JOURNAL OF PLANKTON RESEARCH | VOLUME 33 | NUMBER 1 | PAGES 3–12 | 2011

HORIZONS

Unveiling the mysteries of phytoplankton life cycles: patterns and opportunities behind complexity

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Received June 30, 2010; accepted in principle September 17, 2010; accepted for publication September 25, 2010

Corresponding editor: William K.W. Li

Life cycles of phytoplankton species have been selected over a long evolutionary history and represent a key element for our understanding of their ecology and natural history and for improving our comprehension of ocean functioning. A species can alternate in its life cycle between four distinct major phases: growth, sex, quiescence and cell death. This implies that the population of a phytoplankton species found in any particular water sample will contain cells that undergo different fates, have strong differentiation in physiology and have different functional roles even if they are genetically identical. The factors regulating transitions among the different phases are still largely unknown but have direct impacts on the ecological distribution of species and on their biogeochemical function. Focused research efforts in recent years have begun to reveal emerging patterns in the variability of phytoplankton life cycle traits. This research has relied both on careful observations in culture and at sea and on making use of new genomics- and transcriptomics-based tools. The study of phytoplankton in the context of their life cycle characteristics opens up new opportunities to address fundamental questions about the physiology and cell biology of these important organisms and creates a new evolutionary and ecological framework for defining phytoplankton functional groups.

KEYWORDS: phytoplankton; genomics; life cycle; evolution

Phytoplankton are unicellular phototrophs estimated to be responsible for approximately half of global primary production. Some species are harmful, disrupting ecosystems and hampering human exploitation of marine resources. Phytoplankton are composed of very diverse ancient lineages of eukaryotic and prokaryotic life (Brodie and Lewis, 2007; Falkowski and Knoll, 2007). Unraveling the basic biology of these organisms offers key insights into the evolutionary history of life on earth and is essential for improving our understanding of ocean functioning.

doi:10.1093/plankt/fbq137, available online at www.plankt.oxfordjournals.org. Advance Access publication October 25, 2010

Phytoplankton cells can undergo transitions between an actively growing phase during which biomass is intrinsically increasing (in the absence of external losses), and other life phases in which cells are dormant or quiescent, undergo sexual reproduction or die. These phase transitions represent an organism's life cycle. This means that phytoplankton populations contain cells that can undergo different fates, show strong differentiation in physiology and have different functional roles even if they are genetically identical.

Life cycles have been selected over a long evolutionary history and represent a key element for our understanding of species ecology and natural history. However, it is often difficult or even impossible to identify or preserve the various ephemeral phases with classical plankton observation methods, and phase transitions are often difficult to induce in the laboratory. Thus, life cycles remain one of the least studied and most poorly understood aspect of phytoplankton biology.

Since the 1950's, biological oceanography has focused heavily on bulk measurements of phytoplankton (pigments, ^{14}C fixation) and less on the autecology of individual species. However, functioning of phytoplankton communities may be greatly influenced both by which particular species are present and by the total diversity of the community: closely related species can differ in functional properties such as production of toxins or secondary metabolites and this has implication for pelagic food webs (e.g. Wichard *et al.*, 2005; Touzet *et al.*, 2010). At a broader level, microbial diversity may affect the functioning of pelagic ecosystems (Ptacnik *et al.*, 2008). Life cycle studies are fundamental to the development of a species-focused biological oceanography that aims to understand how the astonishing diversity of planktonic organisms structure the oceans (Smetacek *et al.*, 2002). In this article, we review the life cycles of eukaryotic phytoplankton, focusing on major gaps in current knowledge and highlighting new approaches and perspectives in life cycle research that promise to greatly advance our understanding of the general biology, ecology and evolution of these organisms.

