop directly into gametophytes) occurs is very low. Haploid parthenosporophytes appear to reproduce in the next winter season, as do the diploid sporophytes, so that they are likely to obey the same functional relationship between mass and fitness. In contrast, when they occur, parthenogametophytes reproduce in the same spring season with their parents (male and female gametophytes) because all gametophytes disappear in summer; they are likely to have a different relationship between mass and fitness.

First, we label the two mating types arbitrarily $X$ and $Y$, corresponding to our aim of deriving conditions under which either isogamy and/or anisogamy may become equilibrium states, with symmetrical conditions for the two types (note that $X$ and $Y$ are indeed just labels, as used in previous models on this topic: they have no connection to, e.g., $X$ and $Y$ chromosomes). The probability that a given $X$ gamete fuses with a $y$ gamete is $p_x$, and the probability that given $y$ gamete fuses with an $x$ gamete is $p_y$, leading to the sexual pathway. The zygote goes through its various stages to produce gametophytes, and we derive a fitness component achieved through the sexual cycle. A gamete remains unfused with probability $(1 - p_x)$ or $(1 - p_y)$ for $X$ and $Y$ gametes, respectively, and we similarly derive fitness components achieved through the asexual cycles. Fitness for the asexual cycle is further multiplied with a coefficient $c$, which primarily accounts for lower survivorship of parthenosporophytes relative to zygotes (in addition to a survival difference that might arise from their size difference). For example, $c = 1$ indicates that all unfertilized gametes enter parthenogenesis and have no survival disadvantage for the asexual cycle, whereas $c = 1/2$ corresponds to a 50% survival decrease for the asexual cycle. Secondarily, $c$ accounts for the possibility that not all unfertilized gametes enter parthenogenesis in the first place. There is empirical justification for the coefficient $c$: in the green alga *Monostroma angicava*, the probability that a parthenogamete survives to develop into a (haploid) parthenosporophyte is lower than the probability that a zygote of the same size develops into a (diploid) sporophyte, which also appears to have greater zoospore release success (T. Togashi and Y. Horinouchi, unpublished manuscript).
Figure 1: Schematic diagram of a haplodiplontic algal life cycle in which both x and y gametes can reproduce parthenogenetically by haploid parthenosporophytes (asexual pathway: red) or undergo syngamy to produce diploid sporophytes (sexual pathway: blue), which later undergo meiosis. The x and y pathways represent female and male sexes in anisogamous species or mating types in isogamous species. Ploidy is shown as n or 2n. The haploid adult x and y gametophyte thalli (black broken squares) form gametangia, which broadcast gametes; these enter the sexual and asexual pathways with different probabilities (sexual $p_x$, $p_y$ and asexual $1 - p_x$, $1 - p_y$), respectively, for x and y). In the sexual pathway, after fusion (syngamy) the diploid zygote typically grows considerably to form a (diploid) sporophyte that undergoes a meiotic division, ending in many cell divisions to produce many small haploid zoospores (e.g., Horinouchi et al. 2019), each of which grows into an adult gametophyte thallus, so gametogenesis and meiosis are not directly linked in haplodiplontic cycles. In the parthenogenetic (asexual) cycle, an x or y gamete may develop into a (haploid) parthenosporophyte, which releases zoospores as in the sexual pathway, each of which grows to form a new gametophytic adult. In certain algae, parthenogenetic gametes may form parthenogametophytes, which develop directly into haploid adult gametophytes without forming zoospores (not included here; see text); in others, only one sex may show parthenogenesis. In our model, we focus on the parthenosporophyte asexual pathway (in both x and y) because it is identical to the sexual pathway after the release of zoospores (see text).
We use fertilization functions to keep track of successful fertilizations and fertilization probabilities, thus maintaining internal consistency of the model so that the fate of all gametes is accounted for. Fertilization functions are mathematical models that estimate the number of successful fertilizations based on gamete numbers and other assumptions. Initially created for studies in marine invertebrate ecology (Rothschild and Swann 1951) and artificial insemination of livestock (van Duijn 1964), they now have great flexibility regarding biological settings and can be applied to models of behavioral and evolutionary ecology with relative ease (Lehtonen and Dardare 2019).

In the parthenosporophyte asexual pathway, zoospores are released that then develop into gametophytes, as in the sexual cycle. Our models focus on species utilizing this asexual pathway (fig. 1), and we make the same assumption about how the mass of the propagule (diploid sporophyte or haploid parthenosporophyte) contributes to fitness across both sexual and asexual pathways. This simplification seems justified since (i) only the parthenosporophyte pathway appears to be present in some algae (e.g., the brown alga *Ectocarpus* [Lipsinska et al. 2015; Mignoret et al. 2019] and the green alga *Bryopsis* [Okuda 1994]) and (ii) parthenosporophytes in many species are indistinguishable both morphologically and functionally from diploid sporophytes (Lipsinska et al. 2015). For both sexual and asexual pathways we employ common assumptions about the relationship between propagule (i.e., zygote or parthenosporophyte) size and propagule fitness (see, e.g., Vance 1973; Levitan 2000; Bulmer and Parker 2002; Lehtonen and Kokko 2011; Lehtonen and Parker 2019). To cover the costs of parthenogenesis, we impose an additional size-independent cost to the asexual pathway (parameter \( c \) described above).

