Thoughts on the evolution and ecological niche of diatoms

MICHAEL J. BEHRENFELD, KIMBERLY H. HALSEY, EMMANUEL BOSS, LEE KARP-BOSS, ALLEN J. MILLIGAN, AND GRAHAM PEERS

1Department of Botany and Plant Pathology, Oregon State University, 4575 SW Research Way, Corvallis, Oregon 97333 USA
2Department of Microbiology, Oregon State University, Nash Hall 226, Corvallis, Oregon 97331 USA
3School of Marine Sciences, University of Maine, 5706 Aubert Hall, Orono, Maine 04469-5706 USA
4Department of Biology, Colorado State University, Biology Building, Room 111, 1878 Campus Delivery, Fort Collins, Colorado 80523-1878 USA

Citation: Behrenfeld, M. J., K. H. Halsey, E. Boss, L. Karp-Boss, A. J. Milligan, and G. Peers. 2021. Thoughts on the evolution and ecological niche of diatoms. Ecological Monographs 00(0):e01457. 10.1002/ecm.1457

Abstract. Diatoms are the most recent major algal lineage added to the geological record, appearing more than 200 million years ago. They are stramenopile protists resulting from a secondary endosymbiotic event that yielded the only photosynthetic protistan lineage expressing external siliceous cell wall structures called frustules. Many diatoms also have large internal vacuoles, and a common assumption in the literature is that success of the diatoms is largely attributable to these two morphological inventions: the frustule for defense and vacuole for luxury nutrient uptake. Here, we revisit the evolution of these inventions, propose sequential steps in frustule development, replace luxury nutrient uptake with predator defense and buoyancy control as the driver of vacuole expansion, and suggest that perhaps the greatest significance of the frustule for diatom evolution is the secondary consequence of enhancing sexual reproduction. In this synthesis, we emphasize a distinction between the “general” success of diatoms and the success of “bloom-forming” species, as the physiological and morphological drivers of these successes differ. Importantly, the bloom-forming species are responsible for the major role of diatoms in aquatic biogeochemical cycles. The bloom-forming habit we ascribe to specific physiological attributes that, at their core, revolve around influencing the balance between diatom growth and losses to predators. We propose that these physiological adaptations are linked to size-dependent maximum division rates in bloom-forming diatoms, because of size scaling of predator–prey interactions. The existence of these bloom-forming species yields an apparent allometric relationship that has previously been interpreted in terms of nutrient acquisition. Our analysis yields insights into species successions during blooms, considers the fundamental benefit of blooming (and subsequent sinking) from a reproductive standpoint, and provides some reinterpretation of diatoms success over geologic time and in the modern ocean.

Key words: diatoms; evolution; phytoplankton blooms; succession.

INTRODUCTION

The North Atlantic Aerosol and Marine Ecosystem Study (NAAMES; Behrenfeld et al. 2019) entailed four field campaigns, each targeting specific events in the annual cycle of phytoplankton of the western subarctic Atlantic. The second of these campaigns took place during the spring bloom climax and one expectation (perhaps naive) was that we would encounter phytoplankton populations dominated by large diatoms. We did not (Bolaños et al. 2020). This surprise sent us down a rabbit hole of reading and thinking about the ecophysiology of diatoms, how physiological and morphological inventions allowed for their late emergence in the geological record, and how these inventions define the success of diatoms in the modern world. Our literature review yielded some important pieces to the puzzle, some conflicting concepts, some reoccurring ideas that need revisiting, and some missing pieces. The current manuscript represents an attempt to tell the diatom story through stepwise inventions and in a manner that distinguishes general attributes from those associated with specific
groups of diatoms. This narrative begins by setting the stage with photoautotroph evolution and diatom emergence and diversification. We then outline a sequence of evolutionary steps leading to the success of diatoms and cast in the framework of primary morphological inventions. A summary “Intermission” is then provided before digging into the more specific question of key adaptations of bloom-forming diatom species, which are summarized in a second Intermission. We then attempt to bring all of the parts together to provide some insights on diatoms over geologic time scales and in the modern oceans, finishing with some thoughts on why we did not observe dominant large diatoms during the NAAMES bloom climax expedition.

**SETTING THE STAGE**

The tree of life and the dates of major evolutionary events are constantly changing as new information and technologies become available. With respect to major developments in photosynthetic organisms, it is currently thought that the first anoxygenic prokaryotic phototrophs emerged around 3 billion years ago (Ba) (Hohmann-Marriott and Blankenship 2011, Fischer et al. 2016). The energetic coupling of two photosystems (Photosystem I and II) to oxidize water gave rise to the oxygenic cyanobacteria between 2.4 and 2.6 Ba (Farquhar and Wing 2003, Buick 2008). The first primary endosymbiotic event producing oxygenic photoautotrophic eukaryotes happened around 1.5–2 Ba, yielding the glaucophyte, red algal, and green algal lineages (Yoon et al. 2004, Parfrey et al. 2011, Ku et al. 2014). This endosymbioses likely involved a bi-flagellated, heterotrophic host, capable of phagocytosis and a cyanobacterium, which ultimately became the chloroplast. A second primary endosymbiotic event occurred very recently (~6 million years ago [Ma]) and gave rise to the genus *Paulinella* (Keeling 2013). The green algal lineage, from which all land plants descend, is thought to have dominated eukaryotic phytoplankton populations from ~600 Ma until a few hundred million years ago (Knoll et al. 2007), with planktonic red algal species being of secondary importance.

At least four, if not more, secondary endosymbiotic events occurred, yielding photosynthetic protists with red algal symbionts (Keeling 2013). Lineages descending from these events that are prominent in modern marine systems are the haptophytes, dinoflagellates, and diatoms. Cryptophytes, which also arose from a red algal secondary endosymbiosis, tend to be less common in natural aquatic systems, have no fossil record, and are estimated to have emerged anywhere from 500 to 200 Ma (Zauner et al. 2000). However, the fossil record has provided clear evidence of dinoflagellates at ~200 Ma and haptophyte coccoliths at ~220 Ma, but biomarker evidence suggests a much earlier appearance of >450 Ma for the dinoflagellates, and molecular clock estimates suggest haptophytes may have an even earlier emergence (Delwiche 2007, De Vargas et al. 2007). Diatoms are clearly a late arrival in the geologic record, with an emergence as early as 240 Ma based on molecular clock data (Kooistra and Medlin 1996, Medlin et al. 1997) and are recorded in fossil records back to ~190 Ma (Sims et al. 2006). A common attribute of these three photosynthetic protistan groups is that they all have significantly armored representatives: cellulose thecal plates in dinoflagellates, calcite scales in haptophytes, and silica frustules in diatoms. Comparable armament is generally not found in the planktonic green algae or cryptophytes, suggesting that the heterotrophic hosts of the secondary endosymbiotic events yielding the haptophytes, dinoflagellates, and diatoms were either armored themselves or carried important precursory metabolisms that enabled evolution of protective structures.