LIFE CYCLES: A HIERARCHY OF PLASTICITY

Modern phytoplankton groups have followed distinct evolutionary trajectories and current life cycle traits of a species will be influenced both by evolutionary history and by on-going selective forces. One example of this principle is the planktonic raphid pennate diatoms, such as the genus *Pseudo-nitzschia*, that arose from benthic ancestors during the last 20 million years (Sims *et al.*, 2006). In this particular instance, questions arise as to how characters such as motility, chain formation and mating behavior reflect modern adaptations to a planktonic existence versus retention of more ancient adaptations to a benthic existence. Looking across eukaryotic phytoplankton and their relatives, we can see that clear patterns governing evolutionary variability of phytoplankton life cycles are beginning to emerge as a result of focused research relying both on improved observations in culture and at sea, and on newly available molecular and genomics-based techniques. We define transitions between four basic life cycle phases (Fig. 1), growth, sex, quiescence and cell death, and outline the main types of life cycle plasticity around each phase.

Growth

Growth is the vegetative phase in which cells reproduce asexually (mitosis) with a concomitant increase in biomass. If growth is only expressed in haploid (1N) cells, the life cycle is haplontic. If diploid (2N) cells undergo growth, but not 1N cells, the life cycle is diplontic. If both 1N and 2N cells can undergo growth, the life cycle is haplo-diplontic (Fig. 1). All diatoms exhibit diplontic life cycles (Round *et al.*, 1990; Chepurnov *et al.*, 2004), although polyploidization may occur (von Dassow *et al.*, 2008; Koester *et al.*, 2010). Chlorophytes, prasinophytes and most dinoflagellates seem to be haplontic (Graham and Wilcox, 2000). The Prymnesiophyceae are generally haplo-diplontic, but observations are still limited. The 1N and 2N cells of haplo-diplontic organisms can be physiologically distinct, differentially susceptible to pathogens and allow a species to occupy different ecological niches (Nöel *et al.*, 2004; Houdan *et al.*, 2005, 2006; Frada *et al.*, 2008).

The life cycle type (haplontic, diplontic or haplodiplontic) appears to be one of the least plastic characters defining large taxonomic groups (Otto and Gerstein, 2008). However, we do have examples of variability. Two groups within the normally haplontic dinoflagellates, the Noctilucales (Fukuda and Endoh, 2006) and Pyrocystales (Seo and Fritz, 2006), appear to have independently evolved a diplontic life cycle. The diplontic diatoms are thought to have arisen from a haplontic stramenopile ancestor (Kooistra *et al.*, 2007). Multicellular stramenopiles are haplo-diplontic, however many have reduced the 1N gametophyte and Fucales are essentially diplontic (Coelho *et al.*, 2007).

Sex

Sex is the phase(s) in which fusion of 1N cells (mating, syngamy) and meiosis (sexual recombination and