Our goal is to model \( x \) and \( y \) fitnesses of the form

\[
\begin{align*}
{w_x} &= \left( \frac{1}{2} \right) p_x n_x s_{xp} + \left( 1 - p_x \right) n_x c_s, \\
{w_y} &= \left( \frac{1}{2} \right) p_y n_y s_{yp} + \left( 1 - p_y \right) n_y c_s,
\end{align*}
\]

where \( x \) and \( y \) refer to mating types. The logic of these equations is easiest to follow with reference to figure 1. The first term in \( w_x \) or \( w_y \) represents fitness via the sexual cycle, and the second represents fitness via the asexual cycle. Begin the analysis with a focal adult \( x \) gametophyte, which produces \( n_x \) gametes, each with probability of fertilization \( p_x \). Hence, \( p_x n_x \) is the average number of fertilized gametes per focal gametophyte, and \( s_{xp} \) is the size-dependent survival of each diploid zygote thus produced. The coefficient 1/2 arises from the assumption that half of the offspring resulting from sexual reproduction are of type \( x \) (see fig. 1, “Fitness via \( x \) meiotic products”), and because we further assume strong linkage between the mating type locus and the locus for gamete size (as assumed in most anisogamy models from Charlesworth [1978] onward), the two are inherited together and hence all type \( x \) offspring carry the same allele for gamete size as did the parent. In other words, if an \( x \) adult gametophyte carries a mutation for a deviant gamete size, a fraction 1/2 of its zoospores via the sexual pathway will be of type \( x \) and carry the same mutation. For the second term of \( w_x \), the average number of unfertilized gametes per focal gametophyte is \( (1 - p_x) n_x \), and these offspring are all of type \( x \). We use the same size-survival relationship \( s_{xp} \) for the parthenogamete to zoospore release in the sporophyte stage (see fig. 1, “Fitness via \( x \) parthenosporophytes”), but this can be further reduced by coefficient \( c \), which accounts for potentially lower survivorship of parthenosporophytes relative to zygotes and their lower zoospore release, as described above. Similar derivations apply to the \( y \) type throughout: the left side (\( y \)) of figure 1 is symmetrical with the right side (\( x \)).

Note that (depending on the species) the zygote or parthenogamete often increases in mass to the sporophyte stage, followed by zoospore release (after meiosis in the sexual pathway); zoospores then grow into gametophytes (see fig. 1).

In summary, the model assumes that (1) each \( x \) or \( y \) mature haploid gametophyte produces an equal number of gametes, which may enter either the sexual or asexual pathway; (2) zygote/parthenogamete survival is size-dependent, increasing with the mass of the two fusing gametes or of the single parthenogamete, following the size-survival relationship \( s_{xp}, s_{yp} \); (3) relative fitness in the asexual pathway is potentially further reduced by coefficient \( c \), which accounts for the additional lower survival of pathenogametes and the reduced zoospore output of surviving parthenosporophytes, as described above; (4) at meiosis in the sexual pathway, the diploid sporophyte produces an equal number of \( x \) and \( y \) zoospores and hence gametophyte parental haplotypes; and (5) there is complete linkage between mating type and gamete size loci.

We next derive each component in item 1 separately from the perspective of a focal mutant individual, indicated by a hat. Notation is presented in table 1.

Using the notation given above, we have the following relations for a mutant \( x \) individual (partly following usual GD conventions):

\[
\hat{n}_x = \frac{M}{m_x}
\]  

(the usual GD size/number trade-off),

\[
\hat{s}_x = \exp \left( -\frac{b}{m_x + m_y} \right)
\]  

(the Vance-Levitan survival function; Vance 1973; Levitan 2000; Bulmer and Parker 2002), and
\[ \hat{s}_p = \exp \left( -\frac{b}{m_s} \right), \]  

where the survival function \( \hat{s}_p \) is for a zygote formed by a mutant gamete and \( \hat{s}_p \) is for a mutant parthenosporophyte. For parthenosporophytes, this survival probability is further multiplied by the coefficient \( c \) (see above and table 1 for an explanation). The probabilities \( p_x \) and \( p_y \) of gamete fusion (and hence probabilities of absence of fusion \( 1 - p_x \) and \( 1 - p_y \)) arise as an emergent property of the \( x \) and \( y \) gamete densities and the aptitude for fusion, \( a \). Decreasing \( a \) reduces the probability of fusion and hence increases the probability that a gamete will develop parthenogenetically.

The main models assume that gametes in a very large population of adults are broadcast into a gametic pool in which the gametes of the entire population are well mixed before fusion (an alternative model, including group structure for gamete mixing, is developed below). A consequence of the assumption of panmixia is that the fertilization probability of a rare mutant gamete (and any other gamete) is determined by the population resident strategy only. While in small groups the differing gamete numbers of a mutant may have some influence on fertilization probability, in a large, well-mixed population this effect is negligible.

If there is a 1:1 sex ratio of adults in the population (see the section on sex ratio below), the density of gametes (for some standard volume) in the medium is \( n_x = M/m_x \), and \( n_y = M/m_y \). If the sex ratio differs from 1:1 (see below and sec. 1 of the supplemental PDF, available online), the gamete densities must be weighted by the sex ratio.

We can then use a fertilization function \( f \) to compute the number of successful fertilizations per unit volume:

\[ f(n_x, n_y, a) = n_x n_y \frac{\exp(an_x) - \exp(an_y)}{n_x \exp(an_x) - n_y \exp(an_y)}. \]  

This symmetrical fertilization function has been derived in previous work for the purpose of modeling fertilization for the entire range from isogamy to extreme anisogamy (Togashi et al. 2007; Lehtonen 2015; Lehtonen and Dardare 2019), which makes it particularly suitable for a model of anisogamy evolution. The parameter \( a \) can be used to adjust fertilization efficiency to simulate scenarios from extreme gamete limitation to ones where all gametes of the less numerous type are fertilized. Because there are \( n_x \) and \( n_y \) gametes of the two types per unit volume, the probability of fertilization per gamete for these types is

\[ p_x = \frac{f(n_x, n_y, a)}{n_x}, \]

\[ p_y = \frac{f(n_x, n_y, a)}{n_y}. \]

Because of the assumption of panmixia, this probability is the same for resident and mutant gametes. Computed in this way, the probabilities remain consistent and account for changes in gamete size and number in each type.

