Received: 28 March 2024 | Accepted: 24 April 2024

DOI: 10.1111/jpy.13462

PERSPECTIVE

Let's talk about sex: Why reproductive systems matter for understanding algae

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Funding information
Division of Environmental Biology, Grant/Award Number: DEB-2141971 and DEB-2113745

Editor: M.A. Coleman

Abstract

Sex is a crucial process that has molecular, genetic, cellular, organismal, and population-level consequences for eukaryotic evolution. Eukaryotic life cycles are composed of alternating haploid and diploid phases but are constrained by the need to accommodate the phenotypes of these different phases. Critical gaps in our understanding of evolutionary drivers of the diversity in algae life cycles include how selection acts to stabilize and change features of the life cycle. Moreover, most eukaryotes are partially clonal, engaging in both sexual and asexual reproduction. Yet, our understanding of the variation in their reproductive systems is largely based on sexual reproduction in animals or angiosperms. The relative balance of sexual versus asexual reproduction not only controls but also is in turn controlled by standing genetic variability, thereby shaping evolutionary trajectories. Thus, we must quantitatively assess the consequences of the variation in life cycles on reproductive systems. Algae are a polyphyletic group spread across many of the major eukaryotic lineages, providing powerful models by which to resolve this knowledge gap. There is, however, an alarming lack of data about the population genetics of most algae and, therefore, the relative frequency of sexual versus asexual processes. For many algae, the occurrence of sexual reproduction is unknown, observations have been lost in overlooked papers, or data on population genetics do not yet exist. This greatly restricts our ability to forecast the consequences of climate change on algal populations inhabiting terrestrial, aquatic, and marine ecosystems. This perspective summarizes our extant knowledge and provides some future directions to pursue broadly across micro- and macroalgal species.

KEYWORDS

clonality, fertilization, mating system, meiosis, seaweed, sex

INTRODUCTION

Bell (1982) considered the “casualness of the few attempts to provide a functional account of haploidy and diploidy [i.e., sex]…a major scandal” (p. 443). Over 40 years later, we have yet to resolve the evolutionary enigma of sex. The life cycle is nevertheless one of the most fundamental biological features influencing ecological and evolutionary processes. In eukaryotes, growth and reproduction are linked together through

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Abbreviations: AFLPs, amplified fragment length polymorphisms; ESTs, expressed sequence tags; TSAR, Telonemids, Stramenopiles, Alveolates, and Rhizaria.

The title was inspired by Spencer Barrett's (2011) excellent book chapter on why reproductive systems matter for invasion biology of plants.

sex: fusion (i.e., fertilization or syngamy), rearrangement (i.e., recombination), and reduction (i.e., meiosis). The cycles of growth and reproduction, in turn, link individuals to population dynamics (Bonner, 1965). The alternation in ploidy—often diploid and haploid—constitutes a major genomic change directly affecting the phenotype.

Sex is often easier to observe in large multicellular taxa (e.g., mammals). However, for most eukaryotes, sex is not always tied to a reproductive process (see Beukeboom & Perrin, 2014). We are accumulating evidence for the occurrence of sex across taxa with ever-expanding genomic capabilities, but these observations are nevertheless indirect, such as the identification of functional meiotic genes (Bhattacharya et al., 2013; de Silva & Machado, 2022; see also Beukeboom & Perrin, 2014) or the calculation of population genetic summary statistics (Duminil et al., 2007; Ellegren & Galtier, 2016; Tibayrenc & Ayala, 1991). Our knowledge of sex in nature remains rudimentary outside of taxa of economic, ecological, or epidemiological importance and ease of laboratory-based cultivation (Aanen et al., 2016). Even in putative asexual lineages, meiotic machinery has been observed, suggesting a need to assume sex occurs, even if rarely, as the default unless other evidence is determined to show it has been entirely lost (Hofstatter & Lhahr, 2019).

Studying sex in nature is complicated by the fact that the majority of eukaryotes are partially clonal, engaging in both sexual and asexual reproduction (Beukeboom & Perrin, 2014). Asexual reproduction can range from agametic modes that only involve somatic tissue (e.g., fragmentation) to gametic modes that involve germline tissues (see Orive & Krueger-Hadfield, 2021 for a brief summary and further reading). The occurrence of various manifestations of sexual and asexual reproduction complicates the use of traditional approaches to population genetics and their interpretation because they were built on the assumptions of obligate sexuality or obligate asexuality (Arnaud-Haond et al., 2007; Halkett et al., 2005; Krueger-Hadfield, Guillemin, et al., 2021; Stoeckel, Arnaud-Haond, & Krueger-Hadfield, 2021; Stoeckel, Porro, & Arnaud-Haond, 2021). Moreover, the literature is overwhelmingly dominated by studies on animal behaviors associated with sex (Lane et al., 2011) or the relative rates of self-fertilization (i.e., selfing) versus outcrossing in angiosperms (Barrett, 2002; Whitehead et al., 2018). The life history traits that affect the reproductive system (sensu Barrett, 2011: [i] sexual vs. asexual reproduction *and* [ii] selfing vs. outcrossing) are evolutionarily labile and vary tremendously within and between taxa (Barrett, 2014). Further, the reproductive system influences the partitioning of genetic diversity within and among populations (Hamrick & Godt, 1996) and the maintenance of genetic associations (Otto & Marks, 1996). The balance between sexual and asexual reproduction strongly influences ecological (Halkett et al., 2005; Silvertown, 2008) and evolutionary success (Orive et al., 2017, 2023).

This knowledge gap is all the more critical as climate change can affect the life history traits that influence population-level responses, including by shifting the prevailing reproductive mode (Sandrock et al., 2011). This has direct consequences for forecasting how a changing climate will affect populations of most eukaryotic lineages, even including well-studied groups like the angiosperms (see discussion in Rushworth et al., 2022). The ease with which we can generate genetic data is rapidly increasing and, thus, so is what we can learn about the partitioning of genetic diversity, although it remains important to couch all these data firmly in natural history (Travis, 2020). In Bell (1994; p. 6), figure 2 was described as a "pocket summary of eukaryotic life cycles." To borrow his eloquent turn of phrase, so too should be this perspective, in which the subsections are pocket summaries of what we know about algal reproduction. Where there are excellent reviews, they are noted, and interested readers should delve into the work by those authors, as the level of detail here is not equaled nor is it intended to be. This perspective can also serve as a preliminary translation of these data for our understanding of the evolution of reproductive systems in this polyphyletic group of eukaryotes. Hopefully, it spurs attention to the central role reproductive systems play in algal evolutionary ecology.

THE ROLE OF ALGAE IN UNDERSTANDING EUKARYOTIC REPRODUCTIVE SYSTEMS

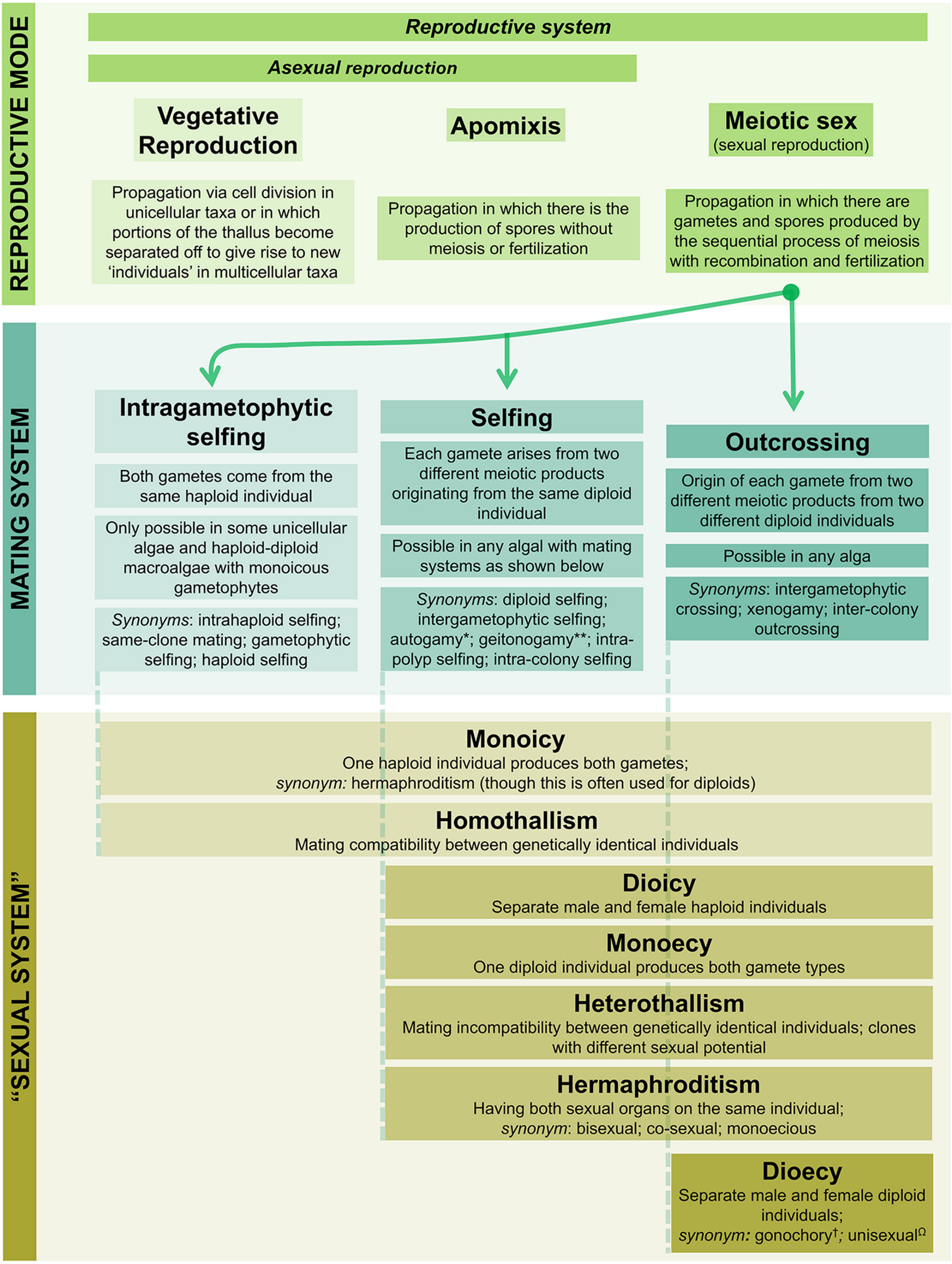
Algae occupy a central role in our understanding of the evolution of reproductive system, especially against the backdrop of a changing climate (see Coleman, 2024, for an introduction to these perspectives). Micro- and macroalgae are observed in almost every major eukaryotic lineage, including Telonemids, Stramenopiles, Alveolates, and Rhizaria (TSAR), Haptista, Cryptista, Archaeplastida, and the "Excavates" (see Burki et al., 2020), enabling powerful insights into convergent evolution (Qiu et al., 2012). Moreover, the algae are the most speciose group following angiosperms and fungi, but important gaps in our understanding of these taxa remain despite their importance to eukaryotic evolution (Guiry, 2024). Further, many aspects of algal reproductive systems differ significantly from those of animals and angiosperms, challenging traditional understanding and the utility of common proxies to describe patterns in nature (Krueger-Hadfield, 2020; Krueger-Hadfield et al., 2019; Krueger-Hadfield, Guillemin, et al., 2021; Krueger-Hadfield & Hoban, 2016). For example, Stoeckel, Arnaud-Haond, and Krueger-Hadfield (2021) recently demonstrated that the combined effects of the proportion of the haploid phase, the rate of clonality, and the relative strength of mutation versus genetic drift substantially influence the distribution of common population genetic indices in haploid–diploid macroalgae, rendering it difficult to use the population genetic knowledge accumulated from animals and angiosperms (see also Krueger-Hadfield, Guillemin, et al., 2021). In addition, in algae with haploid phases of long duration, two types of selfing are possible. Intragametophytic selfing occurs in monoicous haploids and results in instantaneous, genome-wide homozygosity (Klekowski, 1969). Although selfing in a hermaphroditic individual is the same in so far as both gametes are made by the same individual, in diploid taxa, heterozygosity is not lost after a single fertilization event. Separate sexes (i.e., dioecy) prevent selfing in diploid taxa, but this is not the case in haploid–diploid taxa in which intergametophytic selfing is possible despite separate sexes (i.e., dioicy, Klekowski, 1969). Thus, separate sexes cannot be used as a proxy by which to describe the reproductive system without tools of population genetics (see, as an empirical example, Krueger-Hadfield et al., 2015). Finally, separate cytological and morphological phases can be studied in a single species (Dring, 2003). Studies on the life cycles of algae can help resolve the long-standing conflict between ecological and genetic hypotheses (Albecker et al., 2021; Krueger-Hadfield, 2020). Therefore, insights gleaned from algae may therefore aid in the development of better theoretical predictions for patterns of population genetics that are relevant broadly across eukaryotes. These data will be critical for our understanding of how algal populations—and eukaryotes by extension—will respond to the effects of climate change (see Krueger-Hadfield, 2020).