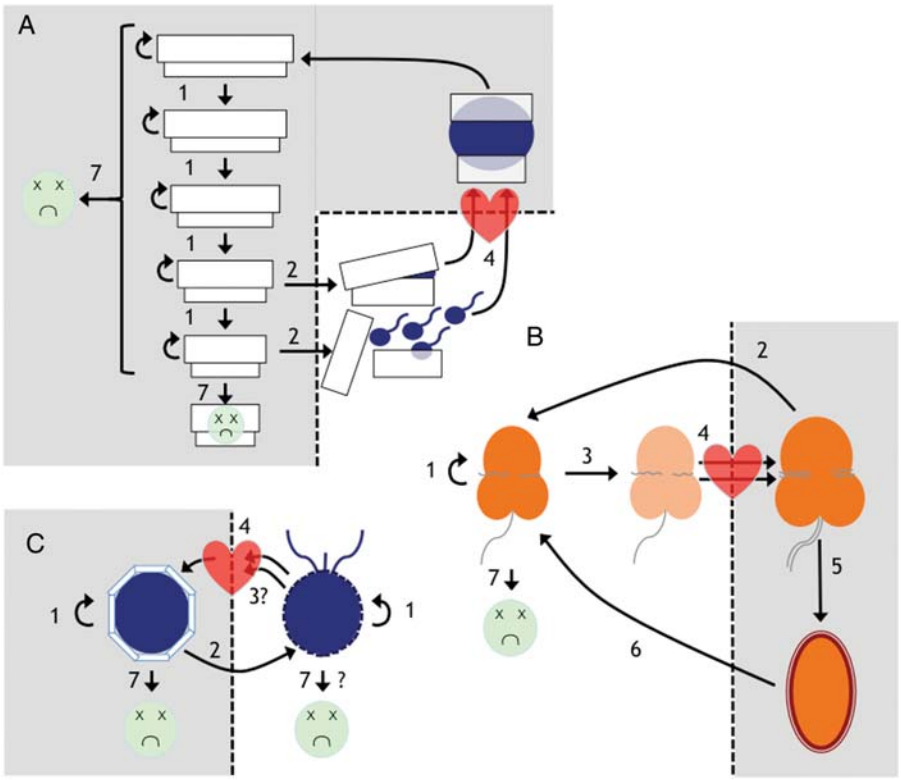

Fig. 1. Schematic drawings illustrating the main features of the archetypal life cycles of (**A**) diplontic centric diatoms, (**B**) haplontic dinoflagellates and (**C**) haplo-diplobiontic coccolithophores (Prymnesiophyceae). The grey shading delimits diploid stages. Arrows mark the points in the life cycle where a change of state is possible. (1) The cell can divide (growth) or enter a resting phase (quiescence). In the archetypal diatom life cycle, each cell division produces one daughter cell of the same size and one daughter cell of a smaller size than its parent; (2) the cell can undergo meiosis; (3) further differentiation of haploid cells into gametes may occur (e.g. dinoflagellates), (4) the gamete can find a compatible partner (syngamy, shown by the 'heart' symbol); (5) the cell (zygote) can transform into a resting cyst (dinoflagellates); (6) the resting cyst (zygote) can undergo meiosis and produce haploid vegetative cells; (7) the cell death may occur, either due to external cues or to failure to restore cell size (diatoms) (shown by the "unhappy face" icon).

division of 2N cells into 1N cells) occurs. Sex can be a single phase, if meiosis is followed immediately by syngamy or syngamy is followed immediately by meiosis, or syngamy and meiosis can occur in separate phases separated either by quiescent (resting) phase or, in a haplo-diplontic life cycle, by growth phases (Fig. 1). The sexual phase involved in syngamy also defines the life cycle, which is homothallic if mating can occur between two cells of the same clonal lineage, and is heterothallic if there are separate sexes (mating types) and a cell must mate with another cell of a different mating type. In complex heterothally, many mating types can exist.

The last decade of research on both diatoms and dinoflagellates has revealed that the mating system is highly diverse, thus suggesting that heterothally and sex-determining mechanisms have evolved independently multiple times among eukaryotes. Pennate diatoms show a tendency towards heterothally, but they arose from a completely homothallic background in the centric diatoms (Kooistra *et al.*, 2007). However, homothallic species can be closely related to heterothallic species (Montresor and Lewis, 2006; Quijano-Scheggia *et al.*, 2009) and a continuum between homothallism and heterothallism has been recently reported for the dinoflagellate *Gymnodinium catenatum* (Figueroa *et al.*, 2009). Directed evolution experiments in the chlorophyte *Chlamydomonas reinhardtii* showed that switches between heterothally and homothally could occur in less than 100 generations (Bell, 2005). The mating system is a fundamental control of syngamy and its plasticity might be a common mechanism to erect breeding barriers at early stages of speciation.