Plugging these components into equation (1) results in the following:

| Table 1: Notation and parameters |
|----------------------------------|
| Notation | Description of parameter, variable, or equation |
| \( x, y \) | Mating types \( x \) and \( y \) |
| \( m_x, m_y, m_x, m_y \) | Gamete sizes of \( x \) residents, \( y \) residents, \( x \) mutants, and \( y \) mutants, respectively |
| \( M \) | Total resources available for gamete production per adult |
| \( n_x, n_y \) | Densities of gametes in the panmictic model |
| \( N_x, N_y \) | Densities of gametes in the group-structured model |
| \( a \) | Aptitude for gametic fusion—sets the “efficiency” of fertilization; increasing \( a \) means that more fusions occur at a given density of \( x \) and \( y \) gametes |
| \( f \) | Function that estimates the number of successful fertilizations as a function of gamete densities and parameter \( a \) |
| \( b \) | Parameter determining the zygote/parthenosporophyte survival function \( s \); increasing \( b \) means that more mass is required for a given level of zygote/parthenosporophyte survival (or other measure of fitness) |
| \( s = s(b, m_x, m_y) = \exp \left( -\frac{b}{m_x + m_y} \right) \) | Survival probability of a zygote as a function of parental gamete sizes and a zygote resource requirement parameter; for a parthenosporophyte’s survival, set either \( m_x \) or \( m_y \) to zero and include the multiplicative cost \( c \) (see text) |
| \( \delta \) | Minimum gamete size for viability (assumed in several previous gamete dynamics models) |
| \( c \) | Multiplicative coefficient to account for possible extra survival disadvantage for parthenogametes and the reduced zoospore output of surviving parthenosporophytes |
| \( p_x, p_y \) | Probability of fertilization per \( x \) and \( y \) gamete |
Sex Ratio with Parthenogenetic Gametes

Parthenogenetic gametes pose two kinds of interesting sex ratio questions, and although a full analysis is beyond the scope of this article, it is important to openly discuss the consequences they may have for our models. One is an issue over evolutionary time, the other over ecological time.

In a typical sexually reproducing organism, long-term evolution selects for 1:1 sex ratios (Fisher 1930; West 2009). This raises the question of whether the possibility of parthenogenetic reproduction alters this theoretical prediction. Should we expect the sexual cycle to lead to a 1:1 ratio of the two types (whether they are mating types or diverged sexes)? As far as we know, this is theoretically an unexplored question. But empirically, evidence suggests that the sexual cycle produces a 1:1 ratio of mating types/sexes (Togashi and Cox 2008), and we base our model on this assumption.

Even if the sexual cycle always produces equal numbers of both types, there is another issue lurking over shorter timescales. This is perhaps easiest to see with the following thought experiment: consider a situation of extreme gamete limitation, where the proportion of fertilized gametes approaches zero. Now the sexual cycle would still produce a 1:1 ratio of types, but there is effectively no reproduction via this pathway. Essentially all gametes remain unfertilized and develop parthenogenetically into adults of their own type. This implies that if the parthenosporophytes of either mating type have even a small overall advantage over the other, that type will dominate the population more and more in each generation. The end result can be that the sex ratio spirals into complete dominance of one type or the other over a relatively short number of generations (i.e., over ecological time) even when there is no evolutionary change in the sex ratio.

We developed two solutions to the second (ecological timescale) sex ratio problem. Both are in their essence game theoretical models (Maynard Smith 1982), but they are implemented in different ways, with different advantages. One is a continuous model where we make the simplifying approximation that the sex ratio over ecological time remains at 1:1. The other is an invasion grid approach inspired by Togashi et al. (2012) and Lehtonen and Parker (2019) but further modified so that the ecological timescale sex ratio is calculated explicitly for each node in the grid using an iterative procedure. The grid approach therefore explicitly accounts for the ecological timescale sex ratio, whereas the continuous model does not. It is possible to do this for the invasion grid approach because there are a finite number of points for which the sex ratio must be iterated, while in the continuous approach there are effectively an infinite number of points for which this would need to be done. However, with the two approaches we are able to present a combination of results that take into account the actual ecological sex ratio (invasion grid) and results that are more approximate in nature but visually very clear and based on well-established methods (continuous model). Together the two methods confirm that results are not significantly altered by variations in the sex ratio that arise under the parameter values examined here.

Although the invasion grid method is arguably the more "correct" one, both are by their nature somewhat prospective qualitative models offering a first approach for modeling anisogamy evolution in this reproductive system. The continuous model is in many ways the clearer approach and allows for very fast computation of results, while the invasion grid conforms that the results are not significantly altered by the ecological sex ratio effect. Hence, both approaches are valuable and will potentially be useful in future explorations of the problem.

Panmictic Model 1: Invasion Grid with Discrete Gamete Sizes

The invasion grid approach (including the sex ratio iteration) is described in further detail in section 2 of the supplemental PDF. Here, we present an outline of how the procedure works. The procedure begins with computation of properties of the resident population, followed by calculation of the fitnesses of possible mutants in such a resident population. The mutant versus resident fitnesses are then contrasted to determine which invasions are possible. This is all done over a "grid" of 21 × 21 gamete sizes, ranging from size 1.5 to 21.5 with increments of 1 unit, resulting in a grid with 441 points for any given parameter combination.

The first step is to compute the resident sex ratio that stabilizes over ecological timescales, given assumptions of the sexual pathway producing x or y offspring in a 1:1 ratio, while parthenosporophytes always generate the type of their parent. This is achieved by iterating equation (6) until the sex ratio stabilizes; this iteration is repeated for each of the 441 grid points (for further details on the sex ratio iteration and invasion grid calculations, see secs. 1 and 2 of the supplemental PDF).
The resident sex ratio found using the iteration above is used to compute gamete densities for each mating type, and subsequently these results can be used to compute resident fitness following equation (6). For each point in the grid there are at least two and at most four possible mutant types that can potentially invade. When such mutants are rare in a well-mixed environment, their per-gamete fertilization probabilities are determined by properties of the resident population. Hence, we can again use equation (6) to compute the fitness of each such rare mutant, and if the mutant fitness is higher than the fitness of the resident population in which it arises, an arrow is drawn from the resident to the mutant size in the grid, indicating a possible invasion.

The entire procedure is repeated for all 441 points in the grid, and all resulting arrows are drawn. Once the process is complete, stable gamete sizes are identified by finding points in the grid that have arrows pointing toward them and no arrows pointing away (i.e., no adjacent mutant can invade).