The late rise of diatoms in the geological record suggests physiological or morphological inventions that allowed diatoms to compete for environmental niches previously occupied by both unarmored and armored species. Understanding what these inventions are and the sequence in which they arose is thus of fundamental importance. A current issue in the oceanographic and limnological literature, however, is that diatom success is too often focused on factors that enable them to dominate bloom biomass periodically, rather than other metrics of success (a topic we will return to later). For example, extant diatoms are extremely diverse taxonomically, with recent estimates ranging from tens of thousands to hundreds of thousands of species (Kooistra et al. 2007). Within the planktonic diatoms alone, on the order of 10,000 species have been estimated morphologically and more recent molecular studies are identifying vast numbers of semicryptic and cryptic species (Massana et al. 2004, Kooistra et al. 2007, Malviya et al. 2016). This diversity dwarfs that of all other phytoplankton species combined (Kooistra et al. 2007). Diatoms also span a tremendous size range of <1 μm to a few millimeters (Hasle et al. 1983, Round et al. 1990, Snoeijis et al. 2002) and can be found in almost all illuminated aquatic environments (Mann 1999, Medlin 2016), including wet terrestrial habitats and even hot springs (Richardson et al. 1983). Within this tremendous diversity, only a small fraction of species are known to dominate phytoplankton blooms. Indeed, there appears to be comparable diatom diversity in the oligotrophic ocean (where blooms are rare) as there is at higher latitudes where major blooms are common (Malviya et al. 2016). Thus, the question of what attributes allow some diatom species to dominate blooms is only a subelement to what attributes led to the overall success of diatoms. Here, we start with thoughts on the latter question framed around the unique morphological attributes of diatoms before moving on to the former question.

**MORPHOLOGICAL INVENTIONS: THE FRUSTULE**

Diatoms are stramenopile (or heterokont) protists. A deep branch within the stramenopile tree separates the...
plastid-containing lineages (diatoms, bolidophytes, eustigmatophytes, chrysophytes, phaeophytes, and raphidophytes) from nonplastid lineages. This branch thus corresponds to the secondary endosymbiotic event within the stramenopiles. The host of this endosymbiosis was almost certainly capable of silica metabolism, as siliceous structures (exterior scales, internal skeletons, cysts, frustules) are broadly found in plastid-containing stramenopiles (Bacillariophyceae, Dictyochophyceae, Synuraphyceae, Chrysophyceae, Parmeophyceae, Xanthophyceae; van den Hoek et al. 1995, Graham and Wilcox 2000, Sims et al. 2006). It is unclear whether silica metabolism in this host provided armament (e.g., scales) or served another function, such as a bioactive surface for reactions (i.e., an “inorganic enzyme”) or to improve survival of resting forms (Medlin 2002, Sims et al. 2006). It is interesting that multiple plastidic stramenopile lineages lost the capability for silica metabolism, including the closest relative to the diatoms, the Bolidophyceae. Of those capable of silica metabolism, only the diatoms produce a continuous siliceous cell wall (composed of two valves and girdle bands), although a few Xanthophyceae (i.e., “yellow–green algae”) have valve-like overlapping silicified cell wall structures. The production of external siliceous cell walls, scales, or similar structures is not found in the aplastidic stramenopiles or in any nonheterokont photosynthetic protistan group.

The earliest generally accepted fossil record of diatoms dates back to 190 Ma and includes two distinct species (Sims et al. 2006). This finding, along with the molecular clock date of 240 Ma for the emergence of the diatom line, suggests that a wide diversity of species likely existed before the earliest fossilized specimens. So why are there no older fossils? One potential explanation is that diatoms did not dominate plankton communities for a long time, so the probability of their fossilization (and finding those fossils) is low. Alternatively, early diatoms may have only proliferated in very specialized habitats (making the likelihood of discovering these fossils low), and the emergence of diatoms in the fossil record simply marks a time when sufficient diversification had broadened their niches of success enough that the likelihood of finding fossils became significant. Alternatively, the apparent late arrival of diatom fossils may be linked to the evolution of the frustule itself, its original dominant function, and how this function changed with the evolution of diatom predators.

In the modern ocean, the entire biomass of phytoplankton is consumed and reproduced on average every 2–6 d (Behrenfeld and Falkowski 1997) and it is very likely that a similar high rate of predation existed during the rise of diatoms. In such tightly coupled predator–prey ecosystems, even a modest reduction in loss rates can convey a significant advantage for perpetuating a species (Smetacek 1999). All known diatoms have frustules (although a few modern species can grow when available silica is extremely low [Cylindrotheca fusiformis] or completely absent [Phaeodactylum tricornutum]) and frustules are so precisely constructed and consistent in basic form across genera that it could only have evolved once (Round et al. 1990). It therefore seems far more likely that a siliceous encasement arose at the very beginning of the diatom lineage than that species lacking such an encasement existed and diversified for tens of millions of years with no living representatives. Accepting that the invention of a frustule defined the diatom lineage does not, however, mean that the original frustule was the same as those found today. It may instead be imagined that this first frustule was much thinner than most modern frustules. As noted above, dinoflagellates and haptophytes had already invented armor, almost certainly resulting in the coevolution of a grazing population equipped to handle their armament. If so, then a thin frustule of the original diatoms would likely have conveyed only modest protection against grazers, but the unique structure of this fused encasement would have presented a formidable defense against pathogens (Hamm and Smetacek 2007, Kranzler et al. 2019). And it is this advantage that may have originally opened a niche for the diatoms.

While a thin and fused silica cell wall provides an energetically cheap (Raven 1983) barrier to pathogens compared to the cellulose plates of dinoflagellates (Hamm and Smetacek 2007), it was also accompanied by some significant challenges. First, vegetative diatom cells lack flagellae (only the sperm of centric diatoms remain flagellated), so frustules not only decreased available surface area for nutrient uptake, but the loss of active swimming diminishes nutrient acquisition in patchy environments and limits options for grazer avoidance. A second challenge is that the opal encasement increased cell density and this increased propensity to sink could not be counteracted by flagellar swimming. Fortunately, frustule ballasting (even for the thick frustules of modern diatoms) is only significant (compared to unarmored cells) for diatoms greater than ~10–20 μm in diameter (Munk and Riley 1952, Waite et al. 1997). To overcome this size threshold, diatoms had to either counteract the ballasting effect (see next section) or assume a benthic (or at least, shallow water) lifestyle. Taken together, we might thus envision the first diatoms as small, thin-walled, and likely pelagic. As such, they would sink slowly through the deep ocean, have a high probability of silica dissolution and diagenetic transformation, and thus a very low probability of preservation in sediments of deep ocean plates (which have largely subducted since the time of the early diatoms; Sims et al. 2006). It might also be imagined that the abundance of these early diatoms was modest, as is generally the case for diatoms in today’s oligotrophic regions. Given these considerations, it may not be surprising if fossils of these early diatoms are never found.