Quiescence

The quiescent phase refers to any cell stages that adopt a greatly reduced metabolic rate and cease division but remain viable. The quiescent phase can refer to a cyst or a spore that has undergone a noticeable

differentiation to be covered in a resistant cell wall. Vegetative cells may also enter a state of strongly decreased metabolic activity without obvious morphological differentiation. Such quiescent cells can remain viable, able to resume growth or sex in response to abiotic cues and/or a biological clock (Montresor and Lewis, 2006). Formation of resting spores in centric diatoms is not directly connected to sex, with the exception of *Leptocylindrus danicus* (McQuoid and Hobson, 1996). In contrast to diatoms, the resting stages in dinoflagellates and chlorophytes are typically formed by the diploid zygotes after syngamy. However, the dinoflagellate *Scrippsiella hangoei* has been shown to be capable of asexual formation of resting cysts (Kremp and Parrow, 2006). Moreover, the formation of resting cysts is not an obligate outcome of zygote formation in several dinoflagellates, where the newly formed zygote can either immediately enter meiosis or form cysts, the choice depending on environmental factors (Figueroa and Bravo, 2005; Figueroa *et al.*, 2006). The capacity to form morphologically differentiated resting phases is widespread in centric diatoms and in dinoflagellates, but does not appear to be present in the majority of species. It has been suggested that most of the diatoms that survived the K-T event 65 Mya (which killed off dinosaurs) were spore-formers (Sims *et al.*, 2006). The ability to form resting spores or cysts may have been secondarily lost in many lineages. Diatoms also form resting cells, which are morphologically indistinguishable from vegetative ones but physiologically differentiated, and several dinoflagellates also produce short-term cysts (either sexually or asexually) that lack the full morphological differentiation of resting cysts. The life cycle of microalgae thus can include resting stages characterized by a broad range of morphological and functional differentiation, which act to buffer the environmental variability over timescales ranging from short-term perturbations to longer decadal time scales. Resting stage formation appears to exhibit a high degree of plasticity.

Cell death

A surprising result of the past decade of research is that many phytoplankton species, including dinoflagellates, diatoms, coccolithophores and even filamentous cyanobacteria can undergo controlled, genetically programmed cell death (PCD) (Vardi *et al.*, 1999; Bidle and Falkowski, 2004; Franklin *et al.*, 2006; Vardi *et al.*, 2007; Bidle and Bender, 2008). A key conceptual characteristic of PCD is that the triggers do not act directly to kill the cell but instead stimulate an intracellular biochemical program in which death is the end result. The hallmarks of PCD are that chromatin and organelles are first subjected to autocatalytic degradation mediated by homologs of the caspase protease family, long before cellular membranes are compromised and lysis occurs.

PCD in phytoplankton has generally been investigated as a response to acute adverse abiotic or biotic stressors, but it is important to note that cell death can conceivably also be an intrinsic outcome of certain cell life cycles, with or without the specific characteristics of PCD. Asymmetric division in budding yeast results in a mother cell producing smaller daughters at every division (which can then grow to become mother cells as well). Each mother cell has a limited replicative lifespan, after which the cell dies, possibly via PCD (Steinkraus *et al.*, 2008). As we will see below, the life cycles of diatoms typically result in the production of non-viable cells at the end of the asexual growth phase.

Forms of controlled cell death thus may be viewed either as alternative paths or inherent parts of phytoplankton life cycles. It remains to be documented how much variability there is in PCD expression among different species and between different cells of the same population. A better understanding of cell death processes in phytoplankton will provide insight into the mechanisms that govern bloom termination, species succession and intercellular signaling, which ultimately drive carbon cycling in the oceans.

CELL FATES AND CONSEQUENCES FOR GENOMES AND BIOGEOCHEMICAL FLUXES

If we follow the individual genome of a protist as it is passed from cell to cell by descent, we see that it is confronted with a series of fate determining steps influencing representation of the genome in future populations (Fig. 1). A growing cell can continue dividing asexually, nearly exactly replicating the genome (with low rates of mitotic mutation), or it chooses to enter into either a sexual, quiescent or cell death phase. The genomes of senescent cells are destroyed. In the quiescent phase, the genome is essentially frozen; its representation in future populations depends on the rate of mortality and the induction of a transition to growth or sex. The induction of sex means that the individual genome will be altered by syngamy (fusion with a parallel genome) and meiotic recombination.