**Panmictic Model 2: Continuous Gamete Sizes**

For the continuous models we incorporate aspects of game theory and adaptive dynamics (Maynard Smith 1982; Parker and Maynard Smith 1990; Dieckmann and Law 1996; Lehtonen and Maynard Smith 1990; Dieckmann and Law 1996; Leh-

tonen 2018). Evolutionary trajectories and end points are approximated by examining fates of mutants in both mating types that deviate from the resident gamete size strategy. Mutations have small effects on gamete size, modeled by differentiating equation (6) for \( m_x \), \( m_y \), \( \hat{m}_x \), and \( \hat{m}_y \). The results are then used to estimate evolutionary trajectories and end points (for further details on this procedure, see sec. 3 of the supplemental PDF, and for a recent example of a related application of this method, see, e.g., Lehtonen and Parker 2019). Note that gamete numbers inside the fertilization functions in brackets in the panmictic model are not mutant values. They are calculated using the resident strategy value \( m_s \) or \( m_r \).

**Group-Structured Population: Analytical Model with Continuous Gamete Sizes**

We can extend the continuous model to include a simple group structure, similar to that in Lehtonen and Kokko (2011). Instead of panmixia, we now assume that spawning occurs in isolated groups of only one individual of each mating type; the offspring generation then disperses (i.e., gametes are mixed only in a small local spawning population, but zoospores from zygotes are mixed in the global population). In this way, we can examine the two extremes: global gamete competition (panmixia) versus no gamete competition (isolated groups). The rationale for doing so is to compare outcomes to those of Lehtonen and Kokko (2011), where it was shown that gamete limitation can drive the evolution of anisogamy even in the complete absence of gamete competition. Examining the extreme case of groups of one individual of each mating type is sufficient for this purpose, but in section 4 of the supplemental PDF we show how this derivation can be generalized to spawning groups of arbitrary size.

Equation (1) applies, but now group structure must be taken into account when computing the probabilities \( p_s \) and \( p_r \). We can still use an equivalent fertilization function,

\[
\begin{align*}
f(N_s, N_r, a) &= \frac{N_s N_r \exp(a N_s) - \exp(a N_r) N_r}{\exp(a N_s) - N_r \exp(a N_r)} \quad (7)
\end{align*}
\]

but now, instead of population-wide densities, \( N_s \) and \( N_r \) indicate the x and y gamete densities in the local group. An important difference now arises between equations (5) and (7). In equation (5) gamete densities are independent of mutant strategy, but in equation (7) they are increasingly dependent on mutant strategy as group size decreases. For example, if the only \( x \)-type individual in a group is a mutant, the local \( x \) gamete density is indicated by a capital letter, \( N_x \), and similarly for a \( y \)-type mutant. Thus, in contrast to the panmictic model, \( f \) and \( p \) are now functions of the mutant gamete size and number:

\[
\begin{align*}
\hat{p}_s &= \frac{f(N_x, N_y, a)}{N_s} \quad (8)
\hat{p}_r &= \frac{f(N_x, N_y, a)}{N_r} \quad (9)
\end{align*}
\]

We now plug in the group structure–amended \( f \) and \( p \) functions into equation (1):

\[
\begin{align*}
\hat{w}_s &= \left( \frac{1}{2} \right) \left( \frac{f(N_x, N_y, a)}{N_s} \right) \frac{M_c}{m_s} \exp \left( -\frac{b}{m_s + m_r} \right)
+ \left( 1 - \frac{f(N_x, N_y, a)}{N_s} \right) \frac{M_c}{m_s} \exp \left( -\frac{b}{m_s} \right),

\hat{w}_r &= \left( \frac{1}{2} \right) \left( \frac{f(N_x, N_y, a)}{N_s} \right) \frac{M_c}{m_r} \exp \left( -\frac{b}{m_s + m_r} \right)
+ \left( 1 - \frac{f(N_x, N_y, a)}{N_s} \right) \frac{M_c}{m_r} \exp \left( -\frac{b}{m_r} \right).
\end{align*}
\]

We then differentiate for \( \hat{m}_s \) and \( \hat{m}_r \) and use the results to estimate evolutionary trajectories and end points as before, while taking into account that now \( N_s \) is a function of \( \hat{m}_s \). Therefore, when differentiating mutant fitness, the derivatives of the \( f \) functions are not zero, as they were
in the panmictic case. So the equations become considerably more complicated, but otherwise the calculation is as before.

**Results**

We outline outcomes of the two panmixia models in figures 2 and 3. The results of the invasion grid approach (where the actual ecological sex ratio is tracked) are consistent with those of the continuous analytical model (where the sex ratio is approximated as 1:1). The most central outcome from both models is how robust the results remain for the evolution of anisogamy when fertilization is efficient (top rows of figs. 2, 3). Note that this outcome is not obvious: even when fertilization is maximally efficient, there will always be unfertilized gametes entering the asexual pathway under the slightest degree of anisogamy—in other words, even under maximally efficient fertilization, the logical structure of the model does not coincide with earlier models of anisogamy evolution. In the figure panels the importance of propagule size for subsequent survival and fitness (increasing parameter \( b \)) increases to the right, transforming isogamy into anisogamy when there is gamete competition (for a similar model and parameter values but without parthenogenesis, see fig. 3 in Lehtonen and Kokko 2011). Gamete limitation (decreasing parameter \( a \)) increases in figures 2 and 3 from top to bottom panels and in the present model can generate large isogamous equilibria even when size exerts an important effect on propagule fitness. As expected from previous GD studies, when anisogamy evolves, the anisogamy ratio (ratio of female gamete mass to male gamete mass; Parker 1982) increases as the importance of zygote (or parthenosporophyte) provisioning (\( b \)) increases.

Note that if there is no parthenogenetic pathway, as previous GD models have assumed, gamete limitation (i.e., small value of \( a \)) can select for anisogamy in a broadcast-spawning group-structured model (Lehtonen and Kokko 2011).

![Figure 2](image_url)

**Figure 2:** Results of the panmictic invasion grid model for \( c = 0.5 \) (for other \( c \) values, see the supplemental PDF, sec. 5). The importance of propagule size for offspring fitness increases from left to right (by increasing parameter \( b \) from 4 to 10 to 20, as used in Lehtonen and Parker 2019), and fertilization gets less efficient from top to bottom (i.e., gamete limitation increases by parameter \( a \) decreasing from 1 to 0.05). There is a minimum gamete size of 1.5 units (again, as in Lehtonen and Parker 2019). Unshaded areas indicate where intermediate sex ratios are ecologically stable; the shaded areas are approximations of zones where one or the other mating type may go to fixation or close to fixation in ecological time because of parthenogenesis. Large black arrows in unshaded areas indicate some of the invasion trajectories, and circles indicate alternative stable equilibria. For complete information on all trajectories, the image must be magnified. In all panels, \( M = 100 \).
2011). This is because in small groups under gamete limitation a mutant can significantly alter local fertilization success by increasing local gamete concentration. In a panmictic model, this effect is diluted in the very large global population and a mutant cannot significantly change fertilization success, so gamete limitation does not facilitate evolution of anisogamy under panmixia in typical GD models.