An important next step in diatom evolution would be the development of thicker cell walls. A strong selective pressure would exist for thick walls, as it would provide a new protection against grazers (Aitken et al. 2016,
Pancic et al. 2019), as well as viruses able to infect through weak frustules (Kranzler et al. 2019). A secondary consequence of this development would be an increase in sinking rates to the sediments, and thus much higher likelihood of fossil preservation. However, retaining a hold in pelagic ecosystem niches would still require small size until a mechanism for countering sinking evolved. It is noteworthy here that the oldest diatom fossils discovered to date were two species of *Pyxidicula* with robust frustules of 6–14 μm diameter (Sims et al. 2006), which is below the threshold where frustules significantly increase sinking speeds.

An additional consequence of frustule evolution, and one that may in fact be the most important of all, is that it imposed a requirement for sex. The vegetative reproduction cycle of modern diatoms involves the formation of two new theca within the confines of the original two parental theca (Kooistra et al. 2007). Consequently, one of the two daughter cells is smaller than the parent cell by approximately twice the thickness of the theca. After sufficient generations, therefore, vegetative reproduction results in a significant reduction in the average cell size of a given population. Reconstitution to the original parental size requires, at least in most modern species, sexual reproduction (Mann 1999) (note, however, that [1] it is not entirely clear that the same division process and size reduction necessarily occurred across ancient diatom species (Sims et al. 2006), [2] it is possible that size reduction to enhance sexual reproduction is actually an evolutionarily selected trait, and [3] cell size can be expanded asexually in some diatoms; Nagai et al. 1995, Chepurnov et al. 2004). The greater requirement for sex in diatoms (a fortuitous consequence of the frustule) compared to other photosynthetic protists has the very significant advantage of promoting speciation (Mann 1999). For predominantly asexual phytoplankton, speciation potential is largely reflected at the level of genomes (whole organisms) within a population and related to the rate of mutations and gene transfer (McDonald and Linde 2002). In the sexually active diatoms, the more regular genetic recombination implies that speciation potential is better reflected by gene diversity (allele level) and is significantly higher than in asexual lineages (McDonald and Linde 2002). It is further expected that the highest rate of species evolution will exist when asexual reproduction is combined with frequent sexual reproduction, where the sexual phase allows prolonged environmental “testing” (or “amplification”) of recombined genomes before being potentially lost by subsequent recombinations (McDonald and Linde 2002). Indeed, experiments performed on sexual and asexual lines of diplontic yeast suggest that high fitness mutations evolve in parallel if sexual recombination is possible (Leu et al. 2020) In line with these expectations, the most sexually active modern diatom lineages are also the most species-rich (Nakov et al. 2018, 2019).

A related attribute of the diatoms is that all species examined to date are diplontics in their vegetative form (Mann 1999), with only the gametes being haplontic (Sims et al. 2006). This contrasts with many other phototrophic unicellular protists, which are either haplontic or switch between haplontic and diplontic forms (e.g., coccolithophorids, cryptomonads). Although diplody increases the cost of reproduction and may limit the minimum size achievable within the diatoms, it can also have advantages. For example, the number of genetic mutations increases with ploidy level, potentially making diplody advantageous over haploidy for adapting to variable environments (Otto and Gerstein 2008). Diplody also provides an effective means of “masking” deleterious alleles (Crow and Kimura 1965, Otto and Goldstein 1992, Otto and Gerstein 2008) until additional mutations render these beneficial. Haploidy, on the other hand, more rapidly removes deleterious mutations and expresses beneficial mutations in a population (Otto and Goldstein 1992, Otto and Gerstein 2008). In general, diplody is evolutionarily advantageous when (1) deleterious mutations are masked (partially recessive) and (2) there is enough sexual reproduction and recombination in a population (Otto and Gerstein 2008). Thus, for the sexually active diatoms, diplody should be advantageous, whereas haploidy should provide better fitness in the other less-sexual algal lines.

The diatom genome is also noted to have a high number of transposable elements and insertion/deletion mutations (Vardi et al. 2009), and it appears that horizontal gene transfer has been more pervasive than in other phototrophic eukaryotes (Bowler et al. 2008, Keeling and Palmer 2008, Martens et al. 2008). These observations provide additional mechanisms by which diatoms may be able to diversify rapidly.

In summary, a requirement for sex and diplody positioned diatoms for a rapid tempo in speciation, a feature of significant advantage in the pelagic arms race against rapidly coevolving pathogens and grazers (Smetacek 1999) and also for expanding habitat range across diverse coastal and wet terrestrial environments. Indeed, it is in these latter habitats where by far the greatest diatom diversity is found (Kooistra et al. 2007).

**Morphological Inventions: Prominent Vacuoles**

The evolution of vacuoles in diatoms is almost certainly tied intimately to frustule evolution. The previous section proposes an evolution from small pelagic cells with thin frustules to small pelagic cells with thick frustules. A trophic consequence of these latter species would be the evolution of grazers able to “crack” the more robust armament (Hamm et al. 2003). With a finite limit to frustule thickness, this condition would drive diatom evolution toward crossing the size threshold where sinking compromises diatom competitiveness in the pelagic. The advantage of large size, however, is that it increases handling times for grazers and, if sufficiently expanded, can even change the class of grazers to which a given species is susceptible (Kiorboe 1993, 1999).
Transitioning, for example, from fast-growing ciliate and dinoflagellate predators to crustacean predators with complex life cycles can have the very important consequence of making it easier for division rates in a large diatom species to outpace loss rates. This idea and its implications for diatom physiology are developed further in our subsequent sections on phytoplankton blooms and succession.

Attaining great size in a unicellular photoautotroph is problematic if achieved simply through an expansion of cytoplasm volume. Such an approach would be energetically costly if cytoplasmic distances between metabolites and enzymes are to be maintained (i.e., not diluted) and it could cause intracellular self-shading of photosynthetic pigments to increase significantly. Together, these constraints would decrease cell division rates in such a manner that they may completely negate any benefit of reduced grazing with increasing size. Diatoms solved this problem by increasing vacuolar volume in parallel with cell diameter (Fig. 1a). Sicko-Goad et al. (1984) provided a rare data set of diatom vacuole volumes across a range of cell sizes, which was subsequently extended by Raven (1995). Analysis of these data reveals that across three orders of magnitude in cell volume, diatoms maintain a highly constrained average cytoplasmic thickness of ~1–3 μm (Fig. 1b; Strathmann 1967, Hitchcock 1983, Sicko-Goad et al. 1984), which may represent a minimum thickness to accommodate non-scalable cellular components, such as nucleic acids and membrane proteins (Raven 1994, 1998). In other words, cytoplasm is distributed more peripherally along the surface (Litchman et al. 2007) and large size is achieved with minimal impact on required concentrations of cytoplasmic constituents for efficient metabolism (Hitchcock 1983), negligible increases in self-shading (Langdon 1987, Raven 1987, Kooistra et al. 2007), and only a modest reduction in surface area:cytoplasmic volume. The unique ability of diatoms to increase cell size greatly through vacuolar expansions can be credited to their rigid silica exoskeleton scaffolding that allows a large vacuole to be maintained under physical stress and osmotic pressure (Hansen and Visser 2019). One downside of this approach is that large vacuoles add to the energetic cost of cell construction (Raven 1983, 1987).