The genetic cost of sex is high (Otto, 2009): A diploid parent shares only 50% of its genes with each diploid offspring in the next sexual generation,

compared to 100% with offspring produced asexually. This genetic cost is only partly offset if intra-clonal sexual reproduction occurs: each diploid offspring does share 100% of its genes with the parent, but heterozygosity in the parent is diminished by inbreeding.

There are also high energetic costs to sex. Syngamy and meiosis proceed much more slowly than mitosis (Lewis, 1983), and are inherently more complex and prone to error. Syngamy adds a requirement for successful encounter between appropriate mates while, during meiosis, chromosome loss occurs 10 times more frequently than in mitosis (Murray and Szostak, 1985) and new mutations arise at a higher rate (Magni and von Borstel, 1962). Finally, in many organisms two or three of the four nuclear products of meiosis are targeted for controlled destruction. For example, only one or two of the nuclei produced in oogenesis in centric diatoms survives, and most species produce only one egg per mother cell (Round *et al*., 1990; Chepurnov *et al*., 2004).

Despite these high costs, sex is ubiquitous in eukaryotes, and the evolutionary origins and maintenance of sex remain one of the largest mysteries in biology. The most popular explanations invoke long-term adaptive advantages of generating new genetic combinations. Sex can also serve to diminish the genetic load of deleterious mutations (Zeyl and Bell, 1997; Paland and Lynch, 2006; Haag and Roze, 2007). Current evolutionary models provide more specific constraints to the advantages of sexual recombination, predicting that sex is evolutionary stable if selection varies strongly over time and space, populations are not infinite, and sex is induced when the fitness of an asexually reproducing individual declines (Otto, 2009). The condition that populations be finite for evolutionary maintenance of sex is particularly interesting. To a biological oceanographer, phytoplankton populations appear essentially infinite, but perhaps the very existence of sex (and even obligate sexual life cycles) in many phytoplankton species implies that the ocean must be much more highly structured than we have yet imagined.

Condition-dependent sex may be key for the evolutionary success of sexuality (Hadany and Otto, 2009). In many protists, sex is induced by stressful conditions, such as nutrient starvation or changes in the light field. However, sex is often controlled by much more than a condition-dependent stress surveillance system. Diatoms provide possibly the most sophisticated example. When a diatom cell divides asexually, the new wall is formed within the older, parental wall. In most species, this causes one of the daughter cells to have a smaller size than the parent, thus the average cell size decreases with asexual division. Cell size is most commonly restored sexually and cells that fail to restore size eventually die. Cells below a species-specific size threshold, but not larger cells, can be induced to enter into sex, differentiating into gametes which fuse to form an auxospore that enlarges and hosts the formation of a large vegetative cell, deposits a new wall and size is restored. However, being in the right cell size window is the necessary but often not sufficient condition for the induction of the sexual phase and environmental factors and/or chemical interactions between cells can further regulate the process (Chepurnov *et al*., 2004).

The complex size-control of diatom sex appears to ensure that a fraction of a clonal cohort can enter into sexual reproduction only after a threshold number of asexual cell divisions, whereas another fraction continues asexual growth (Lewis, 1984). Curiously, many diatom species appear to have lost or fundamentally modified this "sex clock". Many species, including the first two diatoms to be genome-sequenced, *Thalassiosira pseudonana* and *Phaeodactylum tricornutum*, do not undergo cell size decreases with asexual division, and sexual stages have never been observed (Chepurnov *et al*., 2008). The close relatives of *T. pseudonana*, e.g. *T. punctigera* and *Cyclotella meneghiniana*, clearly display classic size-diminution, gametogenesis and auxosporulation (Schultz and Trainor, 1968; Chepurnov *et al*., 2006). Other diatom species are capable of asexual size restoration mechanisms (Sabbe *et al*., 2004). Facultative or complete loss of sexuality has occurred many times independently in diatoms (Chepurnov *et al*., 2004, 2008). Comparing the ecology of asexual and obligate sexual diatom species would offer new deep insights into the evolutionary forces driving the occurrence of sex in eukaryotes in general, and the ecological diversification of one especially important eukaryotic group in particular.