However, the parthenogenetic pathway provides an alternative way out of the gamete-limited situation, leading to the possibility of large isogamy (figs. 2, 3F). Thus, the combination of gamete parthenogenesis and gamete limitation in the panmictic model decreases the size of the basin of attraction for isogamy (fig. 3F; the basins of attraction are easier to visualize in the continuous model).

So a major effect of including the parthenogenetic pathway in the life cycle is that it can generate and stabilize large isogamy. In contrast, a typical result of previous GD models is that the system either diverges toward anisogamy or remains at small isogamy so that gametes are maintained at their minimum size. Here, decreased fertilization prospects result in an alternative isogamous equilibrium (figs. 2, 3F). The relative disadvantage for parthenogametes/parthenosporophytes (c) is set to 0.5 for the main results. However, all central results remain valid if c is increased to 0.7 (supplemental PDF, sec. 5). With the smaller value c = 0.3, the large isogamy equilibrium disappears (supplemental PDF, sec. 5). This is expected: a c value of 0 means that the parthenogenetic pathway is blocked entirely and the model corresponds to a usual one with sexual pathways only where no large isogamous equilibria exist, and this state is gradually approached when c decreases.

In previous GD models, large isogamy resulted only if there was no gamete competition and no gamete limitation (Lehtonen and Kokko 2011)—that is, when fertilizations involve just a pair of mating types, one x and one y, and fertilization is very efficient. Assuming the parameters are such that anisogamy would evolve without parthenogenesis, in the present models anisogamy evolves predominantly when there is gamete competition with no gamete limitation; reversing these conditions tends toward large isogamy. So under efficient fertilization, the results are similar to the classical results. Slight anisogamy can arise with intermediate values of parameter b (figs. 2, 3B, 3F).

The main message of the group-structured model (i.e., where gamete competition is excluded) is that gamete limitation alone is unlikely to drive the evolution of anisogamy...
when parthenogametes provide an alternative reproductive pathway (fig. 4). The anisogamous equilibrium appears only in panel F, and its basin of attraction is very narrow; anisogamy is therefore unlikely to evolve from ancestral isogamy in this model. The reason this is important is that gamete limitation has previously been shown to be a plausible alternative and nonexclusive pathway to anisogamy besides gamete competition (Lehtonen and Kokko 2011). Yet when parthenogametes are included in the model, gamete competition remains the only feasible pathway to anisogamy evolution (figs. 2, 3). Roughly, the reason for this is that large parthenogametes (which require no fertilization) provide a more efficient way to deal with gamete limitation than increased microgamete numbers. Therefore, under gamete limitation, both gamete types tend to be selected for ample provisioning, resulting in large isogamy.

The Occurrence of Parthenogenetic Gametes in Algae

In some green and brown algae, depending on the taxon, parthenogenetic development of gametes can take place in gametes of isogamous species (i.e., ones lacking a division into female and male gametes, such as the green alga *Blidingia minima*; Tatewaki and Iima 1984), in both male and female gametes of anisogamous species (e.g., the green alga genus *Monostroma*; Tatewaki 1969), or in female gametes only (e.g., the green alga *Bryopsis corymbosa* [Okuda 1994] and the brown alga *Ectocarpus siliculosus* [Mignerot et al. 2019]).

We here mainly focus on ulvophycean marine green algae, a group that closely matches our theoretical model assumptions. As the GD model assumes (Parker et al. 1972), their gametes are released individually into an external medium (seawater) by both sexes (Togashi et al. 2007). Data on gamete size (i.e., length of the major and minor axes of gametes of each sex), habitat, and the parthenogenesis of gametes in each sex were obtained by literature searches (table 2). We calculated the volume of gametes by assuming that each gamete was ellipsoidal in shape (if only the range of the length of the major and minor axes of gametes had been provided, we used the median for each axis). We categorized the depth of habitat as follows: (1) below the intertidal zone, (2) the lower intertidal zone, (3) the middle intertidal zone, and (4) the upper intertidal zone.

**Figure 4:** As figure 3 but with gamete competition excluded: spawning takes place in small groups of just one individual of each mating type. Otherwise, the model and parameters are as in figure 3. The main difference compared with figure 3 is that the evolution of anisogamy is now effectively blocked. Under these conditions anisogamous equilibria exist only in very narrow basins of attraction in F, so anisogamy is unlikely to evolve via gamete limitation in the presence of a parthenogenetic pathway; once evolved it may be technically stable, but it is vulnerable to fairly small deviations, which will lead to isogamy.
Table 2: Gametic systems, occurrence of parthenogenesis, gamete size, and habitat in some ulvophycean algae