The emergence of diatoms with thick cell walls and large size would certainly have presented a major challenge to grazer populations not yet evolved to handle such obstacles. Accordingly, the first opportunity may have opened up for diatoms to, at least periodically, achieve very high concentrations. However, without a means yet to counteract associated enhanced sinking rates, these populations of large diatoms may have effectively been restricted to benthic and neritic (frequent turbulent resuspension) environments. An abundance of large diatoms in shallow waters would have notably enhanced opportunities for preservation. From the fossil record, the first well-preserved diatom deposits are from the Aptian-Albian Age (100–125 Ma) and vast diatomaceous deposits (some exceeding 1 km in thickness) accumulated during the Santonian through Maastrichtian Ages (88–65 Ma; Sims et al. 2006). Rapid diversification of benthic species continued into the Eocene (Young and Hopkinson 2017).

In the modern ocean, large diatoms are commonly found in pelagic environments. Although relatively thin frustules can help reduce sinking rates (e.g., Rhizosolenia sp., Ditylum brightwellii), this pelagic lifestyle is largely

![Fig. 1](https://example.com/fig1.png)

**Fig. 1.** Changes in cytoplasm properties as a function of cell volume in diatoms due to vacuole expansion with increasing size. (a) Cytoplasm as a percent of total protoplast volume. Solid black line is least-squares linear regression (% cytoplasm = −0.093 ln [cell volume] + 1.234; $R^2 = 0.64$). Dashed black line is an independent relationship calculated using data from Menden-Deuer and Lessard (2000; Appendix S1). (b) Average cytoplasmic thickness per unit area of surface area. Data from Sicko-Goad et al. (1984) and Raven (1995).
possible because of the evolution of buoyancy regulation involving the vacuole. The sinking rate of dead or highly stressed diatoms increases with cell size in a manner approximately following Stokes’s law (Waite et al. 1997, Miklasz and Denny 2010). However, in nutrient-replete exponentially growing diatoms of greater than ~20-μm diameter, sinking rate is independent of cell size (Waite et al. 1997). Buoyancy control in diatoms is energy dependent (Waite and Harrison 1992, Waite et al. 1997, Du Clos et al. 2019) and involves cellular ion regulation (Anderson and Sweeney 1978, Woods and Villareal 2008), solute adjustments (Boyd and Gradmann 2002), carbohydrate ballasting (Lavoie et al. 2016), and active water pumping (Raven and Dolbin 2014). Diatoms will actively adjust their sinking rates in response to temperature (Bienfang and Szyper 1982), salinity (Bienfang et al. 1982), irradiance, and nutrient concentration (Bienfang et al. 1983). Regulation of buoyancy is perhaps most elegantly displayed in the very largest diatoms, the oligotrophic species of *Rhizosolenia* and *Ethmodiscus*, that mine nutrients by migrating between the surface ocean and nitracline (Moore and Villareal 1996, Richardson et al. 1996, Villareal et al. 1996, 2014, Kemp and Villareal 2018). The need to control buoyancy is a consequence of diatoms getting large. It is not a fundamental trait that defines the late emergence of diatoms in the geological record, however, as small pelagic diatoms and large benthic and neritic species could still proliferate without the ability to control buoyancy. Instead, development of buoyancy regulation following the emergence of large diatoms allowed these species to claim new niches in the pelagic. Giant forms of other taxa (e.g., *Pyrocystis, Halosphaera*) likewise employ large vacuoles to achieve positive buoyancy, so this basic approach is not unique to diatoms.

By providing an instrument for buoyancy control, expansion of the vacuole both created and eventually solved the sinking problem associated with the rise of large diatom frustules. The presence of a large vacuole has also been repeatedly linked in the literature to diatom success for another reason: luxury nutrient uptake (Stolte and Riegman 1996, Marañón et al. 2012, 2015). Here, the idea is that inorganic nutrients can be stored in excess in the vacuole such that, when external nutrients are depleted, diatoms can continue dividing based on intracellular stores, whereas other phytoplankton species cannot. The value of this luxury uptake has been particularly emphasized for patchy nutrient environments (Katz et al. 2004, Tozzi et al. 2004), and indeed multiple models have been developed with this concept in mind to show the diatoms’ advantage (Tozzi et al. 2004, Litchman et al. 2009). Despite its appeal, these ideas are generally invalid. The first problem is that experimental measurements show that diatoms are not distinguished from other phytoplankton groups (including cyanobacteria) in terms of the number of cell divisions that can be supported by intracellular pools once external macronutrients are exhausted (Raven 1984, 1987). The second issue is that the actual number of divisions that can be sustained by intracellular pools is inconsequential. Although it has often been suggested that this number may be a quadrupling of a population (Tozzi et al. 2004, Koioistra et al. 2007, Kemp and Villareal 2018), four divisions on internal nutrient stores have only been reported once and that example was for one phosphate-limited diatom species (Raven 1987). More typically, and as is always the case for nitrogen-limited phytoplankton, the number of divisions supported by intracellular stores ranges from only ~0.5 to ~2, and these values are not just for diatoms but are consistent across the major taxonomic lineages of phytoplankton (Dortch et al. 1982, 1984, Raven 1987).

Furthermore, in natural ecosystems where phytoplankton division rates are perpetually coupled to similar loss rates (Behrenfeld and Boss 2014, 2018), one or two divisions equate to a negligible change in population abundance. Thus, the general idea of vacuolar storage of inorganic nutrients conveying a unique advantage to diatoms in terms of achieving higher biomass than other phytoplankton taxa does not seem to hold. However, there are some additional aspects that may still be worth considering. For example, it is not yet clear if diatoms have any particular advantage with respect to intracellular storage of iron (Marchetti et al. 2009, Lampe et al. 2018). Also interesting is the proposal of Raven (1984) that storage of nitrogen in an inorganic form rather than organic (as in many nondiatom species) may reduce food quality (and thus attractiveness) of diatoms to grazers. Luxury uptake in large vertically migrating diatoms also allows enough nutrient to be stored for the complete journey between the nutricline and high-light, low-nutrient surface (Richardson et al. 1996, 1998).

Finally and as will be revisited below, vacuolar storage of inorganic nutrients may have some significance for bloom-forming diatom species.

**INTERMISSION I**

Earlier, we raised the question about what invention or inventions allowed the late emergence of diatoms in the geologic record and their subsequent success and we distinguished this question from secondary questions regarding attributes of specific diatom groups, such as the ability to achieve biomass-dominating concentrations during blooms. With respect to the late emergence of diatoms, this was in part defined by the (random) timing of when a silica-metabolizing stramenopile became host to a (red-line) primary endosymbiont. This event gave rise to a diversity of plastid-containing stramenopile lineages, but none have been as successful as the diatoms. Within these groups, multiple extant species exist with armament of silica scales, but only the diatoms adopted a fused silica frustule. Although either scales or frustules may provide protection from grazers, the advantage of a fused encasement (even a thin one) is that it may provide a more effective barrier against
pathogens. In the high-turnover world of the plankton, even this limited advantage of a frustule may have enabled the perpetuation of the lineage. This may be particularly true if species exclusion is based less on resource competition (Siegel 1998) than predator avoidance (Guillard and Kilham 1977). But why would such a meager start lead to the grand success of diatoms? To answer this question, we must evaluate what we mean by “success.”