Different algal lineages have been touted as useful for the study of evolution questions about the life cycle and reproductive system, but information remains disparate and taxonomically restricted (Otto & Marks, 1996; Krueger-Hadfield, 2020; Heesch et al., 2021; Krueger-Hadfield et al., 2024). Olsen et al. (2020) demonstrated that the distributions of the inbreeding coefficient (F_{IS}) among angiosperms, macroalgae (including red, green, and brown algae), and marine invertebrates were comparable, suggesting that similar forces may drive patterns of variation in reproductive systems broadly across taxa. This perspective is meant to provide an overview of what we know and what we do not know for micro- and macroalgae. In the sections for each algal lineage, any group with an asterisk (*) has been subject to explicit studies of the reproductive system using the approaches of population genetics, although not all possible references are included in this perspective. Rather than an exhaustive review, the following sections are divided by group based on Burki et al. (2020). The sad fact is that we simply know too little about too many taxa (see also Beukeboom & Perrin, 2014, as this problem is an acute eukaryotic problem, not restricted to the algae).

A SMALL DEPARTURE IN RESOLVING JARGON

It is necessary to begin with a brief introduction to the meaning of different terms invoked in the following sections. Beukeboom and Perrin (2014) distinguished "sex" from "meiotic sex," arguing sex had often been defined as any genetic exchange, such as the succession of meiosis with recombination and fertilization; however, under such a broad definition, sex could also include transformation or transduction in prokaryotes or transmission in viruses, as these too were forms of genetic exchange. Meiotic sex was therefore a more precise definition of sex: sex by the *occurrence of meiosis*. Thus, self-fertilization is a form of uniparental meiotic sex, as it involves meiosis, recombination, and fertilization, albeit with gametes produced by the same individual. Certain modes of parthenogenesis involving meiosis would also fall under meiotic sex (see de Meeûs et al., 2007; Orive & Krueger-Hadfield, 2021 for descriptions of these modes of parthenogenesis that will not be discussed in detail here). For the purposes of this perspective, I will use the term "meiotic sex" as in Beukeboom and Perrin (2014).

Recently, reproductive systems were reviewed with a focus on freshwater red algae, and readers should refer to table 1 in Krueger-Hadfield et al. (2024) for additional clarification on terminology. However, there is some confusion with terms used for diatoms (see an excellent review by Kaczmarska et al., 2013) versus terms used for macroalgae (Heiser et al., 2023; Krueger-Hadfield, Roze, et al., 2013). Inspired by the review on fungi by Billiard et al. (2012), I have adapted their figure, showing the flow from the reproductive mode to the mating system and, finally, to the "sexual system" (Figure 1). Using the separation of reproductive modes by Fristch (1935) as well as work in the angiosperms (Richards, 1986), three types of reproduction are recognized: vegetative reproduction, apomixis, and meiotic sex. Fristch (1935) used the terms vegetative reproduction and asexual reproduction, but here, I have used the term apomixis to refer to the specific type of asexual reproduction—spore production—in which there is no fertilization, meiosis, or recombination. Both vegetative reproduction and apomixis are forms of asexual reproduction in this context. The contrast is in the production of a spore in apomixis as compared to vegetative reproduction, such as the mitotic divisions of unicellular taxa or fragmentation of the thallus in multicellular taxa. The relative rates of vegetative reproduction, apomixis, and meiotic sex are collectively referred to as the reproductive system (sensu Barrett, 2011). The



Vegetative Reproduction: Propagation via cell division in unicellular taxa or in which portions of the thallus become separated off to give rise to new 'individuals' in multicellular taxa

Apomixis: Propagation in which there is the production of spores without meiosis or fertilization

Meiotic sex (sexual reproduction): Propagation in which there are gametes and spores produced by the sequential process of meiosis with recombination and fertilization

Intragametophytic selfing

Both gametes come from the same haploid individual

Only possible in some unicellular algae and haploid-diploid macroalgae with monoicous gametophytes

Synonyms: intrahaploid selfing; same-clone mating; gametophytic selfing; haploid selfing

Selfing

Each gamete arises from two different meiotic products originating from the same diploid individual

Possible in any algal with mating systems as shown below

Synonyms: diploid selfing; intergametophytic selfing; autogamy*; geitonogamy**; intra-polyp selfing; intra-colony selfing

Outcrossing

Origin of each gamete from two different meiotic products from two different diploid individuals

Possible in any alga

Synonyms: intergametophytic crossing; xenogamy; inter-colony outcrossing

Monoicy: One haploid individual produces both gametes; *synonym:* hermaphroditism (though this is often used for diploids)

Homothallism: Mating compatibility between genetically identical individuals

Dioicy: Separate male and female haploid individuals

Monoecy: One diploid individual produces both gamete types

Heterothallism: Mating incompatibility between genetically identical individuals; clones with different sexual potential

Hermaphroditism: Having both sexual organs on the same individual; *synonym*: bisexual; co-sexual; monoecious

Dioecy: Separate male and female diploid individuals; *synonym:* gonochory†; unisexualΩ

FIGURE 1 A synthetic view of different possible reproductive modes, mating systems, and sexual systems for algae adapted with permission from Billiard et al. (2012). Terms and definitions are taken from Beukeboom and Perrin (2014), Billiard et al. (2012), Kaczmarska et al. (2013), Klekowski (1969), Krueger-Hadfield et al. (2024), and Olsen et al. (2021). *Autogamy refers to self-fertilization within the same flower in angiosperms; this is still distinct from monoicy or homothallism as gametes are produced from meiosis; **Geitonogamy refers to self-fertilization with gametes produced by different flowers on the same plant; † term used in animals; Ω Unisexual can sometimes by a synonym for parthenogenetic or uniparental reproduction. [Color figure can be viewed at wileyonlinelibrary.com] mating system refers specifically to meiotic sex and the relative rates of selfing and outcrossing. Finally, the "sexual system" is defined as the distribution of male and female functions (see also Barrett, 2002). Here, I used quotes, as homothallism and heterothallism do not strictly define male and female functions, for example, in diatoms (Kaczmarska et al., 2013) or in fungi (Billiard et al., 2012). However, homothallism and heterothallism do refer to the compatibility of different mating or cell types (e.g., + or −). Thus, they would fit under the umbrella term of the sexual system sensu lato. The sexual system is also influenced by the life cycle. If sex is determined in the haploid phase, then the haploid phase (often a gametophyte) would be considered monoicous or dioicous (Beukeboom & Perrin, 2014). If sex is determined in the diploid phase, then the diploid phase (often a sporophyte for plants and algae) would be considered monecious (or hermaphroditic) or dioecious. Monoicous and homothallic species can undergo intragametophytic selfing, selfing, and outcrossing. Dioicous, monoecious, hermaphroditic, and heterothallic species can only undergo selfing and outcrossing. Finally, dioecious species can only undergo outcrossing (see Figure 1).

Curiously, Fristch (1935) described the sporophytes in many macroalgae as "asexual individuals" and the gametophytes as the "haploid [phase] bearing gametes" or the "haploid individuals bearing the sex organs" (Fristch, 1935; p. 52). This does not accurately describe meiotic sex and the life cycle of many red, green, and brown macroalgae. Sex is not simply a synonym for fertilization or the phase in which "sex organs" are observed. The gametophytes produce gametes via mitosis. The zygote is formed by fertilization, and its fate depends on the type of macroalga (e.g., florideophyte carposporophyte development vs. germination into the sporophyte in brown algae). The resulting sporophyte (or tetrasporophyte in many red algae) is neither female nor male, but this does not make the sporophyte asexual. Meiosis and recombination—critical processes in meiotic sex—occur at the (tetra)sporophyte phase, producing haploid spores that will germinate into gametophytes. This terminology still occurs in the phycological literature and should not be confused with actual asexual reproduction through various vegetative or apomictic processes in the sporophyte phase.

CYANOBACTERIA

The cyanobacteria include representatives across all biomes, including extreme habitats (see Komárek & Johansen, 2015a, 2015b), and are responsible for a sizeable fraction of global photosynthesis (reviewed in Biller et al., 2014). Unlike all other algae, the Cyanobacteria are prokaryotes and do not undergo meiotic sex. This does not mean that bacteria do not possess mechanisms that are similar to meiosis. Transformation, as an example, is thought to be a possible precursor to eukaryotic meiosis (Berstein & Berstein, 2010). Cyanobacteria, like other prokaryotes, can take up DNA from the environment, often a conspecific bacterium, and that DNA becomes integrated into the DNA of the original host's cell in a form of genetic exchange. The Cyanobacterium *Synechococcus elongatus* is naturally competent and an emerging model for circadian rhythms that drive transformation (Taton et al., 2020). Viral transduction can allow gene transfer as well, such as shown in *Prochlorococcus*, leading to niche differentiation in bacterial lineages (Coleman et al., 2006). Cyanobacteria can also bud, undergo binary fission or thallus fragmentation, or form specialized structures (reviewed in Komárek & Johansen, 2015a, 2015b; Warren et al., 2019). Environmental sampling with molecular tools will be key to answering questions about cyanobacteria in natural environments, including the frequencies at which transformation, transduction, the production of dormant cells, or binary fission occur. Understanding the relative frequency of these process will shed light on how they affect standing genetic diversity within and among cyanobacterial "populations."

TSAR—ALVEOLATA

Dinoflagellates*

Dinoflagellates include heterotrophic, mixotrophic, and photosynthetic forms, ranging from species causing harmful algal blooms to invertebrate symbionts. Unlike in other unicellular algae, meiotic sex is thought to be much more widespread among the dinoflagellates (Graham et al., 2022). Dia et al. (2014) interpreted data on dinoflagellate population genetics, including the absence of multilocus linkage disequilibrium and high genotypic richness, as evidence for recombination in *Alexandrium minutum*. Recently, Lin et al. (2022) reported the upregulation of meiotic genes during bloom events, suggesting meiosis could also occur during blooms. Traditionally, meiosis has been thought to occur following encystment of the diploid zygote. Likewise, Figueroa et al. (2015) suggested that *A. minutum* may have a haploid life cycle but instead is biphasic due to patterns of planozygote division whereby encystment is skipped and planktonic divisions of the zygote occur. In the Symbiodiniaceae, gamete fusion and meiosis have yet to be demonstrated, but Shah et al. (2020) provided genomic evidence for meiotic sex based on transcriptomic data from the genera *Cladocopium*, *Breviolum*, *Durusdinium*, and *Symbiodinium*.

Depending on the taxon, gametes can be morphologically similar (isogamous) or distinct (anisogamous). Meiotic sex is described as homothallic (gametes produced from the same parental cell) or heterothallic (gametes produced from two different cells). Homothallism in dinoflagellates could erode genetic diversity, particularly if certain genotypes are selected during bloom events (see discussion in Dia et al., 2014). However, population sizes are thought to be so large that fusion of two gametes from the same parental cell may be rare. Few studies exist exploring the reproductive system in detail in dinoflagellates, and those that do exist rely on culture-based approaches (Dia et al., 2014). In coral, dinoflagellate clonality has been assessed by the presence of one allele per locus in DNA extracted from the host including the symbiont (Baums et al., 2014). Thornhill et al. (2017) further supported meiotic sex occurring despite vegetative mitotic divisions driving the symbiont biomass in a coral host. Based on the critical role dinoflagellates play in forming blooms and integral symbiotic relationships with ecosystem engineers (e.g., coral), it is critical to fill in missing gaps about the reproductive system in this unicellular algal lineage.