| Order, species | Gametic system (ref.) | Parthenogenesis (ref.) | Gamete size, length × width, μm (ref.) | Habitat (ref.) |
|----------------|-----------------------|------------------------|----------------------------------------|----------------|
| Cladophorales: |                       |                        |                                        |                |
| *Anadyomene wrightii* | Isogamy (Enomoto and Hirose 1970) | Both sexes (Enomoto and Hirose 1970) | 10.0−12.0 × 4.0−6.0 (Enomoto and Hirose 1970) | Below intertidal zone (Enomoto and Hirose 1970) |
| *Cladophora surera* | Isogamy (Parodi and Cáceres 1995) | Both sexes (Parodi and Cáceres 1995) | 13.0−15.0 × 7.9−10.0" (Parodi and Cáceres 1995) | Freshwater river (Parodi and Cáceres 1995) |
| *Dictyosphaeria cavernosa* | Isogamy (Enomoto and Okuda 1981) | Both sexes (Enomoto and Okuda 1981) | 8.0−9.5 × 5.0−6.0 (Enomoto and Okuda 1981) | Middle, lower, and below intertidal zone (Hunter and Evans 1995) |
| *Willella japonica* | Isogamy (Chihara 1965) | Both sexes (Chihara 1965) | 8.0−12.5 × 6.0−7.5 (Chihara 1965) | Below intertidal zone (Chihara 1965) |
| Ulotrichales: |                       |                        |                                        |                |
| *Capsosiphon groenlandicus* | Isogamy (Tatewaki 1969) | Both sexes (Tatewaki 1969) | 5.7−9.8 × 2.5−4.8 (Tatewaki 1969) | Upper littoral zone (Tatewaki 1969) |
| *Spongomorpha spiralis* | Isogamy (Miyaji 1996) | Both sexes (Miyaji 1996) | 5.0−7.0 × 2.0−3.0 (Miyaji 1996) | Middle and lower intertidal zone (Miyaji 1996) |
| Ulvales: |                       |                        |                                        |                |
| *Blidingia minima* | Isogamy (Tatewaki and Iima 1984) | Both sexes (Tatewaki and Iima 1984) | 5.0−6.0 × 2.0−3.0 (Tatewaki and Iima 1984) | Upper littoral zone (Iima 1989) |
| *Ulva compressa* | Isogamy (Kagami et al. 2008a) | Both sexes (Kagami et al. 2008b) | 5.7−7.4 × 2.4−3.1" (Kagami et al. 2008b) | Upper to lower intertidal zone (Steinhagen et al. 2019) |
| *Ulva mutabilis* | Isogamy (Hoxmark and Nordby 1974) | Both sexes (Hoxmark and Nordby 1974) | ... | ... |
| *Ulvaria obscura* | Isogamy (Tatewaki 1969) | Both sexes (Tatewaki 1969) | 4.5−7.6 × 1.5−3.7 (Tatewaki 1969) | Middle or lower intertidal zone (Dube 1967) |
| *Ulva lactuca* | Slight anisogamy (van den Hoek et al. 1995) | Both sexes (van den Hoek et al. 1995) | ... | ... |
| *Ulva ohnoi* | Slight anisogamy (Hiraoka et al. 2004) | Both sexes (Hiraoka et al. 2004) | Male: 6.3 × 2.3; female: 7.1 × 3.5 (Hiraoka et al. 2004) | ... |
| *Ulva pertusa* | Slight anisogamy (Hiraoka et al. 1998) | Both sexes (Yamada and Saito 1938) | Male: 5.8−8.7 × 2.3−3.5; female: 5.8−9.0 × 2.7−5.0 (Hiraoka et al. 1998) | ... |
## Ulotrichales:

| Species               | Photoanisogamy | Sexes          | Male Size (μm) | Female Size (μm) |
|-----------------------|----------------|----------------|----------------|-----------------|
| **Collinsiella cava** | Slight         | Both sexes     | 6.2–8.0 × 2.5–3.7 | 6.8–8.7 × 2.5–3.5 |
| (Chihara 1960)        |                | (Chihara 1960) |                |                 |
| **Collinsiella japonica** | Slight       | Both sexes     | 6.2–8.1 × 2.5–3.5 | 7.3–8.7 × 2.5–3.7 |
| (Chihara 1960)        |                | (Chihara 1960) |                |                 |
| **Collinsiella tuberculata** | Slight     | Both sexes     | 6.3–8.1 × 2.5–3.5 | 7.5–9.4 × 2.5–3.5 |
| (Chihara 1960)        |                | (Chihara 1960) |                |                 |
| **Monostroma angicava** | Slight       | Both sexes     | 3.7–7.6 × 1.5–3.3 | 5.6–10.6 × 2.7–5.3 |
| (Tatewaki 1969;       |                | (Tatewaki 1969)|                |                 |
| Togashi et al. 1997,  |
| 1999)                |                |                |                |                 |
| **Monostroma latissimum** | Slight    | Both sexes     | 6.4 × 2.6;      | 6.9 × 2.5 (Bast et al. 2009) |
| (Bast et al. 2009)    |                |                | female: 6.9 × 2.5 |                 |
| **Urospora penicilliformis** | Slight | Both sexes     | 7.0–9.0 × 2.0–5.0; | 8.0–15.0 × 4.0–6.0 (Lokhorst and Trask 1981) |
| (Lokhorst and Trask  |
| 1981)                |                |                | female: 8.0–15.0 |                   |
| **Urospora neglecta** | Anisogamy     | Female only    | 4.0–6.0 × 3.0–4.0; | 16.0–30.0 × 4.0–7.0 (Lokhorst and Trask 1981) |
| (Lokhorst and Trask  |
| 1981)                |                |                | female: 16.0–30.0 |                   |
| **Bryopsidales:**    |                | Male: 6.9 × 3.2; | 24.5 × 16.8 (Arasaki et al. 1956) |
| **Codium fragile**   | Anisogamy     | Female only    |                |                 |
| (Arasaki et al. 1956) |                | (Prince and   |                |                 |
| Trowbridge 2004)     |                | Trowbridge     |                |                 |
| **Derbesia tenuissima** | Anisogamy | Female only    | 8.0 × 3.0;      | 14.0 × 10.0 (Ziegler and Kingsbury 1964) |
| (Ziegler and Kingsbury 1964) | | (Ziegler and Kingsbury 1964) | | |
| **Bryopsis flaminigii** | Anisogamy    | Both sexes     | 5.0–6.0 × 2.0–3.0; | 10.0–12.0 × 5.0–8.0 (Harper and Pienaar 1985) |
| (Harper and Pienaar 1985) | |                | female: 10.0–12.0 |                   |
| **Bryopsis plumosa**  | Anisogamy     | Both sexes     | 5.0 × 2.4;      | 9.2 × 5.0 (Togashi et al. 1998) |
| (Togashi et al. 1998) |                |                | female: 9.2 × 5.0 |                   |
| **Caulerpa racemosa** | Anisogamy     | Both sexes     | 5.2–7.0 × 2.2–3.0; | 5.8–8.5 × 2.7–3.3 (Ohba et al. 1992) |
| (Ohba et al. 1992)    |                |                | female: 5.8–8.5 |                   |
| **Derbesia marina**   | Anisogamy     | Both sexes     | 5.0–6.0 × 2.0;  | 11.0–13.0 × 6.0 (Kobara and Chihara 1981) |
| (Kobara and Chihara 1981) | |                | female: 11.0–13.0 |                   |
| **Trichosolen myura** | Anisogamy     | Both sexes     | 4.0–5.0 × 2.0;  | 7.0–10.0 × 4.0–5.0 (Chihara and Kobara 1995) |
| (Chihara and Kobara 1995) | |                | female: 7.0–10.0 |                   |