PCD is even more puzzling from an evolutionary perspective. PCD might serve as a mechanism whereby some cells are sacrificed to confer benefits to survival on closely related cells, e.g. by killing infections before they can spread or by releasing nutrients to neighboring cells in famine conditions (Franklin *et al*., 2006). An early observation that such a mechanism might exist in phytoplankton was made in the freshwater planktonic diatom *Asterionella formosa*, in which newly infected cells rapidly die, killing the parasite before infection can spread to other cells (Canter and Jaworski, 1979). However, it is not clear how auto-induced PCD might be selected in normally dilute phytoplankton populations. Except in the case of chain-forming or colonial phytoplankton, kin selection seems unlikely, as it would require that cells undergoing PCD would have some compensatory genetic advantage due to enhanced survival of closely related cells. Population genetics has

revealed that phytoplankton populations are very genetically diverse (Rynearson and Armbrust, 2000; Casteleyn *et al.*, 2009). The probability of sampling the same clone twice is very low, suggesting closely related cells do not remain long in closer proximity than to unrelated cells. If PCD was altruistic, cheater mutations, losing the capacity for PCD, would be expected to have a strong selective advantage and quickly eliminate PCD capacity from the population.

Alternatively, PCD might be simply an unintended consequence of the presence of caspase machinery that normally serves important functions in transitions from growth to quiescence or sex, at which time cells carry out controlled destruction of complex cellular components, e.g. excess nuclei (Ejercito and Wolfe, 2003; Kobayashi and Endoh, 2005). Oxidative stress, which induces PCD, also induces entry into sex in *Volvox* (Nedelcu *et al.*, 2004). PCD can be finally considered a natural mechanism that eliminates a large part of a population at the end of the growth phase.

Life cycle choices can have direct impacts on ecological distribution and biogeochemical function. The 1N and 2N cells of some haplo-diplontic coccolithophores are distinguished by radically different calcite cell coverings: holococcoliths on 1N cells and heterococcoliths on 2N cells. In these species, the holococcolith-covered cells occur with a more shallow depth distribution and in more stratified, oligotrophic waters than the heterococcolith-bearing cells (Cros, 2002). The maximum growth rate of diatoms can change during their life cycle (Amato *et al.*, 2005; von Dassow *et al.*, 2006) and discarding of parental frustules during sex might, at times, be a major source of sinking silica (Crawford, 1995) with a large amount of associated particulate organic carbon. On the other hand, short-lived gametes that fail to mate, or cells that undergo PCD, will lyse and release dissolved organic carbon in the euphotic zone. The frequency and environmental constraints for the occurrence of sex in the natural environment are still largely unknown (D'Alelio *et al.*, 2010; Holtermann *et al.*, 2010; Sarno *et al.*, 2010), but these parameters have implications for the genetic structure of natural populations and for their persistence, at least in the case of diatoms that require sex to regain the large cell size. The choice of who to mate with may help maintain biogeographic boundaries if post-zygotic barriers to mating arise before pre-zygotic barriers. Gametes of toxic Group I and non-toxic Group III *Alexandrium tamarense* can mate to form resting cysts, but the hybrid cysts are nonviable, suggesting hybridization might limit range-expansion between closely related species (Brosnahan *et al.*, 2009).