TSAR—RHIZARIA

Chlorarachniophytes

This group of algae is often amoeboid, with their ultrastructure clearly differentiating them from green algae and the euglenoids (Ichida et al., 2007). They are the only group of algae that are not observed in freshwater, with their distribution likely being strictly marine. They display amazing diversity in their life cycle (see figure 9.6 in Ichida et al., 2007). Grell (1990) made observations in which resting cells were formed and plasmodial cells remained fused with the resting cells, hinting at possible fertilization. Beutlich and Schnetter (1993) used measurements of DNA content and determined the life cycle of *Cryptochlora perforans* was haploid-diploid, in which both phases can have amoeboid and coccoid morphologies. Observations of the haploid and diploid phases were only possible using DNA staining methods, suggesting that molecular markers and single-cell genotyping techniques could help understand the relative importance of mitotic divisions (e.g., vegetative reproduction) and meiotic sex.

TSAR—STRAMENOPILA

The photosynthetic Stramenopiles were organized as in Graham et al. (2022). Certain groups for which no information could be located are not included below, including the Synchromophyceae, Aurearenophyceae, Phaeothamniophyceae, and Schizocladiophyceae.

Bacillariophyceae*

Unlike most algae, diatoms spend the majority of their life cycle in the diploid phase. Meiotic sex in diatoms is widely accepted, as it is the only mechanism by which cell-size reduction is reversed (Davidovich & Davidovich, 2022). Kaczmarska et al. (2013) wrote an excellent review on diatom terminology, and interested readers should consult this resource, as I will not recapitulate here. In addition to sexual auxosporulation, Sabbe et al. (2004) showed that reproduction can also occur via a process that would be akin to apomixis in plants, suggesting that there is a great deal of diversity and lability in the reproductive systems of diatoms. Most studies to date have been on laboratory-based crosses (Godhe et al., 2014) or clonal cultures (Evans et al., 2005; Rynearson & Armbrust, 2000). The latter have shown very high levels of genotypic richness, often viewed as a paradox (see discussion in Krueger-Hadfield et al., 2014). Moreover, Bulnakova et al. (2021) demonstrated mitotic recombination in a series of elegant experiments that might help explain fitness advantages during clonal competition in blooms.

Godhe et al. (2014) demonstrated that the centric diatom *Skeletonema marinoi* was homothallic and auxospores were formed from meiotic sex. It is unclear how centric diatoms mate in nature or what role homothallism plays in the partitioning of genetic diversity. In heterothallic diatoms, clones produce one gamete type, although there does appear to be flexibility for intraclonal reproduction (Kaczmarska et al., 2013). Ultimately, analyses of population genetics are required to explore the lability of diatom reproductive systems without reliance on laboratory-based cultivation to understand the eco-evolutionary consequences in natural populations.

Bolidophyceae

Ichinomiya et al. (2016) provided information on the global distribution of this group of picoplankton based on metabarcoding from the Tara Oceans expedition (https://fondationtaraocean.org/en/expedition/tara-oceans/), but little other data exist about their life cycle or prevailing reproductive mode.

Pelagophyceae

Pelagophytes can form large blooms, sometimes referred to as brown tides. Tang et al. (2019) observed that one species, *Aureoumbra anophagefferens*, had a resting stage in sediments. Ma et al. (2020) followed with experiments on the resting stage and observed it could revert back to cell divisions—akin to vegetative reproduction (Figure 1)—under certain culture conditions. As species in this group can form algal blooms, understanding their basic biology is of importance to investigations of how sexual versus vegetative reproduction structures populations and influences bloom dynamics.

Dictyochophyceae

Silicoflagellates can form blooms that have been associated with fish kills, but little is known about their life cycles. Henrickson et al. (1993) observed different cell types, ranging from skeleton-bearing to naked cells. However, the cell types did not differ in ploidy; thus, the authors concluded that meiotic sex did not occur (Henrickson et al., 1993). Genomic analyses could determine whether meiotic genes persist in silicoflagellate genomes and could be followed by other studies to determine if and how meiotic sex occurs and the frequency of sexual versus asexual reproductive modes.

Chrysophyceae

The Crysophytes are commonly observed in freshwater habitats and produce a resting stage referred to as a stomatocyst (Nicholls & Wujek, 2003). They are thought to spend the majority of the life cycle in the haploid phase. Mitotic divisions lead to the liberation of zoospores and would be analogous to vegetative reproduction. Recently, Kraus et al. (2019) observed evidence for meiotic or meiosis-related genes based on transcriptomic data, suggesting they are “secretly sexual.”

Synurophyceae

Synurophyceans produce stomatocysts like the Chrysophytes, and they too are assumed to be haploid. In a species of *Synura*, fertilization occurred between isogamous gametes and was heterothallic (Sandgren & Flanagin, 1986). There is little information about Synurophycean reproductive system variation, cyst formation, or the prevailing reproductive mode.

Eustigmatophyceae

These yellow-green algae are observed in freshwater or marine habitats. Meiotic sex has not been observed (Amaral et al., 2020; Santos, 1996). There are, thus, rather large gaps in our understanding of how these algae reproduce and the frequency of sexual versus asexual processes in natural populations.

Pinguiophyceae

Kawachi et al. (2002) described this new group of microscopic marine flagellates, but no information exists about their reproductive modes.

Phaeophyceae*

The brown macroalgae include species characterized by microscopic filamentous thalli to giant kelps. The brown algae exhibit incredible diversity of life cycles and variation in reproductive systems (see Bringloe et al., 2020; Heesch et al., 2021). Meiotic sex occurs across the brown algae, but there are multiple examples of vegetative reproduction (e.g., *Fucus* in the Baltic; Tatarenkov et al., 2005) and apomixis (e.g., parthenosporophytes in *Scytosiphon*; Hoshino & Kogame, 2019). Bringloe et al. (2020) located 72 papers published between 1984 and 2019 that provided information on the reproductive system of 37 species of brown algae—20 had diploid life cycles (e.g., fucoids), 13 exhibited a heteromorphic alternation with diploid dominance (e.g., kelps), and four had an "isomorphic" alternation (e.g., Dictyotales and Ectocarpales). Early work focused on the reproductive system of diploid *Fucus* spp. (Billard et al., 2010; Perrin et al., 2007) as well as haploid–diploid kelps (Billot et al., 2003; Robuchon et al., 2014), although most studies have focused on the diploid sporophyte (but see Oppliger et al., 2014). Far fewer studies have investigated the reproductive systems of haploid–diploid brown algae other than in *Ectocarpus* spp. (Couceiro et al., 2015) and *Dictyota dichotoma* (Steen et al., 2019; see also Krueger-Hadfield, Guillemin, et al., 2021). Nevertheless, the brown macroalgae are promising models for exploring transitions from monoicy to dioicy as well as from monoecy to dioecy (Heesch et al., 2021). Future work needs to assess the relative rates of sexual versus asexual reproduction across brown algae not only to understand population-level responses to a changing climate but also to test predictions about reproductive systems and life cycles (Otto & Marks, 1996).

Raphidophyceae*

Raphidophytes can form intense blooms that can cause adverse effects to water bodies, such as lakes. Apomictic and sexual cyst formation has been described for *Gonyostomum semen* (Cronberg, 2005;

Figueroa & Regenfors, 2006). Lebret et al. (2012) suggested that patterns of genetic diversity in phytoplankton, such as *G. semen*, could be closely related to their life cycle, highlighting the important role of and feedback between the life cycle and the reproductive mode. The relative frequencies of sexual versus asexual reproduction require more attention in the Raphidophytes.

Xanthophyceae

These yellow-green algae produce apomictic spores or cysts depending on conditions. Meiotic sex has only been described in *Tribonema*, *Botrydium*, and *Vaucheria* (Ott & Oldham-Ott, 2003). The life cycle is thought to be haploid with variation in isogamy and anisogamy. Species of *Vaucheria* can be monoicous or dioicous (as monoecious or dioecious, Ott & Hommersand, 1974). In Florida, several *Vaucheria* species were thought to overwinter as zygotes (Gallagher & Humm, 1981). Nevertheless, there is very little information on the relative frequency of sexual versus asexual reproduction in natural populations. Yet, monoicy and dioicy will have profound consequences on the distribution of genetic diversity in haploid species (see Krueger-Hadfield et al., 2024).

HAPTISTA

Haptophytes*

The haptophytes include species that play important roles in global biogeochemical cycles and can form blooms seen from outer space. Haploid and diploid cells are often morphologically distinct; in Gephyrocapsa huxleyi (*E. huxleyi)*, for example, the naked haploid cell is phenotypically and ecologically distinct from the coccolith-bearing diploid cell (Frada et al., 2008, but see Frada et al., 2017; Mordecai et al., 2017). Both haploid and diploid cells are capable of vegetative reproduction through mitotic divisions. However, there have been numerous questions raised about the amount of genotypic diversity in blooms when asexual processes should lead to many repeated genotypes (Iglesias-Rodriguez et al., 2006). Krueger-Hadfield et al. (2014) demonstrated multiple repeated genotypes when isolates from a single bloom event of *G. huxleyi* were genotyped. Previous work combined isolates from different geographic locations and years in which unique genotypes would be expected. Since many haptophytes are thought to be haploid–diploid, it is possible that selfing can occur if the two haploid cells share the same diploid parental cell (analogous to intra- or intergametophytic selfing in macroalgae, or homothallism in diatoms or dinoflagellates; see also Figure 1). Understanding the relative rates of sexual versus asexual reproduction is critical for understanding how genetic diversity is partitioned in these algae. Moreover, von Dassow et al. (2015) showed that *G. huxleyi* haploid cells can lose flagella in oligotrophic waters, posing questions as to whether meiotic sex can be lost.

CRYPTISTA

Cryptomonads

Cryptomonads are small flagellates that are important in natural systems and aquaculture (Graham et al., 2022). Vegetative reproduction via mitotic divisions is thought to be the only mechanism of reproduction. Yet, Kugrens and Lee (1988) observed fusing gametes in a *Cryptomonas* sp. using electron microscopy. The life cycle is poorly understood but could be haploid–diploid, in which haploid and diploid cells may have even been classified as different taxa (Hoef-Emden & Melkonian, 2003). Kugrens and Lee (1988) posed a handful of questions at the end of their paper that appear to remain unresolved, such as when meiosis occurs, the fate of meiotic products, and the environmental conditions that induce fertilization. Novorino (2012) reviewed cryptomonad taxonomy and raised similar questions about the alternation of different cell types as well as the frequency of meiotic sex. Several cryptomonad genomes have been sequenced and published (Lane et al., 2005), and searching for homologs of meiotic genes is an important next step.

ARCHAEPLASTIDA—GLAUCOPHYTA

Glaucophytes

The Glaucophytes share a common ancestor with the red algae and the Chloroplastida (including green algae and land plants) and form a monophyletic group (Adl et al., 2012). Jackson et al. (2015) provided a review about this lineage of archaeplastid algae and noted that there were no reports of meiotic sex, whereas apomixis occurred through the production of motile zoospores or non-motile autospores. Indeed, few morphological and molecular studies exist, but these data are critical not only for describing the life cycle of the Glaucophytes but also for understanding eukaryotic and archaeplastid evolution more thoroughly. More recent molecular data have uncovered protein families important in fusion during fertilization (Speijer et al., 2015). Although this is not conclusive evidence of meiotic sex, Speijer et al. (2015) conclude that even limited recombination can be considered a form of sex.

ARCHAEPLASTIDA—RHODOPHYTA

The Rhodophyta are organized in this section as in Graham et al. (2022). Certain groups for which no information could be located are not included below, including the Rhodellophyceae. Hansen et al. (2019) observed two distinct growth phases in a new species of Stylonematophyceae, but no information on the life cycle or reproductive system for this species or group is available.