* The width of gametes was measured from micrographs.

b The values are of mean gamete size from different strains.

c A stigma possibly present in male gametes.
Various gametic systems (isogamy, anisogamy) are found in this class. Particularly, differing from many other biological groups, many isogamous or slightly anisogamous species exist. Figure 5 shows female gamete size plotted against male gamete size; isogamous species lie on the broken line. In isogamous species, we observe a wide range of gamete size from small isogamy to large isogamy. In most such species—including Blidingia minima, which produces small isogametes—gametes of both mating types develop parthenogenetically (the anisogamy ratio is significantly different among the parthenogenetic systems; see the supplemental PDF, sec. 6). The depth of habitat appears to be positively related to the size of isogametes (fig. 6); although the trend in figure 6 is not significant, this may be because the sample size is too low in the data; see the supplemental PDF, sec. 6). Slightly anisogamous species (e.g., Monostroma angicava) also produce parthenogenetic male and female gametes. In anisogamous species, the anisogamy ratio varies widely depending mainly on female gamete size. In many moderately anisogamous species (e.g., Bryopsis plumosa), parthenogenetic gametes are not found in both sexes. In contrast, in some strongly anisogamous species (e.g., Codium fragile), gamete parthenogenesis is observed only in females. Thus, in ulvophycean marine green algae, parthenogenesis of gametes seems to link to gametic systems (table 2).

Discussion

Sex Ratio and Extra Costs of Parthenogenesis

Our models focus on one asexual pathway (the parthenosporophyte pathway; fig. 1), since the second pathway (the parthenogametophyte pathway) is absent in many
species, and in the others the probability that it occurs is very low. They include two costs for parthenogenetic propagules: (i) lower viability, a result of their smaller size relative to zygotes (this cost emerges implicitly via function $s$); and (ii) reduced relative survivorship, $c < 1$, accounting for lower survivorship of parthenosporophytes relative to zygotes, including the possibility that not all unfertilized gametes enter parthenogenesis (in addition to the survival difference arising from the size difference in cost i) and their potentially reduced zoospore release.

That only those gametes that fail to undergo syngamy enter the asexual pathway suggests that this involves an extra cost compared with the sexual pathway. It is also possible that they might be functionally different in some way (Hoxmark and Nordby 1974). When denied the opportunity to fuse sexually, a significant proportion of unfused gametes of the green alga *Monostroma angicava* fail to enter the parthenogenetic pathway, and those that form parthenosporophytes release less zoospores than sporophytes in the sexual pathway (T. Togashi and Y. Horinouchi, unpublished observations). Whatever the reason, an extra cost seems likely and appears to be necessary to stabilize sexual reproduction in algae with parthenogenetic gametes, and investigation of both this aspect and the evolution of sex ratio requires further study.

**Figure 6:** Relation between habitat and gamete volume in isogamous ulvophycean marine algae.

*Model Predictions and Ulvophycean Reproduction*

In the most ancestral species of green algae, gametes might have had the ability to develop parthenogenetically, since such species would have been unicellular and isogamous (Hanschen et al. 2018). We outline here how ulvophycean algae offer good prospects for testing the predictions of our models.

That isogamy/slight anisogamy with parthenogenetic gametes of both sexes is most common in ulvophycean marine algae is evident in figure 5 (see the supplemental PDF, sec. 6). Isogamous or slightly anisogamous species often appear to inhabit shallow waters (fig. 6; table 2), often in high population densities (see the supplemental PDF, sec. 6). In such habitats, conditions would be more favorable for gathering resources and receiving sunlight, enhancing photosynthesis. Hence, less resources may be required for a zygote or parthenosporophyte to develop safely (i.e., smaller $b$). In nature, the gametes of these species are released synchronously, stimulated by daytime low tide (e.g., Togashi and Cox 2001). They have an eyespot and show positive phototaxis (e.g., Togashi et al. 1997). Positive phototaxis by gametes is useful for effective fusion (Togashi et al. 1999). Therefore, these species are unlikely to be strongly gamete limited, and they probably experience...
gamete competitive conditions in nature. This combination of conditions (low $b$ despite high $a$) is likely to result in small gametes that are isogamous (figs. 2A, 3A) or slightly anisogamous (figs. 2B, 3B).

However, some isogamous or slightly anisogamous marine ulvophyceans are found under rather less favorable deeper conditions (fig. 6; table 2), where the reduced environmental resources and sunlight imply that a higher zygote size is favored (high $b$) because of the need for more chloroplasts and so on. Their gamete densities—and hence the fusion probability per gamete—may be lower (variation in density is not explicitly presented in our results, but low density has an effect similar to a low value of parameter $a$). Under these conditions, our results might explain the evolution of large isogamy (figs. 2F, 3F). Some moderately and strongly anisogamous species often also inhabit deeper waters (e.g., bottom of tide pools; Chapman et al. 1964); our results indicate that under gamete-limited conditions, anisogamy and large gamete isogamy can be a simultaneous attractors, although the basin for attraction for anisogamy is smaller (fig. 3F). However, these species might be under less gamete-limiting conditions for various reasons: for example, female gametes have a large target size (Levitan et al. 1991); gametes are synchronously released in both sexes, stimulated by sunlight (Togashi et al. 1998); and female gametes use a sexual pheromone to attract male gametes that lack a phototactic system (Togashi et al. 1998). Under such conditions, figure 2B and 2C and figure 3B and 3C converge to classical models without parthenogenesis to explain the evolution of anisogamy (Togashi et al. 2012).