The formation of resting stages represents a key-life cycle trait linking pelagic and benthic phases with implications for population dynamics, species succession patterns and biogeochemical processes. Massive cyst formation can be responsible for bloom termination (Ishikawa and Taniguchi, 1996), and cyst production also represents a survival strategy for the healthy fraction of the population after massive synchronized cell death (Vardi *et al.*, 1999). Benthic stages are 'time travelers', constituting reservoirs of populations/genotypes that can germinate and re-colonize the water column in subsequent years (Wyatt and Jenkinson, 1997), at times with a surprisingly regular timing (Matrai *et al.*, 2005). Cysts and spores are 'resistant' stages that can survive in apparently hostile environments (e.g. ballast waters) and be transported through space, colonizing distant areas. Life strategies including quiescent/resting stages represent a selective adaptation to the variable aquatic environment and allow partitioning the genotype in two different environments, the sediments and the water column, and in different seasons, thus favoring the maintenance of the high diversity of unicellular organisms (Jones and Lennon, 2010).

BECOMING VOYEURS INTO THE PRIVATE LIVES OF PHYTOPLANKTON

Our understanding of the functioning of life cycles in phytoplankton ecology and evolution has been severely limited by lack of data on the life cycle capacities of most species and the difficulty of observing the various life cycle stages and the transitions among them in the natural environment.

Whole genome sequencing has opened great new possibilities to investigate the hidden lives of phytoplankton. *Ostreococcus* and *Micromonas* are abundant prasinophyte members of the picophytoplankton. Sex has never been observed in the lab and would probably be extremely difficult to detect with classic light microscopy in these minuscule cells. Yet whole genome sequencing has revealed a set of genes specific to meiosis conserved between plants, animals and fungi, suggestive of a yet unobserved sexual phase (Derelle *et al.*, 2006; Worden *et al.*, 2009). Genomics-based targeted sequencing of a large number *Ostreococcus* strains recently provided convincing evidence that meiotic recombination is on-going in natural populations of this smallest known free-living eukaryote (Grimsley *et al.*, 2010). As more and more whole genomes of phytoplankton become available, such population-genomics approaches will permit detecting the extent to which meiotic recombination is on-going in other phytoplankton populations.

Another newly available approach to detect life cycle transitions is offered by transcriptomic-based approaches. For example, the 1N cells of the bloom-forming coccolithophore *Emiliania huxleyi* are essentially invisible in the environment by classical techniques, as they cannot be distinguished from other small flagellates or non-calcified 2N *E. huxleyi* cells. Hence, we have no information on the occurrence of 1N cells of this important species. Transcriptomic comparison of 1N and 2N *E. huxleyi* recently revealed that thousands of genes might be only expressed in 1N, but not in 2N cells (von Dassow *et al.*, 2009). Detection of highly 1N-specific mRNAs or proteins (e.g. using QRT–PCR or antibodies) in environmental samples would permit the investigation of the natural history of *E. huxleyi* populations. Similarly, a smaller-scale transcriptomic study of spermatogenesis of the diatom *Thalassiosira weissflogii* revealed the SIG family of genes specifically expressed in centric diatom sperm (Armbrust, 1999), now known to encode the flagellar mastigonemes (Honda *et al.*, 2007). Large-scale transcriptomic sequencing of alternate life cycles of diatoms and dinoflagellates is now on-going. Such studies are now possible because of a dramatic increase in the ability to manipulate phytoplankton life cycles in the laboratory (Chepurnov *et al.*, 2008) and will offer a very extensive molecular toolkit for detecting life cycle phase transitions in phytoplankton in nature.

Deep study of different life cycle phases also offers essential keys for understanding phytoplankton biology and ecology in other ways. Ecophysiologically important characters, including biomineralization, photophysiology, signaling and pathogen susceptibility, vary strongly over phytoplankton life cycles. For example, transcriptomic comparison of 1N and 2N *E. huxleyi* revealed a large number of Ca^{2+}, H^{+} and bicarbonate transporter homologs highly specific for 2N cells and likely involved in calcification in coccolithophores (von Dassow *et al.*, 2009). As another example, the mating system is among the most variable characters between closely related phytoplankton, and gamete recognition genes are among the most rapidly evolving genes in animals and plants (Swanson and Vacquier, 2002). Gamete recognition genes in phytoplankton would offer molecular markers that correlate exactly with the biological species definition. Phytoplankton diversity studies would be revolutionized by a toolkit mechanistically matching a functional definition of the fundamental unit of biological diversity.