Cyanidiophyceae

Until the work of Hirooka et al. (2022), meiotic sex was unknown in this group of unicellular red algae. The genus *Galdieria* exhibits an alternation of a cell-walled diploid and cell wall-less haploid phases, both of which are capable of vegetative reproduction through mitotic divisions. The diploid phase is what appears to dominate in natural populations and gametes are isogamous (Hirooka et al., 2022). The alternation between a diploid and a haploid phase may be ancestral prior to the divergence of other red algae and the lineage that includes the green algae and plants. The relative frequencies of haploid and diploid cells as well as sexual versus asexual reproduction are unknown.

Porphyridiophyceae

Bhattacharya et al. (2013) have observed genetic evidence of meiotic machinery in the full genome sequence of *Porphyridium purpureum*, suggesting the occurrence of meiotic sex. The life cycle and relative contributions of sexual versus asexual reproduction are not known in natural populations.

Compsopogonophyceae

The two monospecific genera, *Compsopogon* and *Boldia*, are thought to reproduce solely by the production of monospores (i.e., apomixis). The ploidy for both taxa is unknown. As cryptic meiotic sex has been observed in other Rhodophyte taxa, empirical evidence of the reproductive mode is necessary in these two algal genera (see also Krueger-Hadfield et al., 2024).

Bangiophyceae*

The Bangiophytes undergo a biphasic alternation between a gametophytic blade and a filamentous sporophyte (called the conchocelis). Drew (1949) demonstrated the connection between the two phases in *Porphyra*, revolutionizing nori aquaculture. Bangiophytes can undergo both apomixis and meiotic sex. Archespores are produced in specialized sporangia in *Bangia* and *Neopyropia* as well as spores on the edges of *Porphyra* blades (Graham et al., 2022). Much of the work on these algae has focused on taxonomy (Brodie et al., 2008), with far fewer studies investigating the structure of population genetics. Blouin and Brawley (2012) concluded that there was evidence for apomixis based on the resampling of genotypes using amplified fragment length polymorphisms (AFLPs). Eriksen et al. (2016) and Cao et al. (2018) also interpreted their results as evidence for apomixis, but both studies were based on a handful of markers only. The former used three microsatellite loci derived from expressed sequence tags (ESTs) and, therefore, the loci were unlikely to be neutral. The latter used only five single nucleotide polymorphisms (SNPs) derived from an RNA-seq dataset. The resampling of the same multilocus genotype is likely due to poor polymorphism with such a small set of molecular markers (see Arnaud-Haond et al., 2007) as well as working with a haploid phase in which only one allele will be observed per locus (see, as an example in a Florideophyte red alga, Lees et al., 2018). Yet, Varela-Álvarez et al. (2018, 2022) described polyploidy in the supposedly haploid gametophytic blade of *Porphyra* spp. in the North Atlantic (although they referred to gametophytes as monoecious and dioecious). This raises questions about the ploidy of each phase and across taxa. Angiosperms and ferns are almost all polyploid (Soltis et al., 2015), but the role of polyploidy and reproductive system variation (see discussion in Kearney, 2005) is still poorly understood in algae. Genotyping the conchocelis and gametophytic phases of the Bangiophytes is critical for accurately assessing the relative rates of sexual and asexual processes as well as employing methods (e.g., flow cytometry, Varela-Álvarez et al., 2018) to determine ploidy levels as well.

Florideophyceae*

Most Florideophytes undergo a “triphasic” alternation of the gametophyte, the carposporophyte, and the tetrasporophyte. Cytologically, the life cycle is triphasic, but genetically and ecologically, the life cycle is biphasic as the carposporophyte remains on the maternal gametophytic thallus. Maggs (1988) highlighted the spectacular diversity in red algal reproduction, and this has been shown based on a survey of studies using population genetic tools (Krueger-Hadfield, Guillemin, et al., 2021). Krueger-Hadfield et al. (2024) recently drew attention to the lineages of freshwater red algae, and specifically the Batrachospermales, in which there are switches between sister taxa in monoicy and dioicy that are representative of that described in brown algae (Heesch et al., 2021).

Data on population genetics in *Batrachospermum gelatinosum* are forthcoming (see Crowell et al., 2024).

Patterns of geographic parthenogenesis via apomixis have been shown in Florideophytes in both gametophytes (e.g., *Mastocarpus* spp., Fierst et al., 2010; Krueger-Hadfield, Kübler, & Dudgeon, 2013) and tetrasporophytes (Gabrielson et al., 2002). Fragmentation is also common in many taxa, including economically and ecologically important species, such as those in the Gracilariales (Guillemin et al., 2008; Krueger-Hadfield et al., 2016). Sexual reproduction has been demonstrated through both direct (i.e., paternity analyses) and indirect approaches (i.e., population genetic summary statistics) in *Gracilaria gracilis* (Engel et al., 1999, 2004) and *Chondrus crispus* (Krueger-Hadfield et al., 2011, 2015; Krueger-Hadfield, Roze, et al., 2013). Gamete unions in *G. gracilis* were allogamous; in other words, they occurred between unrelated gametophytes (outcrossing in Figure 1). By contrast, in the same intertidal zone and in *C. crispus*, gamete unions were mostly between sibling gametophytes (selfing in Figure 1; more accurately endogamous and intergametophytic selfing). Recently, Heiser et al. (2023) observed evidence for both vegetative reproduction and selfing in a *Plocamium* sp. in Antarctica. Unlike in the gametophyte-dominated *C. crispus*, the *Plocamium* sp. sites were dominated by tetrasporophytes. The contrast between the phase dominance in *C. crispus* and *Plocamium* sp. highlights some of the inherent challenges to working on haploid–diploid algae and using tools of population genetics (see discussion in Krueger-Hadfield & Hoban, 2016). Unfortunately, there are too few datasets (see review in Krueger-Hadfield, Guillemin, et al., 2021, and more recent work by Williams et al., 2024) in which these tools have been used to explore the tremendous diversity of reproductive modes described by direct observation by earlier authors (Hawkes, 1990; Maggs, 1988). Thus, at present, we cannot conclude whether *G. gracilis* and *C. crispus* represent end points on a spectrum of reproductive system diversity.

ARCHAEPLASTIDA—CHLOROPHYTA

The Chlorophytes are organized in this section as in Graham et al. (2022). The Prasinophytes are included under this subheading, subsuming a great deal of diversity (see Graham et al., 2022). Certain groups for which no information could be located are not included below, including the Pedinophyceae and the Chlorodendrophyceae.

Prasinophytes

Prasinophytes are known to produce resting cysts, also observed in many other unicellular algae. The first evidence for meiotic sex was provided by Suda et al. (1989) in *Nephroselmis olivaceae*, in which morphologically similar gametes were produced and thought to be heterothallic. Upon fertilization, the zygote underwent meiosis, producing four daughter cells. Suda et al. (2006) subsequently compared vegetative cell division and sexual cell fusion. The diploid phase for Prasinophytes is thought to be the zygote with the rest of the life cycle spent in the haploid phase (Niklas & Kutschera, 2009).

Trebouxiophyceae

This group of algae live mainly in terrestrial habitats and includes many unicellular taxa as well as more complex colonial and filamentous forms. Fuckikova et al. (2015) compiled all indirect, direct, and genetic/genomic evidence of meiotic sex in this group. The life cycle is presumably haploid. Very little work exists documenting the variation in life cycle or reproductive system in natural populations.

Ulvophyceae*

This group of green algae attracted the attention of Otto and Marks (1996) as a group of eukaryotes with which to test the hypothesis that the reproductive system is correlated with the life cycle. Variation in the life cycle includes diploids (e.g., *Caulerpa*, *Avrainvillea*), "isomorphic" alternations between gametophytes and sporophytes (e.g., *Ulva*), and the alternations between a haploid phase and a unicellular diploid zygote called the codiolum phase (i.e., in the Ulotrichales). Most data on green algae to date are based on direct observations in which all reproductive modes—vegetative reproduction, apomixis, and meiotic sex—are known to occur.

Vegetative reproduction through fragmentation or patch expansion of holdfasts is known in many Ulvophytes, including *Caulerpa taxifolia* (Phillips, 2009), *Cladophoropsis membrancacea* (van der Strate et al., 2002), and, more recently, *Avrainvillea lacerata* (Thornton et al., 2024). Many taxa are also capable of producing gametes or spores through apomixis, which has been shown using data on population genetics in *Ulva* sp. (as *Enteromorpha linza*, Innes & Yarish, 1984). In *C. membranacea*, as vegetative growth filled in space, vegetative reproduction also led to the spatial distribution of repeated genotypes, and due to these asexual processes, intergametophytic selfing and inbreeding are likely, although all mats were composed of multiple genotypes (van der Strate et al., 2002). Many taxa are also capable of producing gametes or spores through apomixis, which has been shown in *Ulva* sp. (as *Enteromorpha linza*, Innes & Yarish, 1984). In *Ulva* sp., the apomictic thalli are diploid and likely bypass meiosis to produce zoospores (Ichihara et al., 2019). Few other population genetic studies exist in which both gametophytes and sporophytes have been studied in haploid–diploid Ulvophytes. Arnaud-Haond et al. (2017) observed evidence of higher genotypic diversity in the native range of the diploid *Caulerpa taxifolia* in Australia as compared to the Mediterranean Sea into which it has been introduced. Yet, the relative frequency of asexual versus sexual reproduction in many *Caulerpa* populations remains largely unknown. This is broadly a problem across all Ulvophyte algae despite the elapse of almost 30 years since Otto and Marks (1996) highlighted the role of these algae for understanding variation in reproductive systems.

Chlorophyceae

Chlorophytes include a remarkable diversity of unicellular and filamentous taxa (Graham et al., 2022). In addition to mitotic cell divisions or fragmentation (depending on the type of alga as a form of vegetative reproduction), chlorophytes also produce zoospores, aplanospores, and autospores. Chlorophytes are thought to be haploid, and meiotic sex has been described, for example, in *Chlamydomonas reinhardtii* (see summary in Graham et al., 2022). Different species can be homothallic or heterothallic. However, there are few studies that have investigated natural populations to determine the relative amounts of sexual versus asexual reproduction. One study, Brown et al. (2016), used the diversity in the internal transcriber spacer rRNA region 2 (ITS2) in a bloom of a snow alga to determine that the bloom was dominated by vegetative reproduction (i.e., mitotic cell divisions). However, the ITS2 rRNA region cannot be used to determine whether a form of asexual reproduction is occurring, as many individual cells within a bloom will share the same ribotype even if meiotic sex occurs during blooms. This barcode gene is not dissimilar to the CMM gene used in the haptophyte *E. huxleyi* bloom by Krueger-Hadfield et al. (2014), in which there were unique genotypes and repeated genotypes that shared the same CMM. Thus, polymorphic markers and appropriate sampling tools are needed to resolve these questions in the Chlorophytes.

ARCHAEPLASTIDA—STREPTOPHYTA

The Streptophyte algae are composed of several important lineages. Meiotic sex is not known in the Mesostigmatophyceae, Chlorokybophyceae, and Klebsormidiophyceae (Graham et al., 2022).

Zygnematophyceae

Species can be unicellular and filamentous species with no flagellated gametes. Mating occurs with the physical pairing of filaments or single cells in a process known as conjugation (see Graham et al., 2022). Vegetative reproduction occurs through fragmentation in filamentous forms or the production of spores from unpaired cells. The relative frequency of meiotic sex, or conjugation, in natural populations is unknown as sexual stages are unknown for many taxa (see review by Coesel & Krienitz, 2008 for more information and relevant citations of mating experiments).

Coleochaetophyceae

Species are periphytic, growing on both living and nonliving substrates. Zoospores are produced through apomixis and can rapidly increase in population size. Meiotic sex occurs with unflagellated egg cells and flagellated sperm cells. In some species, eggs are not released, similar to in land plants (Graham et al., 2022); however, the relative frequencies of different reproductive modes in nature are poorly described.