In terms of number abundance, diatoms as a group are unremarkable. In large parts of the ocean (particularly oligotrophic regions), diatoms represent a diverse but background assemblage that sustains its existence in part simply through rarity, which makes them difficult targets for grazers and pathogens because of low encounter probabilities (e.g., Kiorboe 1993). On occasion, some diatom species achieve more impressive numbers, but only transiently, and rarely rivaling the sustained abundance of prokaryotic photoautotrophs and often even chlorophytes and haptophytes (e.g., Liu et al. 2004, Bolaños et al. 2020). And again, the occasional prominence of one or a few diatom species is a subelement in the broader question of diatom success. To this latter question, one metric of success by which diatoms are the uncontroversial champions is species diversity. This success cannot be directly attributed to the diatoms’ two unique morphological inventions: the frustule and large vacuole. As discussed above, evolution of the vacuole in diatoms was likely linked to sequential successes in different environments, but we lack experimental evidence that the vacuole provides an advantage over other photosynthetic protists with respect to nutrient storage, and there is no clear evidence that diatom species diversity changes across the spectrum of nonvacuolated to highly vacuolated cells. With respect to the frustule, its existence does not directly predicate high species diversity, although it can be a platform for diversification (Smetacek 1999).

What we propose here is that the great diversity of the diatoms is a consequence of the enhanced requirement for sexual reproduction because of thecal size reduction during replication and to the endosymbiotic stramenopile host’s retention of diplontic vegetative cells. These two attributes foster enhanced genetic diversity and speciation through rapid evolution of structural defenses (e.g., specific morphologies of the frustule) and biochemistries, with the latter likely being the basis of the large number of semicryptic and cryptic diatom species (Sims et al. 2006).

Hansen and Visser (2019) considered the two defining physical traits—the silica shell and vacuole—as central to the success of diatoms and asked why, if their success is instead due to physiological properties, such attributes have not equally been exploited by nondiatom species. The answer likely lies in the integration of the novel metabolisms between the endosymbiotic host and the engulfed alga. In the case of diatoms, evolution had yielded a host stramenopile that was diplontic and had developed silica metabolism for success as a heterotroph. Following acquisition of a plastid, these attributes enabled the rise of diatoms. Additional host-inherited metabolisms have likely also played an important role in diatom success, such as their complete urea cycle, which, in addition to providing important precursors for silica precipitation proteins, enhances nitrogen and carbon recycling efficiencies (Allen et al. 2011). As discussed in detail in the next section, unique photosynthetic properties of diatoms may be of central importance for bloom-forming species. In summary, endosymbiosis represents an evolutionary quantum leap that is otherwise unlikely, because it merges complex metabolisms of a host and symbiont that have each evolved independently and are based on separate selective pressures. Of the two, it is the unique attributes of the host that are likely most important, because many of the symbiont’s traits will be common with its free living relatives and the plastids of other endosymbioses. We might thus equally assign the rise of dinoflagellates and haptophytes to evolved properties of their respective hosts.

We are now in a position to begin addressing secondary questions regarding the adaptations of some diatom species that allow them to dominate phytoplankton biomass during blooms and what advantage this accomplishment conveys. Here, we adopt the view of Behrenfeld and Boss (2018) where “bloom” is a qualitative term referring to an elevated phytoplankton abundance, rather than assigning an arbitrary quantitative biomass threshold to define a bloom. Also following Behrenfeld and Boss (2018), we focus on processes that allow blooming, which is the condition of temporal increases in phytoplankton biomass that lead to a bloom. Relatively few species within the large diversity of diatoms actually form blooms. So, it is unlikely that the mechanisms permitting these bloom formers are conserved within all diatom species (vacuole size, silicification). This is akin to attributing invasive behavior in some weedy species of plants to characteristics found in all Spermatophytes (e.g., vasculature, seeds, and lignin). However, these characteristics are essential to the success of the group as a whole. Furthermore, cyanobacteria, dinoflagellates, and chlorophytes, which lack these two morphological attributes, are also capable of forming blooms (Langdon 1987, Smayda 1997, Anderson et al. 2012, White et al. 2018). So here again, the most likely explanation for the success of bloom-forming diatoms is physiological.

**HOW AND WHEN TO BLOOM?**

A common statement in the literature is that diatoms dominate blooms because they have maximum division rates ($\mu_{\max}$) that are higher than other phytoplankton groups (Raven and Geider 1988, Mizuno 1991, Snoeijis et al. 2002, Hansen and Visser 2019). But what does this mean? For a given species, $\mu_{\max}$ is defined as the rate of cell division under conditions of saturating light, replete nutrients, and optimal temperature. In classic phytoplankton bloom regions such as the subarctic Atlantic,
the springtime rise in phytoplankton concentration is realized under mixed layer conditions that are largely light limiting. In other words, if \( \mu_{\text{max}} \) for a given species is ever achieved (i.e., nutrients are not exhausted first), it is typically only realized just before the demise of the bloom. Clearly, the simple explanation that diatoms dominate blooms because of their high \( \mu_{\text{max}} \) is insufficient. However, a link between successful bloom-forming diatoms and a high \( \mu_{\text{max}} \) may still exist, but we need to consider the issue in greater detail.

From a photosynthetic perspective, the rate of carbon fixation at low light is, to first order, determined by the total light-harvesting capacity of a given cell’s photosynthetic membranes (“first order” because there are additional pathways besides carbon fixation [e.g., nitrogen reduction, Mehler reaction, midstream oxidases, substrate shuttles, etc.] that can utilize the immediate products of photosynthetic electron transport [plastoquinol, ATP, NADPH; Behrenfeld et al. 2008, Halsey et al. 2010, 2011, 2013, 2014, Halsey and Jones 2015]). At light saturation, the rate of carbon fixation is generally viewed as being limited by the summed turnover capacity of the Calvin–Benson–Bassham (CBB) cycle, in particular the enzyme ribulose bis-phosphate carboxylase-oxygenase (RuBiSCO), the concentration and/or activity of which may be adjusted in response to changing light conditions (Beardall and Morris 1976, Glover and Morris 1979, Steinbiss and Zetsche 1986, Sukenik et al. 1987, Fisher et al. 1989, Glover 1989, Rivkin 1990, Orellana and Perry 1992, Flynn and Raven 2017). Thus, for a diatom species (or any phytoplankton species for that matter) with a high \( \mu_{\text{max}} \), one prerequisite is a high CBB cycle capacity for carbon fixation. In addition, such a species would also have to have a matching uptake and assimilation capacity for nutrients. It can also be advantageous to have a high conversion efficiency between gross carbon fixation (GCF) and net carbon fixation (NCF), with the latter term when divided by cellular carbon biomass being equal to division rate. In diatoms, this ratio can at times exceed 50% (Wagner et al. 2006, Fisher and Halsey 2016). Additional relevant physiological properties of diatoms are summarized in Table 1.