The different phases and stages of the life cycle of unicellular organisms reflect both evolutionary history and adaptations to specific ecological conditions. Molecular techniques and genomic approaches now provide new tools to gain information about the functional role of the different life cycle stages, to track them in the natural environment and to approach comparative studies among the phylogenetic diversity of aquatic protists. The apparent high plasticity of phytoplankton genome structures, supported by the existence of transposable elements (Palenik *et al.*, 2007; Maumus *et al.*, 2009) and the occurrence of polyploidization (von Dassow *et al.*, 2008; Koester *et al.*, 2010), suggests genome reorganization might occur at a high rate compared to the rate of morphological evolution in microalgae. Biologically isolated populations might thus be common within the same morpho-species (e.g. Amato *et al.*, 2007). Different life cycle traits evolved over different time scales and show different levels of plasticity (Fig. 2). Plasticity is high at the level of the mechanisms that regulate gamete recognition and/or mating systems: here changes occur over relatively short time scales (Bell, 2005) and lead to the erection of reproductive barriers. Plasticity in life cycle traits is present at the species and supra-specific level, but differences also arise over longer evolutionary timescales. Species can differ in the complexity of their life cycle, in the number of stages and phases included, and in the kind of biotic and abiotic cues that regulate the transition between distinct phases. Finally, the general patterns of

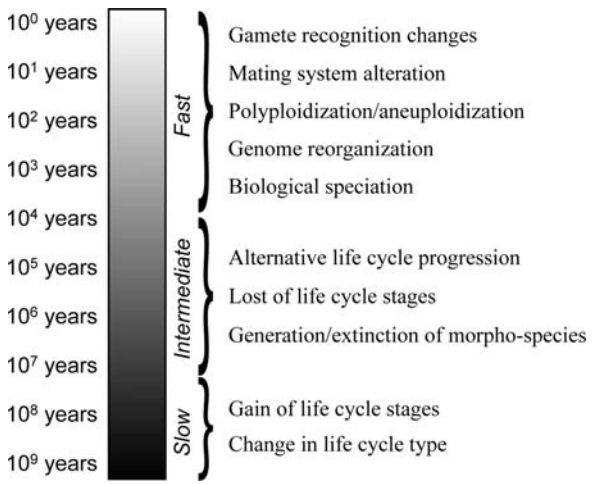

Fig. 2. Timescales at which life cycle variations arise. Fast timescale: mating system changes can occur within 100 s of generations (months to years) in lab populations. Genome duplication may have led to speciation in the diatom *Ditylum brightwellii* on timescales of $\leq 10^4$ years. Intermediate timescale: new coccolithophore and diatom morpho-species appear at time scales of 10^5 to 10^7 years. Alternative life cycle progressions differentiating species must have occurred on timescales equal to or less than that. Slow time scale: addition of new life cycle stages and/or changes in life cycle type (e.g. haplontic to diplontic) are least frequent and differentiate lineages at the class level. These changes appear to arise at time scales on the order of 10^8 years.

life cycle organization, haplontic, diplontic and haplodiplobiontic, are relatively conserved, evolved over considerably longer timescales and characterize groups at the level of high taxonomic ranking (Fig. 2). These considerations shape how we expect adaptation to different environmental conditions to be reflected in distinct modes of life and we will hopefully soon be able to define functional groups of microalgae not only based on their size and/or cell wall covering but also based on their life cycle traits. We are now faced with the achievable challenge of building an ecological and evolutionary framework for unicellular microalgae rooted in their life history traits.

ACKNOWLEDGEMENTS

We thank R. Harris for the invitation to write this article and two anonymous reviewers for constructive comments that improved the manuscript.

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