Charophyceae*

Named for the genus *Chara*, these species are ecologically important in lakes and streams, and a few species exist in brackish habitats. Vegetative reproduction can occur from rhizoids and bulbils (Graham et al., 2022). Charophytes produce visible gametangia that make sperm or eggs. Following fertilization, the zygote is a thick-walled cell that may be resistant to environmental stress. Meiosis is thought to occur in the zygote, and only one meiotic product survives. Thus, adult Charophytes are thought to be haploid and can be either monoicous or dioicous. (Note: This is often written as monoecy and dioecy when describing the Charophytes, Proctor, 1971a). Proctor (1971b) described crosses between various populations of *Chara* and observed patterns of reproductive isolation, suggesting these taxa are not cosmopolitan. Schaible et al. (2011) observed two distinct populations, one cluster composed of sexual *Chara* (including males and females), and the other composed of apomictic females. Tests of variation in the reproductive system in a haploid taxon would shed light on patterns observed in other macroalgae. Yet, Haig (2010) questioned how much we really know about Charophyte life cycles and advocated for a reappraisal of these taxa.

DISCOBA

Euglenophyceae

The Euglenoids are single-celled flagellates. Meiotic sex is thought to occur rarely, if at all (e.g., see Graham et al., 2022). Indeed, Rosowski (2003) concluded that vegetative reproduction through mitotic cell divisions is the only mode of reproduction. Moestrup and Enveldson (2019) recently drew attention to the overlooked and forgotten work of Biecheler (1937), in which the fusion and formation of cysts were observed in a species of *Euglena*. As meiotic sex has been observed in other Euglenoids that are human parasites, it is plausible that it also occurs in photosynthetic species. Speijer et al. (2015) showed that homologs of proteins involved in fusion are present in the Euglenozoa, but this may refer to human parasitic taxa, as there is no specification as to the types of Euglenoids in their figure. Since meiotic sex is presumed to be ancestral in all eukaryotes and putative genetic machinery for meiotic sex has been observed in the Euglenoids, it follows that meiotic would also occur in the photosynthetic lineages. With the recent publication of the *Euglena gracilis* genome (Ebenezer et al., 2019), it will be possible to search for meiotic machinery accompanied by further study to explore meiotic sex broadly across this group, including the photosynthetic taxa.

FUTURE DIRECTIONS

Our understanding of algal reproductive systems is critical for predicting algal evolution. This knowledge gap is all the more critical because we are living in a period of rapid environmental change that will profoundly influence algal evolutionary ecology. This perspective is part of a larger set of papers published in 2024 that addresses different aspects of algal biology in light of climate change (Coleman, 2024). Here, the general dearth of information about reproductive modes broadly across algae is obvious. We need to quantitatively assess the prevailing reproductive mode, which directly affects a population's ability to respond to environmental change through phenotypic evolution (Orive et al., 2017). However, most eukaryotic taxa, including many of the unicellular algae described in this perspective, cannot be cultured in the lab (del Campo et al., 2014). Tools developed in multicellular animals and angiosperms—or even the macroalgae for which data on population genetics exist—are often not tractable in microscopic organisms where generation times are short, population sizes are large, and DNA extraction from single cells (i.e., unique individuals) is difficult. When we can grow microalgae in the laboratory, we impose artificial selection that leads to limited and often unrepresentative views of natural diversity (see discussion in Krueger-Hadfield et al., 2014). As such, the characterization of microalgal reproductive modes cannot be predicted by the observation of organisms themselves, especially for the unculturable majority. Therefore, characterizing microalgal reproductive modes in natural populations, and this is true for the majority of macroalgae as well, is only possible through approaches using population genetics (Tibayrenc, 1997). Yet, it is curious that in some taxa, such as in dinoflagellates, the cryptic nature of sex is accepted despite the similarity between gametes and vegetative cells, while in other lineages, such as euglenoids, it is assumed to be absent even though it has been observed in related taxa of the same lineage. In other eukaryotes, such as *Candida* species (Sherwood & Bennett, 2009), parasexual processes may occur with limited recombination. Speijer et al. (2015) concluded that this could be considered a form of sex. The remarkable plasticity in the fungi (Sherwood & Bennett, 2009) suggests that we may observe similar diversity in other unicellular taxa, such as unicellular algae, that do not fit our conventional views of meiotic sex.

It is an exciting time to combine ecology and genetics in phycology. The boundaries of population genetics are constantly being pushed (see as an example, Stoeckel, Arnaud-Haond, & Krueger-Hadfield, 2021). More and more algal genomes are rapidly emerging through projects like Phaeoexplorer (Denoeud et al., 2024; https://phaeoexplorer.sb-roscoff.fr/home/) or Rhodoexplorer (Lipinska et al., 2023; https://rhodoexplorer.sb-roscoff.fr/home/). Additionally, new tools with which to distinguish phases based on sex determination systems are available (e.g., Ahmed et al., 2014; Krueger-Hadfield, Flanagan, et al., 2021; see also Coelho & Umen, 2021). Finally, appropriate methods that facilitate the characterization of asexual (i.e., clonal) lineages are available (e.g., HiPlex SNP genotyping, Delord et al., 2018) that do not require the same laborious development as microsatellite loci. This will rapidly expand the capacity with which to explore patterns in populations genetics in taxa for which molecular markers do not yet exist. We are at an opportune time to apply something Haig (2010) wrote about Charophyte life cycles: "Common knowledge is sometimes collective misinformation, and it is worthwhile to occasionally subject what everybody knows to critical reappraisal" (p. 861).

AUTHOR CONTRIBUTIONS

Stacy A. Krueger-Hadfield: Conceptualization (lead); data curation (lead); funding acquisition (lead); writing – original draft (lead); writing – review and editing (lead).

ACKNOWLEDGMENTS

I dedicate this perspective to Myriam Valero—one of my PhD advisors—for all her insights and guidance for nearly two decades. I thank Mel Coleman for the invitation, encouragement, and particularly the patience for this perspective. I appreciate feedback on earlier drafts of this manuscript from Richard Snyder, Karolina Fučíková, and another anonymous reviewer. Finally, I acknowledge the National Science Foundation (NSF) CAREER Award (DEB-2141971) and an EAGER (DEB-2113745) award for support.

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REFERENCES

Aanen, D., Beekman, M., & Kokko, H. (2016). Weird sex: The underappreciated diversity of sexual reproduction. *Philosophical Transactions of the Royal Society B*, *371*, 20160262.

Adl, S. M., Simpson, A. G. B., Lane, C. E., Lukeš, J., Bass, D., Bowser, S. S., Brown, M. W., Burki, F., Dunthorn, M., Hampl, V., Heiss, A., Hoppenrath, M., Lara, E., le Gall, L., Lynn, D. H., McManus, H., Mitchell, E. A., Mozley-Stanridge, S. E., Parfrey, L. W., … Spiegel, F. W. (2012). The revised classification of eukaryotes. *Journal of Eukaryotic Microbiology*, *59*, 429–493.

Ahmed, S., Cock, J. M., Pessia, E., Luthringer, R., Cormier, A., Robuchon, M., Sterck, L., Peters, A. F., Dittami, S. M., Corre, E., Valero, M., Aury, J. M., Roze, D., van de Peer, Y., Bothwell, J., Marais, G. A. B., & Coelho, S. M. (2014). A haploid system of sex determination in the brown alga *Ectocarpus* sp. *Current Biology*, *8*, 1945–1957.

Albecker, M. A., Wilkins, L. G. E., Krueger-Hadfield, S. A., Bashevkin, S. M., Hahn, M. W., Hare, M. P., Kindsvater, H. K., Sewell, M. A., Lotterhos, K. E., & Reitzel, A. M. (2021). Does a complex life cycle affect adaptation to environmental change? Genome-informed insights for characterizing selection across complex life cycle? *Proceedings of the Royal Society B*, *288*, 20212122.

Amaral, R., Fawley, K. P., Němcová, Y., Ševčíková, T., Lukešová, A., Fawley, M. W., Santos, L. M. A., & Eliáš, M. (2020). Toward modern classification of Eustigmatophytes, including the description of Neomonodaceae fam. nov. and three new genera. *Journal of Phycology*, *56*, 630–648.

Arnaud-Haond, S., Aires, T., Candeias, R., Teixeira, S. J. L., Duarte, C. M., Valero, M., & Serrão, E. A. (2017). Entangled fates of holobiont genomes during invasion: Nested bacterial and host diversities in *Caulerpa taxifolia*. *Molecular Ecology*, *26*, 2379–2391.

Arnaud-Haond, S., Duarte, C. M., Alberto, F., & Serrao, E. A. (2007). Standardizing methods to address clonality in population studies. *Molecular Ecology*, *16*, 5115–5139.

Barrett, S. C. H. (2002). Evolution of sex the evolution of plant sexual diversity. *Nature Reviews Genetics*, *3*, 274–284.

Barrett, S. C. H. (2011). Why reproductive systems matter for the invasion biology of plants. In D. M. Richardson (Ed.), *Fifty years of invasion ecology: The legacy of Charles Elton* (pp. 195–210). Wiley.

Barrett, S. C. H. (2014). Evolution of mating systems: Outcrossing versus selfing. In J. Losos (Ed.), *The Princeton guide to evolution* (pp. 356–362). Princeton University Press.

Baums, I. B., Devlin-Durante, M. K., & Lajeunesse, T. C. (2014). New insights into the dynamics between reef corals and their associated dinoflagellate endosymbionts from population genetic studies. *Molecular Ecology*, *23*, 4203–4215.

Bell, G. (1982). *The masterpiece of nature: The evolution and genetics of sexuality* (635 pp.). University of California Press.

Bell, G. (1994). The comparative biology of the alternation of generations. In M. Kirpatrick (Ed.), *Lectures on mathematics in life sciences: The evolution of haplo-diploid life cycles* (pp. 1–26). American Mathematical Society.

Berstein, H., & Berstein, C. (2010). Evolutoinary origins of recombination during meiosis. *Bioscience*, *60*, 498–505.

Beukeboom, L., & Perrin, N. (2014). *The evolution of sex determination* (pp. 222). Oxford University Press.

Beutlich, A., & Schnetter, R. (1993). The life cycle of *Cryptochlora perforans* (Chlorarachniophyta). *Botanica Acta*, *106*, 441–447.

Bhattacharya, D., Price, D., Chan, C., Qiu, H., Rose, N., Ball, S., Weber, A. P. M., Arias, M. C., Henrissat, B., Coutinho, P. M., Krishnan, A., Zäuner, S., Morath, S., Hilliou, F., Egizi, A., Perrineau, M.-M., & Yoon, H. S. (2013). Genome of the red alga *Porphyridium purpureum*. *Nature Communications*, *4*, 1941.

Biecheler, B. (1937). On the existence of copulation in a green euglenoid and the global conditions that determine copulation. *Proceedings of the Sciences of the Biological Society*, *124*, 1264–1266.

Billard, E., Serrão, E., Pearson, G., Destombe, C., & Valero, M. (2010). *Fucus vesiculosus* and *spiralis* species complex: A nested model of local adaptation at shore level. *Marine Ecology Progress Series*, *405*, 163–174.

Biller, S. J., Berube, P. M., Lindell, D., & Chisholm, S. W. (2014). *Prochlorococcus*: The structure and function of collective diversity. *Nature Reviews Microbiology*, *13*, 13–27.

Billiard, S., López-Vilaviencio, M., Hood, M. E., & Giraud, T. (2012). Sex, outcrossing and mating types: Unsolved questions in fungi and beyond. *Journal of Evolutionary Biology*, *25*, 1020–1038.

Billot, C., Engel, C., Rousvoal, S., Kloareg, B., & Valero, M. (2003). Current patterns, habitat discontinuities and population genetic structure: The case of the kelp *Laminaria digitata* in the English Channel. *Marine Ecology Progress Services*, *253*, 111–121.

Blouin, N. A., & Brawley, S. H. (2012). An AFLP-based test of clonality in widespread, putatively asexual populations of Porphyra umbilicalis (Rhodophyta) in the Northwest Atlantic with an in silico analysis for bacterial contamination. *Marine Biology*, *159*, 2723–2729.

Bonner, J. T. (1965). *Size and cycle: An essay on the structure of biology*. Princeton University Press.