In ulvophyceans, one or both sexes may not show parthenogenesis; when only one sex is parthenogenetic it is the female, and the macrogametes are large (fig. 5; table 2). However, the probability that the small male gametes in these species will fail to fuse is high, so it is not clear why they have (presumably) lost the ability for parthenogenetic development, particularly as other ulvophyceans with isogametes of similar size retain it (fig. 6; table 2), suggesting an interesting question for future theoretical study. This consideration aside, it may always pay small male gametes (with very low parthenogenetic viability) to undergo syngamy (with much higher viability prospects) rather than parthenogenesis. But this may not apply to large female gametes, which may do better by parthenogenesis rather than share their resources through syngamy (under anisogamy, the twofold cost of sex applies), implying possible sexual conflict over which pathway (sexual or asexual) to adopt. Recent work on the brown alga _Ectocarpus_ has demonstrated male fitness costs of parthenogenesis, where parthenogenesis may be under both sex-specific selection and generation/ploidally antagonistic selection (Mignerot et al. 2019).

**How Does Gamete Parthenogenesis Affect GD Theory?**

Our analyses show that GD theory remains a likely explanation for the evolution of anisogamy from isogamy, even when (as seems quite probable for certain algal taxa) the ancestral isogamous state involved parthenogenetic development of gametes. However, gamete parthenogenesis modifies GD predictions. First, anisogamy is likely to arise only through gamete competition, not gamete limitation, particularly from an isogamous ancestor (in the absence of gamete parthenogenesis, strong gamete limitation and weak gamete competition can generate anisogamy; Lehtonen and Kokko 2011). Second, under gamete-limited conditions, gamete parthenogenesis generates isogamy, with isogamete size increasing as the importance of size/complexity (parameter $b$) increases, so that large isogamy now becomes possible. In GD models without parthenogametes, large isogamy is an unlikely outcome and appears only in the absence of both gamete competition and gamete limitation (fig. 5a in Lehtonen and Kokko 2011), whereas in the present model large isogamy is typically a stable outcome when gamete limitation is present. An alternative explanation of large isogamy, particularly in species without gamete parthenogenesis, is that anisogamy may be prevented because of a constraint on minimum gamete size. In volvocines, gametes of isogamous species have a chloroplast, but the chloroplast of microgametes of anisogamous species is degenerate; such microgametes are smaller than isogametes of comparable species (da Silva and Drysdale 2018).

We summarize how the presence or absence of parthenogenesis affects the evolution of anisogamy/isogamy in our panmixia model compared with the model with group structure in table 3. In this first theoretical approach to anisogamy evolution in species with parthenogenetic gametes, we have mainly focused on a panmictic scenario with high gamete competition, with the aim of exploring how classic results are affected by parthenogenetic gametes. Additionally, we have examined the opposite extreme of no gamete competition, with variation in gamete limitation. Modeling intermediate values of gamete competition is possible, as we detail in the section 4 of the supplemental PDF, but such an analysis would again face the limitation of being restricted to a 50:50 sex ratio. Modeling variation in gamete competition while accounting for the ecological sex ratio would pose significant technical challenges, and we leave this question for future work. Note that our models do not investigate the strategic evolution of parthenogenesis in gametes; we assume (following evidence) that gametes fuse if possible and resort to parthenogenesis only if they fail to fuse. Thus, if the sexual pathway is rare relative to the parthenogenetic pathway (likely under gamete limitation), we get isogamy;
the rare zygotes formed will be well above (almost twice) the optimal size for development, since the parthenogametes will approach the Smith-Fretwell (1974) optimum. If the parthenogenetic pathway is rare relative to the sexual pathway (i.e., the maximal number of gametes fuse), we get the classical results found in previous GD articles. Assuming that parameters are such that anisogamy could evolve, under panmixia the principal change is that parthenogenesis has the effect that anisogamy is much less likely to evolve in the presence of strong gamete limitation, which is consistent with our comparative data in ulvophyceans (see above). Adding strategic choices of syngamy and parthenogenesis would greatly complicate analyses. The models could also be expanded to include further effects, such as might occur in the case where species show two asexual pathways—that is, both the parthenosporophyte pathway and the parthenogametophytic pathway—which does not include the production of zoospores.

How irreversible is anisogamy? Parker’s (1982) models suggest that the strong anisogamy seen in Metazoa is very stable. But parthenogenesis of gametes may change this conclusion and explain some transitions found in algae. For example, in brown algae, separate sexes (Luthringer et al. 2014) with oogamy (Silberfeld et al. 2010) is claimed to be the ancestral state; presumably an isogamous ancestor evolved toward oogamy before the brown algae arose, but there have been subsequent transitions back to isogamy. Possibly this has been facilitated by gamete parthenogenesis; some brown algae have parthenogenesis in both male and female gametes; if conditions became gamete limited, this would generate selection for large isogamy.

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Statement of Authorship

The project was conceived by G.A.P. and T.T. The models were developed and analyzed by J.L. and G.A.P. Empirical data were analyzed by Y.H. and T.T. All authors wrote the original draft, reviewed and edited the manuscript, and approved the final manuscript for publication.

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Table 3: Predictions of gamete dynamics models with and without parthenogenesis and with and without group structure, assuming parameters are otherwise such that anisogamy could evolve

| Gamete competition level | Gamete limitation level | Outcome with sexual pathway only | Outcome with both sexual and asexual pathways |
|-------------------------|------------------------|----------------------------------|-----------------------------------------------|
| Highest—panmixia        | Low                    | Anisogamy                        | Anisogamy                                     |
|                         | High                   | Anisogamy                        | Isogamy                                       |
| Lowest—extreme group structure (g = 1) | Low | Isogamy                        | Isogamy                                       |
|                         | High                   | Anisogamy                        | Isogamy                                       |

Note: The most prevalent result is shown here; alternative equilibria with smaller basins of attraction do occur in some cases (see fig. 3).
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“The Xanthocephalus icterocephalus, as this species is called, is one of our handsomest blackbirds, the body being glossy black, the head, neck and breast rich yellow, and the wings having a white spot. The female is smaller than the male, and plain dark brown, with the yellow of the head restricted and clouded. Together with the Lark Finch (Chondestes grammaca) and Prairie Hen, it is one of the earliest indications that the westward bound traveller has of approaching a different ornithological region.” From “The Yellow-Headed Blackbird” by Elliott Coues (The American Naturalist, 1871, 5:195–200).