So if a classic oceanic phytoplankton bloom develops under conditions where light within the mixed layer is largely limiting (i.e., carbon fixation rate is limited by light harvesting), then how would a high CBB cycle capacity (i.e., \( \mu_{\text{max}} \)) provide an advantage? An answer to this question arises when we consider the mixed layer light environment in more detail. At all depths in the mixed layer, carbon fixation is light limited early and late in the photoperiod. Light limitation also prevails at depth. At these depths and times, therefore, a cell must increase its light-harvesting capacity in order to increase carbon fixation rates. However, during the middle of the day and nearer the surface, carbon fixation can become light saturated. At these depths and times, an increase in carbon fixation requires an increase in CBB cycle capacity. Thus, in the highly variable mixed layer light environment, phytoplankton can increase daily photosynthesis and growth through either an increase in pigmentation or an increase CBB cycle capacity (Vincent et al. 1994, Cullen and MacIntyre 1998). We can quantify the trade-off between these two acclimation strategies using a simple time- and depth-resolved model of mixed layer light intensities (see Appendix S2 for model details).

The relative benefit of the two acclimation strategies just identified obviously depends on the depth of mixing and the incident light level. For purposes of illustration, we therefore executed our model for mixed layer depths ranging from 50 to 200 m and noon incident photosynthetically active radiation (PAR) intensities ranging from 25 to 1,500 μmole quanta·m\(^{-2}\)·s\(^{-1}\). The resultant time- and depth-resolved light fields were then applied to a photosynthesis-irradiance (PE) relationship to calculate average daily primary production (NPP) (units m\(^{-3}\)). This “baseline” NPP was then compared to two variants of the PE relationship, one where the light-limited slope (α) was increased twofold while the light-saturated rate (\( P_{\text{max}} \)) was held constant and one where \( P_{\text{max}} \) was increased twofold while α was held constant. The salient outcome of the model is that, for all mixing depths, a twofold increase in \( P_{\text{max}} \) yields a significantly greater increase in carbon fixation (i.e., growth rate) than an equivalent increase in α at all daily PAR levels greater than ~5 mole quanta·m\(^{-2}\)·d\(^{-1}\) (Fig. 2), which is a very low light level rarely experienced in the global oceans. Only under extreme low light conditions does the model show a significant advantage of increasing light harvesting over the CBB Cycle capacity. To bring these findings back into context, it is often noted that diatoms dominating blooms are those with high \( \mu_{\text{max}} \) (Raven and Geider 1988, Mizuno 1991, Snoeijjs et al. 2002, Hansen and Visser 2019). However, the significance of this correlation is not that bloom-forming diatoms are growing at \( \mu_{\text{max}} \). Instead, this property equates to an elevated CBB cycle capacity (Table 1) that essentially allows the cells to “make hay when the sun shines” despite an overall low-light mixed layer environment (note that elevated α and \( P_{\text{max}} \) are not mutually exclusive and diatoms with high \( \mu_{\text{max}} \) also increase light-harvesting capabilities in response to decreasing growth irradiance just as in species that have lower CBB cycle capacities; Richardson et al. 1983, Langdon 1987, 1988).

In addition to photosynthetically making the most out of an often deeply mixing and generally light-limiting environment, bloom-forming species must also match enhanced primary production with enhanced nutrient uptake and assimilation. However, although light levels vary greatly with time and depth within the mixed layer over the course of a day, nutrients will likely be uniformly distributed over this layer and, during blooming periods of the annual cycle, generally replete in concentration. This difference will drive contrasting strategies for photosynthesis and nutrient uptake (Clark et al. 2002). As discussed above, making hay when the
sun shines can be effective for enhancing daily photo-
synthesis, but the opposite approach of sustained lower-
level rates is likely most advantageous for nutrient
uptake. Minimizing nutrient uptake transporter sites
and enzymes for assimilation allows a greater fraction of
net primary production to be invested in cell growth. In
diatoms, nutrient uptake into the vacuole and subse-
tive assimilation in the cytoplasm continues in the
dark (fueled by stored photosynthate; Cullen and
MacIntyre 1998, Clark et al. 2002) and provides a means
for minimizing nutrient transporter costs under condi-
tions of energy-limited division (note that dark nutrient
uptake and assimilation is also observed in vertically
migrating dinoflagellates; Cullen and MacIntyre 1998).

At this point, we have discussed in this section physio-
logical attributes of diatoms that can enhance division
rates for a given mixed layer environment. Let us now
consider an environment such as the subarctic Atlantic,
where mixed layer depths shoal and incident sunlight
increases during the spring. The above analysis implies
that, under these conditions, the division rate of a
phytoplankton species with high CBB cycle capacity
and sustained low-level nutrient uptake rates will be fas-
ter at any given time than a neighbor species without
these adaptations (even though both species are experi-
encing identical daily light exposures) and that this dif-
ference will increase through the spring with increasing
PAR and shallower mixing (Fig. 2). However, what this
prediction does not yet tell us is how these differences in
division rate (μ) are related to changes in biomass
because the biomass accumulation rate (l) is also depen-
don loss rates (r):

\[ r_i = \mu_i - l_i, \]  

where the \( t \) subscript refers to a given point in time. For
the perpetually quasiequilibrium predator–prey state of
planktonic ecosystems, the value of \( l \) is related to \( \mu \)
through a temporal offset (i.e., changes in loss rates are
time-lagged with respect to \( \mu \); Behrenfeld 2014, Behren-
feld et al. 2017, Behrenfeld and Boss 2018). Thus, Eq. 1
can be rewritten as

| Table 1. Physiological properties of diatoms and potential relevance to population success. |
|---------------------------------------------------------------|
| Diatom Property                                                | Relevance                                                                 |
| Tightly appressed chloroplast and mitochondria                 | Enhances metabolic coupling of organelles allowing rapid burst exploitation of transient light exposures and fine tuning of energy balance. |
| Rapid response of pigment and nonphotochemical quenching capacity | Rapid photoacclimation maximizes carbon fixation under dynamic mixed layer light conditions. |
| Growth efficiencies                                            | Elevated net/gross carbon fixation ratio enhances division rates for a given light environment. |
| Calvin–Benson–Bassham cycle under allosteric and transcriptional control | Dampens temporal variability in carbon fixing capacity to sustain high \( P_{max} \) values under dynamic mixed layer light conditions. |
| Peroxisomal photorespiration                                   | Enhances net carbon fixation in dynamic mixed layer light conditions. |
| Carbon stored as chrysolaminarin and lipids in cytosol         | Lower density storage product compared to starch contributes to buoyancy. |
| Full glycolytic pathway and acyl chain beta-oxidation within mitochondria | Enables efficient and localized pyruvate processing to fuel TCA cycle and oxidative phosphorylation. |
| Possible C4 carbon fixation in centric diatoms                 | Reduces requirements for membrane carbon transport sites. |
| Complete enzyme system needed for a urea cycle                 | Osmolyte function; long-term N storage; efficient C and N recycling; intermediates: Ornithine feeds polyamine cycle to make unusual proteins involved in silica precipitation, arginine feeds nitric oxide cycle in production of pathogen defense. |
| Secondary metabolites                                          | Cell signaling linked to sexual reproduction; grazer deterrents, some of which induce birth defects. |
| Rubisco and CCM diversity                                      | Coevolution of Rubisco kinetics and carbon concentrating mechanism optimized to native environments. |
| Novel integration of metabolism into energy capture reactions  | Efficient redox cycling between organelles using ornithine-glutamine and branched chain amino acids. |