Bringloe, T. T., Starko, S., Wade, R. M., Vieira, C., Kawai, H., de Clerck, O., Cock, J. M., Coelho, S. M., Destombe, C., Valero, M., Neiva, J., Pearson, G. A., Faugeron, S., Serrão, E. A., & Verbruggen, H. (2020). Phylogeny and evolution of the brown algae. *Critical Reviews in Plant Sciences*, *39*, 281–321.

Brodie, J., Mols Mortensen, A., Ramirez, M. E., Russell, S., & Rinkel, B. (2008). Making the links: Towards a global taxonomy for the red algal genus *Porphyra* (Bangiales, Rhodophyta). In M. A. Borowitzka, A. T. Critchley, S. Kraan, A. Peters, K. Sjøtun, & M. Notoya (Eds.), *Nineteenth international seaweed symposium. Developments in applied phycology* (Vol. 2, pp. 489–499). Springer.

Brown, S. P., Ungerer, M. C., & Jumpponen, A. (2016). A community of clones: Snow algae are diverse communities of spatially structured clones. *International Journal of Plant Sciences*, *177*, 432–439.

Bulnakova, P., Sekulic, M., Jallet, D., Nef, C., van Oosterhout, C., Delmont, T. O., Vercauteren, I., Osuna-Cruz, C. M., Vancaester, E., Mock, T., Sabbe, K., Daboussi, F., Bowler, C., Vyverman, W., Vandepoele, K., & De Veylder, L. (2021). Mitotic recombination between homologous chromosomes drives genomic diversity in diatoms. *Current Biology*, *31*, 1–12.

Burki, F., Roger, A. J., Brown, M. W., & Simpson, A. G. B. (2020). The new tree of eukaryotes. *Trends in Ecology & Evolution*, *35*, 43–55.

Cao, Y., Green-Gavieldis, L., Eriksen, R. L., & Klein, A. S. (2018). A pilot study of genetic structure of *Porphyra umbilicalis* Kützing in the Gulf of Maine using SNP marker from RNA-seq. *Journal of Applied Phycology*, *31*, 1493–1503.

Coelho, S. M., & Umen, J. (2021). Switching it up: Algal insights into sexual transitions. *Plant Reproduction*, *34*, 287–296.

Coesel, P. F. M., & Krienitz, L. (2008). Diversity and geographic distribution of desmids and other coccoid green algae. *Biodiversity and Conservation*, *17*, 381–392.

Coleman, M. A. (2024). Algae in the Anthropocene: Managing, conserving, and utilizing algae in an era of rapid environmental change. *Journal of Phycology*, *60*, 1–3.

Coleman, M. L., Sullivan, M. B., Martiny, A. C., Steglich, C., Barry, K., Delong, E. F., & Chisholm, S. W. (2006). Genomic islands and the ecology and evolution of *Prochlorococcus*. *Science*, *311*, 1768–1770.

Couceiro, L., le Gac, M., Hunsperger, H. M., Mauger, S., Destombe, C., Cock, J. M., Ahmed, S., Coelho, S. M., Valero, M., & Peters, A. F. (2015). Evolution and maintenance of haploid-diploid life cycles in natural populations: The case of the marine brown alga *Ectocarpus*. *Evolution*, *69*, 1808–1822.

Cronberg, G. (2005). The life cycle of *Gonyostomum semen* (Raphidophyceae). *Phycologia*, *44*, 285–293.

Crowell, R. M., Shainker-Connelly, S. J., Vis, M. L., & Krueger-Hadfield, S. A. (2024). Microsatellite development in the freshwater red alga *Batrachospermum gelatinosum* (Batrachospermales, Rhodophyta). *Cryptogamie Algologie*, *45*, 5. https://doi.org/10.5252/cryptogamie-algologie2024v45a5

Davidovich, N., & Davidovich, O. (2022). Diatoms with studied sexual reproduction. *Fottea*, *22*, 292–296.

de Meeûs, T., Prugnolle, F., & Agnew, P. (2007). Asexual reproduction: Genetic and evolutionary aspects. *Cellular and Molecular Life Sciences*, *64*, 1355–1372.

de Silva, V. S., & Machado, C. R. (2022). Sex in protists: A new perspective on the reproduction mechanisms in trypanosomatids. *Genetics and Molecular Biology*, *45*, e2022065.

del Campo, J., Sieracki, M. E., Molestina, R., Keeling, P., Massana, R., & Ruiz-Trillo, I. (2014). The others: Our biased perspective of eukaryotic genomes. *Trends in Ecology & Evolution*, *29*, 252–259.

Delord, C., Lassalle, G., Oger, A., Barloy, D., Coutellec, M. A., Delcamp, A., Evanno, G., Genthon, C., Guichoux, E., le Bail, P. Y., le Quilliec, P., Longin, G., Lorvelec, O., Massot, M., Reveillac, E., Rinaldo, R., Roussel, J. M., Vigouroux, R., Launey, S., & Petit, E. J. (2018). A cost-and-time effective procedure to develop SNP markers for multiple species: A support for community genetics. *Methods in Ecology and Evolution*, *9*, 1959–1974.

Denoeud, F., Godfroy, O., Cruaud, C., Heesch, S., Nehr, Z., Tadrent, N., Couloux, A., Brillet-Guéguen, L., Delage, L., Mckeown, D., Motomura, T., Sussfeld, D., Fan, X., Mazéas, L., Terrapon, N., Barrera-Redondo, J., Petroll, R., Reynes, L., Choi, S.-W., … Cock, J. M. (2024). *Evolutionary genomics of the emergence of brown algae as key components of coastal ecosystems*. *bioRxiv*. https://doi.org/10.1101/2024.02.19.579948

Dia, A., Guillou, L., Mauger, S., Bigeard, E., Marie, D., Valero, M., & Destombe, C. (2014). Spatiotemporal changes in the genetic diversity of harmful algal blooms caused by the toxic dinoflagellate *Alexandrium minutum*. *Molecular Ecology*, *23*, 549–560.

Drew, K. (1949). Conchocelis-Phase in the Life-History of *Porphyra umbilicalis* (L.) Kütz. *Nature*, *164*, 748–749. https://doi.org/10.1038/164748a0

Dring, M. J. (2003). *The biology of marine plants*. Cambridge University Press.

Duminil, J., Fineschi, S., Hampe, A., Hampe, A., Jordano, P., Salvini, D., Vendramin, G. G., & Petit, R. J. (2007). Can population genetic structure be predicted from life-history traits? *American Naturalist*, *169*, 662–672.

Ebenezer, T. E., Zoltner, M., Burrell, A., Nenarokova, A., Novák Vanclová, A. M. G., Prasad, B., Soukal, P., Santana-Molina, C., O'Neill, E., Nankissoor, N. N., Vadakedath, N., Daiker, V., Obado, S., Silva-Pereira, S., Jackson, A. P., Devos, D. P., Lukeš, J., Lebert, M., Vaughan, S., … Field, M. C. (2019). Transcriptome, proteome and draft genome of *Euglena gracilis*. *BMC Biology*, *17*, 11.

Ellegren, H., & Galtier, N. (2016). Determinants of genetic diversity. *Nature Reviews Genetics*, *17*, 422–433.

Engel, C. R., Destombe, C., & Valero, M. (2004). Mating system and gene flow in the red seaweed *Gracilaria gracilis*: Effect of haploid–diploid life history and intertidal rocky shore landscape on fine-scale genetic structure. *Heredity*, *92*, 289–298.

Engel, C. R., Wattier, R., Destombe, C., & Valero, M. (1999). Performance of non-motile male gametes in the sea: Analysis of paternity and fertilization success in a natural population of a red seaweed, *Gracilaria gracilis*. *Proceedings of the Royal Society B*, *266*, 1879–1886.

Eriksen, R. L., Green, L. A., & Klein, A. S. (2016). Genetic variation within and among asexual populations of *Porphyra umbilicalis* Kützing (Bangiales, Rhodophyta) in the Gulf of marine, USA. *Botanica Marina*, *59*, 1–12.

Evans, K. M., Kühn, S. F., & Hayes, P. K. (2005). High levels of genetic diversity and low levels of genetic differentiation in North Sea *Pseudo-nitzchia pungens* (Bacillariophyceae) populations. *Journal of Phycology*, *41*, 506–514.

Fierst, J., Kübler, J. E., & Dudgeon, S. (2010). Spatial distribution and reproductive phenology of sexual and asexual *Mastocarpus papillatus* (Rhodophyta). *Phycologia*, *49*, 274–282.

Figueroa, R. I., Dapena, C., Bravo, I., & Cuadrado, A. (2015). The hidden sexuality of *Alexandrium Minutum*: An example of overlooked sex in dinoflagellates. *PLoS ONE*, *10*, e0142667.

Figueroa, R. I., & Regenfors, K. (2006). Life cycle and sexuality of the freshwater raphidophyte *Gonyostomum semen* (Raphidophyceae). *Journal of Phycology*, *42*, 859–871.

Frada, M., Probert, I., Allen, M. J., Wilson, W. H., & de Vargas, C. (2008). The “Cheshire cat” espace strategy of the coccolithophore *Emiliania huxleyi* in response to viral infection. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 15944–15949.

Frada, M. J., Rosenwasser, S., Ben-Dor, S., Shemi, A., Sabanay, H., & Vardi, A. (2017). Morphological switch to a resistant subpopulation in response to viral infection in the bloom-forming coccolithophore *Emiliania huxleyi*. *PLoS Pathogens*, *13*, e1006775.

Fristch, F. E. (1935). *The structure and reproduction of the algae* (Vol. 1). Cambridge University Press.

Fuckikova, K., Pazoutova, M., & Rindi, F. (2015). Meiotic genes and sexual reproduction in the green algal class Trebouxiophyceae (Chlorophyta). *Journal of Phycology*, *51*, 419–430.

Gabrielson, T. M., Brochman, C., & Rueness, J. (2002). The Baltic Sea as a model system for studying postglacial colonization and ecological differentiation, exemplified by the red alga *Ceramium tenuicorne*. *Molecular Ecology*, *11*, 2083–2095.

Gallagher, S. B., & Humm, H. J. (1981). *Vaucheria* (Xanthophyceae, Vaucheriaceae) of the central Florida Gulf Coast. *Bulletin of Marine Science*, *31*, 184–190.

Godhe, A., Kremp, A., & Montresor, M. (2014). Genetic and microscopic evidence for sexual reproduction in the centric diatom *Skeletonema marinoi*. *Protist*, *165*, 401–416.

Graham, L. E., Graham, J. M., Wilcox, L. W., & Cook, M. E. (2022). *Algae* (4th Ed.). LJLM Press.

Grell, K. G. (1990). Some light microscope observations on *Chlorarachnion reptans* Geitler. *Archiv für Protistenkunde*, *138*, 271–290.

Guillemin, M.-L., Faugeron, S., Destombe, C., Viard, F., Correa, J. A., & Valero, M. (2008). Genetic variation in wild and cultivated populations of the haploid-diploid red alga *Gracilaria chilensis*: How farming practices favor asexual reproduction and heterozygosity. *Evolution*, *62*, 1500–1519.

Guiry, M. D. (2024). How many species of algae are there? A reprise. Four kingdoms, 14 phyla, 63 classes and still growing. *Journal of Phycology*, *60*, 214–228.

Haig, D. (2010). What do we know about charophyte (Streptophyta) life cycles. *Journal of Phycology*, *46*, 860–867.

Halkett, F., Simon, J., & Balloux, F. (2005). Tackling the population genetics of clonal and partially clonal organisms. *Trends in Ecology & Evolution*, *20*, 194–201.

Hamrick, J. L., & Godt, M. J. W. (1996). Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions: Biological Sciences*, *351*, 1291–1298.

Hansen, G. I., West, J. A., Yoon, H. S., Goodman, C. D., Louseux-de Goer, S., & Zuccarello, G. C. (2019). *Viator vitreocola* gen. et sp. nov. (Stylonemato-phyceae), a new red alga on drift glass debris in Oregon and Washington, USA. *Algae*, *34*, 71–90.

Hawkes, M. W. (1990). Reproductive strategies. In K. M. Cole & R. G. Sheath (Eds.), *Biology of the red algae* (pp. 455–476). Cambridge University Press.

Heesch, S., Serrano-Serrano, M., Barrera-Redondo, J., Luthringer, R., Peters, A. F., Destombe, C., Cock, J. M., Valero, M., Roze, D., Salamin, N., & Coelho, S. M. (2021). Evolution of life cycles and reproductive traits: Insights from brown algae. *Journal of Evolutionary Biology*, *34*, 992–1009.

Heiser, S., Amsler, C. D., Stoeckel, S., McClintock, J. B., Baker, B. J., & Krueger-Hadfield, S. A. (2023). Tetrasporophytic bias coupled with heterozygote deficiency in the Antarctic *Plocamium* sp. (Florideophyceae, Rhodophyta). *Journal of Phycology*, *59*, 681–697.

Henrickson, P., Knipschildt, F., Moestrup, Ø., & Thomsen, H. A. (1993). Autoecology, life history and toxicology of the silicoflagellate *Dictyocha speculum* (Silicoflagellata, Dictyochophyceae). *Phycologia*, *32*, 29–39.

Hirooka, S., Itabashi, T., Ichinose, T. M., Onuma, R., Fujiwara, T., Yamashita, S., Jong, L. W., Tomita, R., Iwane, A. H., & Miyagishima, S. Y. (2022). Life cycle and functional genomics of the unicellular red alga *Galdieria* for elucidating algal and plant evolution and industrial use. *Proceedings of the National Academy of Sciences of the United States of America*, *119*, e2210665119.

Hoef-Emden, K., & Melkonian, M. (2003). Revision of the genus *Cryptomonas* (Cryptophyceae): A combination of molecular phylogeny and morphology provides insights into a long-hidden dimorphism. *Protist*, *154*, 371–409.

Hofstatter, P. G., & Lhahr, D. J. (2019). All eukaryotes are sexual, unless proven otherwise. Many so-called asexual present meiotic machinery and might be able to have sex. *BioEssays*, *41*, 1800246.

Hoshino, M., & Kogame, K. (2019). Partthenogenesis is rare in the reproduction of a sexual field population of the isogamous brown alga *Scytosiphon* (Scytosiphonaceae, Ectocarpales). *Journal of Phycology*, *55*, 466–472.

Ichida, K., Yabuki, A., & Ota, S. (2007). The chlorarachniophytes: Evolution and classification. In J. Brodie & J. Lewis (Eds.), *Unravelling the algae: The past, present, and future of algal systematics* (pp. 171–182). CRC Press.

Ichihara, K., Yamazaki, T., Miyamura, S., Hiraoka, M., & Kawano, S. (2019). Asexual thalli originated from sporophytic thalli via apomeiosis in the green seaweed *Ulva*. *Scientific Reports*, *9*, 13523.

Ichinomiya, M., dos Santos, A. L., Gourvil, P., Yoshikawa, S., Kamiya, M., Ohki, K., Audic, S., de Vargas, C., Noël, M. H., Vaulot, D., & Kuwata, A. (2016). Diversity and oceanic distribution of the Parmales (Bolidophyceae), a picoplanktonic group closely related to the diatoms. *The ISME Journal*, *10*, 2419–2434.

Iglesias-Rodriguez, M. D., Schofield, O. M., Batley, J., Medlin, L. K., & Hayes, P. K. (2006). Intraspecific genetic diversity in the marine coccolithophore *Emiliania huxleyi* (Prymnesiophyceae): The use of microsatellite analysis in marine phytoplankton population studies. *Journal of Phycology*, *42*, 526–536.

Innes, D. J., & Yarish, C. (1984). Genetic evidence for the occurrence of asexual reproduction in populations of *Enteromorpha linza* (L.) J. Ag. (Chlorophyta, Ulvales) from Long Island sound. *Phycologia*, *23*, 311–320.

Jackson, C., Clayden, S., & Reyes-Prieto, A. (2015). The Glaucophyta: The blue-green plants in a nutshell. *Acta Societatis Botanicorum Poloniae*, *84*, 149–165.

Kaczmarska, I., Poulíčková, A., Sato, A., Edlund, M. B., Idei, M., Watanabe, T., & Mann, D. G. (2013). Proposals for a terminology for diatom sexual reproduction, auxospores and resting stages. *Diatom Research*, *28*, 263–294.

Kawachi, M., Inouey, I., Honda, D., O'Kelly, C. J., Bailey, J. C., Bidigare, R. R., & Andersen, R. A. (2002). The Pinguiophyceae *classis nova*, a new class of photosynthetic stramenopiles whose members produce large amounts of omega-3 fatty acids. *Phycological Research*, *50*, 31–47.

Kearney, M. (2005). Hybridization, glaciation and geographical parthenogenesis. *Trends in Ecology & Evolution*, *20*, 495–502.

Klekowski, E. J. (1969). Reproductive biology of the Pteridophyta. II. Theoretical considerations. *Botanical Journal of the Linnean Society*, *62*, 347–359.

Komárek, J., & Johansen, J. R. (2015a). Coccoid cyanobacteria. In J. D. Wehr, R. G. Sheath, & J. P. Kociolek (Eds.), *Freshwater algae of North America ecology and classification* (pp. 75–133). Elsevier.

Komárek, J., & Johansen, J. R. (2015b). Filamentous cyanobacteria. In J. D. Wehr, R. G. Sheath, & J. P. Kociolek (Eds.), *Freshwater algae of North America ecology and classification* (pp. 75–133). Elsevier.

Kraus, D., Chi, J., Beonigk, J., Beisser, D., Graupner, N., & Dunthorn, M. (2019). Putatively asexual chrysophytes have meiotic genes: Evidence from transciptomic data. *PeerJ*, *6*, e5894.

Krueger-Hadfield, S. A. (2020). What's ploidy got to do with it? Understanding the evolutionary ecology of macroalgal invasions necessitates incorporating life cycle complexity. *Evolutionary Applications*, *13*, 486–499.

Krueger-Hadfield, S. A., Balestreri, C., Schroeder, J. L., Highfield, A., Helaouët, P., Allum, J., Moate, R., Lohbeck, K. T., Miller, P. I., Riebesell, U., & Reusch, T. B. (2014). Genotyping an *Emiliania huxleyi* (Prymnesiophyceae) bloom event in the North Sea reveals evidence of asexual reproduction. *Biogeosciences*, *11*, 5215–5234.

Krueger-Hadfield, S. A., Blakeslee, A. M. H., & Fowler, A. E. (2019). Incorporating ploidy diversity into ecological and community genetics. *Journal of Phycology*, *55*, 1198–1207.

Krueger-Hadfield, S. A., Collén, J., Daguin-Thiébaut, C., & Valero, M. (2011). Distinguishing among genets and genetic population structure in the haploid-diploid seaweed *Chondrus crispus* (Rhodophyta). *Journal of Phycology*, *47*, 440–450.

Krueger-Hadfield, S. A., Flanagan, B. A., Godfroy, O., Hill-Spanik, K. M., Nice, C. C., Murren, C. J., Strand, A. E., & Sotka, E. E. (2021). Using RAD-seq to develop sex-linked markers in a haplodiplontic alga. *Journal of Phycology*, *57*, 279–294.

Krueger-Hadfield, S. A., Guillemin, M.-L., Destombe, C., Valero, M., & Stoeckel, S. (2021). Exploring the genetic consequences of clonality in haplodiplontic taxa. *Journal of Heredity*, *112*, 92–107.

Krueger-Hadfield, S. A., & Hoban, S. M. (2016). The importance of effective sampling for exploring the population dynamics of haploid-diploid seaweed. *Journal of Phycology*, *52*, 1–9.

Krueger-Hadfield, S. A., Kollars, N. M., Byers, J. E., Greig, T. W., Hammann, M., Murray, D. C., Murren, C. J., Strand, A. E., Terada, R., Weinberger, F., & Sotka, E. E. (2016). Invasion of novel habitats uncouples haplo-diplontic life cycles. *Molecular Ecology*, *25*, 3801–3816.

Krueger-Hadfield, S. A., Kübler, J. E., & Dudgeon, S. R. (2013). Reproductive effort in the red alga, *Mastocarpus papillatus*. *Journal of Phycology*, *49*, 271–281.

Krueger-Hadfield, S. A., Roze, D., Correa, J. A., Destombe, C., & Valero, M. (2015). O father where art thou? Paternity analyses in a natural population of the haploid–diploid seaweed *Chondrus crispus*. *Heredity*, *114*, 185–194.

Krueger-Hadfield, S. A., Roze, D., Mauger, S., & Valero, M. (2013). Intergametophytic selfing and microgeographic genetic structure shape populations of the intertidal red seaweed *Chondrus crispus*. *Molecular Ecology*, *22*, 3242–3260.

Krueger-Hadfield, S. A., Shainker-Connelly, S. J., Crowell, R. M., & Vis, M. L. (2024). The eco-evolutionary importance of reproductive system variation in macroalgae: Freshwater reds as a case study. *Journal of Phycology*, *60*, 15–25.

Kugrens, P., & Lee, R. E. (1988). Ultrastructure of fertilization in a cryptomonad. *Journal of Phycology*, *24*, 385–393.

Lane, C. E., Khan, H., MacKinnon, M., Fong, A., Theophilou, S., & Archibald, J. M. (2005). Insight into diversity and evolution of the cryptomonad nucleomorph genome. *Molecular Biology and Evolution*, *23*, 856–865.

Lane, J. E., Forrest, M. N. K., & Willis, C. K. R. (2011). Animal behaviour. *Animal Behaviour*, *81*, 909–917.

Lebret, K., Kritzberg, E. S., Figueroa, R., & Rengefors, K. (2012). Genetic diversity within and genetic differentiation between blooms of a microalgal species. *Environmental Microbiology*, *14*, 2395–2404.

Lees, L. E., Krueger-Hadfield, S. A., Clark, A. J., Duermit, E. A., Sotka, E. E., & Murren, C. J. (2018). Diploid thalli of the ecosystem engineer Gracilaria vermiculophylla are stronger and less nutritious than haploid thalli. *Journal of Phycology*, *54*, 471–482.

Lin, S., Yu, L., Wu, X., Li, M., Zhang, Y., Luo, H., Li, H., Li, T., & Li, L. (2022). Active meiosis during dinoflagellate blooms: A 'sex for prolifertaion' hypothesis. *Harmful Algae*, *118*, 102307.

Lipinska, A. P., Krueger-Hadfield, S. A., Godfory, O., Dittami, S. M., Ayres-Ostrock, L., Bonthond, G., Brillet-Guéguen, L., Coelho, S., Corre, E., Cossard, G., Destombe, C., Epperlein, P., Faugeron, S., Ficko-Blean, E., Beltrán, J., Lavaut, E., Le Bars, A., Marchi, F., Mauger, S., … Valero, M. (2023). The Rhodoexplorer platform for red algal genomics and whole-genome assemblies for several *Gracilaria* species. *Genome Biology and Evolution*, *15*, evad124.

Ma, Z., Hu, Z., Deng, Y., Shang, L., Gobler, C. J., & Tang, Y. Z. (2020). Laboratory culture-based characterization of the resting stage cells of the brown-tide-causing pelagophyte, *Aureococcus anophagefferens*. *Journal of Marine Science and Engineering*, *8*, 1027.

Maggs, C. A. (1988). Intraspecific life history variability in the Florideophycidae (Rhodophyta). *Botanica Marina*, *31*, 465–490.

Moestrup, Ø., & Enveldson, H. (2019). On sexual reproduction in euglenoids, a tribute to Berthe Biecheler. *Phycologia*, *58*, 326–328.

Mordecai, G. J., Verret, F., Highfield, A., & Schroeder, D. C. (2017). Schrödinger's Cheshire cat: Are haploid *Emiliania huxleyi* cells resistant to viral infection or not? *Viruses*, *9*, 51.

Novorino, G. (2012). Cryptomonad taxonomy in the 21st century: The first two hundred years. In K. Wolowski, I. Kaczmarska, J. M. Ehrman & Z. W. Agata (Eds.), *Current advances in algal taxonomy and its applications: Phylogenetic, ecological, and applied perspective*, (pp. 19–52). Szafer Institute of Botany, Polish Academy of Sciences.