References:
- Benson
- Bassham
- Broddrick et al. (2019)
- Cullen and MacIntyre (1998)
- Davis et al. (2017)
- Fisher and Halsey (2016)
- Fisher et al. (2004)
- Furnas (1990), Wagner et al. (2006), Fisher and Halsey (2016)
- Kooistra et al. (2007), Allen et al. (2011)
- Maeda et al. (2017), Kroth et al. (2008)
- Matthews et al. (2015)
- Matz et al. (2009)
- Matsuda and Kroth (2014), Young et al. (2016), Shen et al. (2017)
- Pohnert (2000), Miralto et al. (1999), Ianora et al. (2004), Wichard et al. (2005)
- Prihoda et al. (2012), Bailleul et al. (2015)
- Reinfelder et al. (2000), Reinfelder et al. (2004)
- Smith et al. (2012), Jallet et al. (2020)
- Taddei et al. (2018), Anning et al. (2000), Bailleul et al. (2015)
- Wilhelm et al. (2006), Jensen et al. (2017)
- Young and Hopkinson (2017), Trimborn et al. (2009), Matsuda and Kroth (2014), Young et al. (2016), Shen et al. (2017)
- Penta et al. (2021)
- Behrenfeld and Boss 2018
- Behrenfeld et al. 2017
- Behrenfeld et al. 2014
- Lepetit et al. (2017), Penta et al. (2021)
- Kooistra et al. (2007), Allen et al. (2011)
- Pohnert (2000), Miralto et al. (1999), Ianora et al. (2004), Wichard et al. (2005)
- Behrenfeld 2014, Behrenfeld et al. 2017, Behrenfeld and Boss 2018.
Smith et al. (1983) provided a high temporal resolution description of physiological and biomass properties of a phytoplankton community during a springtime stratification event in Bedford Basin between February 9 and March 21, 1978. At the beginning of the time series, dinoflagellates numerically dominated the phytoplankton community, followed by flagellates and then diatoms (Fig. 3a–c; see Appendix S3 for data details). The concentration of all three populations was exponentially increasing over the first half of the record, with rates of increase following: diatoms > flagellates > dinoflagellates (Fig. 3a–c). The slight advantage of the diatoms under these low light conditions is consistent with the concepts discussed above. The value of $\mu_{\text{max}}$ for dinoflagellates and flagellates is typically lower than bloom-forming diatoms (Chan 1978, 1980) and, for the two former groups, was apparently reached by ~Julian Day 60. With an inability to accelerate $\mu$ further, loss rates quickly caught up and terminated the bloom of these two groups (Fig. 3a, b; for the dinoflagellates, these losses were purportedly dominated by rotifer grazing; Smith et al. 1983). By contrast, higher $\mu_{\text{max}}$ of the diatoms allowed their concentrations to continue rising at a constant rate for the entire observational period (Fig. 3c). As cell division rates were rapidly increasing with time (green line in Fig. 3d), this relatively stable rate of accumulation ($r$) implies that diatom loss rates were only slightly lagged behind division rates (red line in Fig. 3d). As anticipated above, the time-resolved record for $r$ (black line in Fig. 3d) was effectively captured by $\Delta \mu = \frac{\text{d} \mu}{\text{d}t}$ (brown line in Fig. 3d). Thus, the large range between $\mu_{\text{min}}$ and $\mu_{\text{max}}$ and the associated ability to take advantage of brief periods of high light in the mixed layer, allowed the diatoms to sustain accumulations in biomass over a longer period than the dinoflagellates and flagellates and, accordingly, dominate biomass at the end of the observational period. In addition to generally having a lower $\mu_{\text{max}}$ than bloom-forming diatoms, the more abbreviated accumulations in dinoflagellate and flagellate biomass might also reflect a mixotrophy-enabled elevation of winter $\mu_{\text{min}}$ in these taxa, which would also contribute to their smaller $\mu_{\text{min}}$–$\mu_{\text{max}}$ range.

Here, we have focused on specific physiological adaptations associated with photosynthesis and division rates that can favor diatom dominance in classical open ocean blooms. Certainly, additional adaptations can be considered that enable blooming, such as under eutrophic conditions or during a toxic diatom bloom, but a commonality among these physiological approaches is their ability to impact temporal imbalances between division and loss rates.

**Cell Size and Bloom Succession**

Allometric scaling is a common central assumption in trait-based modeling of competition and succession in planktonic ecosystems (Litchman et al. 2009). Although a relationship between metabolic rate and size is
undeniable over a broad range in complex organisms with fractal distributions systems (e.g., blood flow; West et al. 1997, 2002, Agutter and Wheatley 2004), it is not clear that such scaling is applicable to single-celled phytoplankton. Indeed, Raven (1995) has stated that a mechanistic explanation for allometry in phytoplankton has largely evaded us (see also Chisholm 1992, Wirtz 2011). One argument for size-dependent maximum growth rates is that an increase in size decreases the surface:volume ratio and thus limits nutrient uptake.

However, this conclusion depends on an assumption that the cell membrane is saturated with respect to nutrient uptake sites, which is unlikely (Raven 1995) and has not been demonstrated experimentally. With respect to diatoms, it is also important to recognize that the relevant issue is not the surface:volume ratio, but rather the cytoplasmic volume served by a given area of cell surface (Snoeijs et al. 2002, Behrenfeld et al. 2008), which is weakly dependent on cell volume (Fig. 1b). There is also experimental evidence that size-dependent maximum division rates cannot be attributed to simple geometric considerations such as surface:volume ratios. For example, Eppley (1977) found that this size dependence may be observed between species, but it does not exist within a given species that shows a large range in sizes. Bergkvist et al. (2018) observed that large *Chaetoceros* cells assimilated nitrogen significantly faster than the smaller *Skeletonema* cells. Raven (1987) also noted that the concentration of vacuolar nutrients does not vary significantly between different-sized diatoms. This observation implies that, with every division (which will dilute vacuolar nutrients in half for each daughter cell), large diatoms take up significantly more nutrients than smaller diatoms (Lomas and Glibert 2000) to

---

**Fig. 3.** Phytoplankton community properties over a 40 d observational period in Bedford Basin during the spring of 1978. (a) Log of dinoflagellate cell concentration. (b) Log of flagellate cell concentration. (c) Log of dinoflagellate cell concentration. (d; left axis) Phytoplankton specific division rate ($\mu$; green line), specific loss rate ($l$; red line), and specific accumulation rate ($r$; black line) and (right axis) specific rate of change in division ($\Delta \mu$; brown line). Horizontal dashed blue line indicates zero change. Data from Smith et al. (1983).
Concepts & Synthesis

reconstitute original vacuolar concentrations (Dorch
1982), which is an unlikely phenomenon if nutrient
uptake is limiting division for large cells. Direct mea
surements by Marañón et al. (2013) showed that maxi
mum nutrient uptake rates scale linearly with size,
indicating diffusion and membrane uptake are not pri
mary limitations. In his study, intracellular assimilation
of nutrients appeared to be the basis for deceased maxi
mum division rates with increasing size. Clearly, we need
to rethink why a dependence of \( \mu_{\text{max}} \) on size might exist
and what might be the evolutionary driver.