Nicholls, K. H., & Wujek, D. E. (2003). Chrysophycean algae. In J. D. Wehr & R. G. Sheath (Eds.), *Freshwater algae of North America ecology and classification* (pp. 471–503). Academic Press.

Niklas, K. J., & Kutschera, U. (2009). The evolution of the land plant life cycle. *New Phytologist*, *185*, 27–41.

Olsen, K. C., Ryan, W. H., Kosman, E. T., Moscoso, J. A., Levitan, D. R., & Winn, A. A. (2021). Lessons from the study of plant mating systems for exploring the causes and consequences of inbreeding in marine invertebrates. *Marine Biology*, *168*, 39.

Olsen, K. C., Ryan, W. H., Winn, A. A., Kosman, E. T., Moscoso, J. A., Krueger-Hadfield, S. A., Burgess, S. C., Carlon, D. B., Grosberg, R. K., Kalisz, S., & Levitan, D. R. (2020). Inbreeding shapes the evolution of marine invertebrates. *Evolution*, *74*, 871–882.

Oppliger, L. V., von Dassow, P., Bouchemousse, S., Robuchon, M., Valero, M., Correa, J. A., Mauger, S., & Destombe, C. (2014). Alteration of sexual reproduction and genetic diversity in the kelp species *Laminaria digitata* at the southern limit of its range. *PLoS ONE*, *9*, e102518.

Orive, M. E., Barfield, M., Fernandez, C., & Holt, R. D. (2017). Effects of clonal reproduction on evolutionary lag and evolutionary rescue. *The American Naturalist*, *190*, 469–490.

Orive, M. E., Barfield, M., & Holt, R. D. (2023). Partial clonality expands the opportunity for spatial adaptation. *The American Naturalist*, *202*, 587–736.

Orive, M. E., & Krueger-Hadfield, S. A. (2021). Sex and asex: A clonal lexicon. *Journal of Heredity*, *112*, 1–8.

Ott, D. W., & Hommersand, M. H. (1974). Vaucheriae of North Carolina. I. Marine and brakish water species. *Journal of Phycology*, *10*, 373–385.

Ott, D. W., & Oldham-Ott, C. K. (2003). Eustigmatophyte, raphidophyte, and Tribophyte algae. In J. D. Wehr & R. G. Sheath (Eds.), *Freshwater algae of North America ecology and classification* (pp. 423–466). Academic Press.

Otto, S. P., & Marks, J. C. (1996). Mating systems and the evolutionary transition between haploidy and diploidy. *Biological Journal of the Linnean Society*, *57*, 197–218.

Perrin, C., Daguin, C., Van De Vliet, M., Engel, C. E., Pearson, G., & Serrão, E. A. (2007). Implications of mating system for genetic diversity of sister algal species: *Fucus spiralis* and *Fucus vesiculosus* (Heterokontophyta, Phaeophyceae). *European Journal of Phycology*, *3*, 219–230.

Phillips, J. A. (2009). Reproductive ecology of *Caulerpa taxifolia* (Caulerpaceae, Bryopsidales) in subtropical eastern Australia. *European Journal of Phycology*, *44*, 81–88.

Proctor, V. W. (1971a). Taxonomic significance of monoecism and dioecism in the genus *Chara*. *Phycologia*, *10*, 299–307.

Proctor, V. W. (1971b). *Chara globularis* Thuillier (= *C. vragilis* Desvaux): Breeding patterns within a cosmopolitan complex. *Limnology and Oceanography*, *16*, 422–436.

Qiu, Y. L., Taylor, A. B., & McManus, H. A. (2012). Evolution of the life cycle in land plants. *Journal of Systematics and Evolution*, *50*, 171–194.

Richards, A. J. (1986). *Plant breeding systems* (529 pp.). George Allen & Unwin.

Robuchon, M., Le Gall, L., Mauger, S., & Valero, M. (2014). Contrasting genetic diversity patterns in two sister kelp species co-distributed along the coast of Brittany, France. *Molecular Ecology*, *23*, 2669–2685.

Rosowski, J. R. (2003). Photosynthetic euglenoids. In J. D. Wehr & R. G. Sheath (Eds.), *Freshwater algae of North America ecology and classification* (pp. 383–416). Academic Press.

Rushworth, C. A., Wagner, M. R., Mitchell-Olds, T., & Anderson, J. T. (2022). The *Boechera* model system for evolutionary ecology. *American Journal of Botany*, *109*, 1939–1961.

Rynearson, T. A., & Armbrust, E. V. (2000). DNA fingerprinting reveals extensive genetic diversity in a field population of the centric diatom *Ditylum brightwellii*. *Limnology and Oceanography*, *45*, 1329–1340.

Sabbe, K., Chepurnov, V. A., Vyverman, W., & Mann, D. G. (2004). Apomixis in *Achnanthes* (Bacillariophyceae); development of a model system for diatom reproductive biology. *European Journal of Phycology*, *39*, 327–341.

Sandgren, C. D., & Flanagin, J. (1986). Heterothallic sexuality and density dependent encystment in the Chrysophycean alga *Synura petersenii* Korsh. *Journal of Phycology*, *22*, 206–212.

Sandrock, C., Razmijou, J., & Vorburger, C. (2011). Climate effects on life cycle variation and population genetic architecture of the black bean aphid, *Aphis fabae*. *Molecular Ecology*, *20*, 4165–4181.

Santos, L. M. A. (1996). The Eustigmatophyceae: Actual knowledge and research perspectives. *Nova Hedwigia*, *112*, 391–405.

Schaible, R., Bergmann, I., & Schubert, H. (2011). Genetic structure of sympatric sexually and parthenogenetically reproducing population of *Chara canescens* (Charophyta). *ISRN Ecology*, *501838*, 1–13.

Shah, S., Chen, Y., Bhattacharya, D., & Chan, C. X. (2020). Sex in Symbiodiniaceae dinoflagellates: Genomic evidence for independent loss of the canonical synaptonemal complex. *Scientific Reports*, *10*, 9792.

Sherwood, R. K., & Bennett, R. J. (2009). Fungal meiosis and parasexual reproduction – Lessons from pathogenic yeast. *Current Opinion in Microbiology*, *12*, 599–607.

Silvertown, J. (2008). The evolutionary maintenance of sexual reproduction: Evidence from the ecological distribution of asexual reproduction in clonal plants. *International Journal of Plant Sciences*, *169*, 157–168.

Soltis, P. S., Marchant, D. B., Van de Peer, Y., & Soltis, D. E. (2015). Polyploidy and genome evolution in plants. *Current Opinion in Genetics and Development*, *35*, 119–125.

Speijer, D., Lukes, J., & Eliás, M. (2015). Sex is ubiquitous, ancient, and inherent attribute of eukaryotic life. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 8827–8834.

Steen, F., Marc, V., D'Hondt, S., Vieira, C., & De Clerck, O. (2019). *Population structure and geographically structured reproductive strategies of the haplodiplontic seaweed* Dictyota dichotoma. *bioRxiv*. https://doi.org/10.1101/595587

Stoeckel, S., Arnaud-Haond, S., & Krueger-Hadfield, S. A. (2021). The combined effect of haplodiplonty and partial clonality in population genetics. *Journal of Heredity*, *112*, 78–91.

Stoeckel, S., Porro, B., & Arnaud-Haond, S. (2021). The discernible and hidden effects of clonality on the genotypic and genetic states of populations: Improving our estimation of clonal rates. *Molecular Ecology Resources*, *21*, 1068–1084.

Suda, S., Watanabe, M. M., & Inouye, I. (1989). Evidence of sexual reproduction in the primitive green alga *Nephroselmis olivacea* (Prasinophyceae). *Journal of Phycology*, *25*, 596–600.

Suda, S., Watanabe, M. M., & Inouye, I. (2006). Electron microscopy of sexual reproduction in *Nephroselmis olivaceae* (Prasinophyceae, Chlorophyta). *Phycological Research*, *52*, 273–283.

Tang, Y. Z., Ma, Z., Hu, Z., Deng, Y., Yang, A., Lin, S., Yi, L., Chai, Z., & Gobler, C. J. (2019). 3000 km and 1500-year presence of *Aureococcus anophagefferens* reveals indigenous origin of brown tides in China. *Molecular Ecology*, *28*, 4065–4076.

Tatarenkov, A., Bergström, L., Jönsson, R. B., Serrão, E. A., Kautsky, L., & Johannesson, K. (2005). Intriguing asexual life in marginal populatoins of the brown seaweed *Fucus vesiculosus*. *Molecular Ecology*, *14*, 647–651.

Taton, A., Erikson, C., Yang, Y., Rubin, B. E., Rifkin, S. A., Golden, J. W., & Golden, S. S. (2020). The circadian clock and darkness control natural competence in cyanobacteria. *Nature Communications*, *11*, 1688.

Thornhill, D. J., Howells, E. J., Wham, D. C., Steury, T. D., & Santos, S. R. (2017). Population genetics of reef coral endosymbionts (*Symbiodinium*, Dinophyceae). *Molecular Ecology*, *26*, 2640–2659.

Thornton, B. M., Spalding, H. L., Stoeckel, S., Harris, M. L., Wade, R. M., & Krueger-Hadfield, S. A. (2024). *Clonality and polyploidy contribute to the spread of* Avrainvillea lacerata (*Bryopsidales, Chlorophyta) in Hawai'i*. *bioRxiv*. DOI TBD. https://doi.org/10.1101/2024.05.04.592553

Tibaryrenc, M. (1997). Are *Candida albicans* natural populations subdivided? *Trends in Microbiology*, *5*, 253–254.

Tibayrenc, M., & Ayala, F. J. (1991). Towards a population genetics of microorganisms: The clonal theory of parasitic protozoa. *Parasitology Today*, *7*, 228–232.

Travis, J. (2020). Where is natural history in ecological, evolutionary and behavioral science? *American Naturalist*, *196*, 1–8.

van der Strate, H. J., van de Zande, L., Stam, W. T., & Olsen, J. L. (2002). The contribution of haploids, diploids and clones to fine-scale population structure in the seaweed *Cladophoropsis membranacea* (Chlorophyta). *Molecular Ecology*, *11*, 329–345.

Varela-Álvarez, E., Loureiro, J., Paulino, C., & Serrão, E. A. (2018). Polyploid lineages in the genus *Porphyra*. *Scientific Reports*, *8*, 8696.

Varela-Álvarez, E., Meirmans, P. G., Guiry, M. D., & Serrão, E. A. (2022). Biogeographic population structure of chimeric blades of *Porphyra* in the northeast atlantic reveals southern rich gene pools, introgression and cryptic plasticity. *Frontiers in Plant Science*, *13*, 818368.

von Dassow, P., John, U., Ogata, H., Probert, I., Bendif, E. M., Kegel, J. U., Audic, S., Wincker, P., da Silva, C., Claverie, J. M., Doney, S., Glover, D. M., Flores, D. M., Herrera, Y., Lescot, M., Garet-Delmas, M. J., & de Vargas, C. (2015). Life-cycle modification in open oceans accounts for genome variability in a cosmopolitan phytoplankton. *The ISME Journal*, *9*, 1365–1377.

Warren, S. D., St. Clair, L. L., Stark, L. R., Lewis, L. A., Pombubpa, N., Kurbessoian, T., Stajich, J. E., & Aanderud, Z. T. (2019). Reproduction and dispersal of biological soil crust organisms. *Frontiers in Ecology and Evolution*, *7*, 344.

Whitehead, M. R., Lanfear, R., Mitchell, R. J., & Karron, J. D. (2018). Plant mating systems often vary widely among populations. *Frontiers in Ecology and Evolution*, *6*, 38.

Williams, T. M., Krueger-Hadfield, S. A., Hill-Spanik, K. M., Kosaki, R. K., Stoeckel, S., & Spalding, H. L. (2024). The reproductive system of *Chondria tumulosa* (Florideophyceae) at Manawai Atoll, Papahānaumokuākea Marine National Monument. *Phycologia*, *63*, 36–44.

How to cite this article: Krueger-Hadfield, S. A. (2024). Let's talk about sex: Why reproductive systems matter for understanding algae. *Journal of Phycology*, *60*, 581–597. https://doi.org/10.1111/jpy.13462