For this assessment, we have compiled a (nonexhaus
tive) data set of light- and nutrient-saturated division
rates from the literature (Fig. 4). Although these data
may not truly represent \( \mu_{\text{max}} \) values for a given species if
growth conditions were not optimal (e.g., temperature),
if we take these data as representative, then a few funda
mental conclusions can be drawn. First, there is not a
clear dependence of \( \mu_{\text{max}} \) on size, but rather the envelope
under which the \( \mu_{\text{max}} \) values fall roughly decreases with
increasing size at cell diameters greater than \( \sim 5 \mu m \)
(Marañón et al. 2013) (note, \( \mu_{\text{max}} \) decreases in smaller
cells are potentially due to issues with “nonscalable”
components; Raven 1994). In other words, many smaller
species have maximum division rates similar to larger
species, but some smaller species have evolved excep
tional division capacities. Second, the species with
exceptional \( \mu_{\text{max}} \) are often (but not always) diatoms
(Banse 1982, Furnas 1990), noting here that Fig. 4 does
not include documented examples of diatom division
rates exceeding 4 d\(^{-1}\) (e.g., Thomas 1966, Furnas 1990,
Ichimi et al. 2012).

If we ask the question, “why does the envelope for
\( \mu_{\text{max}} \) decrease with increasing cell size?”, our tendency is
to search for an explanation focused on how large size
prevents high division rates, with an example answer
being surface:volume based arguments (see above).
However, what if we reverse the question and ask
instead, “why have some smaller species evolved a capac
ity for very high division rates?” When asked this way,
the focus of the question shifts toward why smaller spe
cies might need to divide faster than larger species and
the problem becomes more of an issue in ecology than
one of physical constraints imposed by large size.

To answer this latter question, we should recall a few
concepts from above. First, the evolution of large size in
diatoms is likely driven primarily by predation, where
increasing size (via an actual increase in cell volume or
an effective increase in size via chain formation, setae,
or organic thread formation; Verity and Villareal 1986)
increases handling times by small predators and can
change the class of primary predator to one with a com
plicated life cycle. Second, \( \mu_{\text{max}} \) is related to CBB cycle
capacity. And third, the biomass accumulation rate for
a given species should, to first order, vary with the acce
leration rate in cell division, because of a temporal lag
between division and loss rates. In Eq. 2, this temporal
lag is represented by \( i' \) and the expectation is that \( i
\) increases with increasing cell size. We can now pull these
concepts together into a simple mathematical model (see
Appendix S4 for model details). In this model, mixed
layer growth conditions improve over time in response
to changes in incident PAR and mixed layer depth that
roughly resemble subarctic Atlantic-type spring condi
tions. We then describe three size classes of bloom-
forming diatoms where \( \mu_{\text{max}} \) decreases from 2 d\(^{-1}\) to 1
d\(^{-1}\) with increasing size and \( i \) increases with size from
1.7 d to 3 d (Appendix S4). For each size class, the divi
sion rate accelerates in time in proportion to \( \mu_{\text{max}} \) and
then the bloom of that size class terminates when \( \mu = \mu_{\text{max}} \).
The outcome of the model is that each size class
achieves essentially the same maximum concentration
(assuming no nutrient exhaustion), but the smaller cells
dominate earlier in the spring, followed by the medium
sized cells and finally the large cells (Fig. 5). This succe
ssion in size class is consistent with classical field observa
tions (Guillard and Kilham 1977, Smayda 1980) and is
opposite the succession expected if size-dependent nutri
tent uptake (i.e., surface:volume arguments) was a pri
mary driver. Thus, the apparent upper envelope in \( \mu_{\text{max}} \)
as a function of cell size (Fig. 4) is a consequence of
small bloom-forming species needing to accelerate divi
sion rates rapidly to outpace closely coupled losses to
rapidly reproducing small predators. For larger cells,
the longer lag between division and loss rates has dimin
ished the selective pressure for very high \( \mu_{\text{max}} \), enabling
bloom-level biomass to be achieved with only modest
investments in CBB cycle capacity (and, accordingly,
modest nutrient assimilation rates as observed by
Marañón et al. 2013). In other words, the apparent allo
metric relationship between \( \mu_{\text{max}} \) and cell size is a conse
quence of predator–prey dynamics, not physical
constraints on nutrient uptake (Guillard and Kilham
1977, Hansen and Visser 2019). Our simple model also
provides some insight on why there are no uber-diatoms
that can exploit all periods of the blooming phase (Guil
lard and Kilham 1977). Specifically, physiological accli
mations that allow early blooming (i.e., enhanced CBB
cycle capacity, enhanced light harvesting) lead to a rapid
achievement of \( \mu_{\text{max}} \) at which point division rate can no
longer accelerate and losses catch up, whereas for larger
species with slower acceleration rates blooming can be
prolonged.

Why Bloom and Why Sink?

It may be envisioned that the act of blooming is one
mechanism to combat extinction, as it ensures that when
the post-bloom period of decreasing abundance ends
and conditions once again become favorable, enough
individuals remain to recreate a bloom and thus con
tinue the cycle. This explanation, however, is inconsis
tent with dominant diatom species during spring blooms
typically being among the least abundant species at
other times of the year. In other words, blooming has
the apparent opposite effect of that suggested above.
and, indeed, it is more often that background species during a bloom climax dominate during winter (e.g., Irigoien et al. 2005, Bolaños et al. 2020). It has therefore been proposed that radical biomass variability over the annual cycle is a central element in the bloom-forming life strategy because of its impacts on predator–prey dynamics (Bakun 1997, Behrenfeld and Boss 2014).

If we think a bit more about the phenomenon of blooming, it could be argued that it is, in fact, a risky life history strategy. By achieving a high concentration, a bloom-forming species ensures that it simultaneously supports the development of a large grazer population that will rapidly decimate bloom biomass postclimax. Reaching a high concentration also makes a species much more susceptible to the density-dependent spread of pathogens. Thus, it may not be surprising at all that dominant bloom-forming diatom species tend to be rare at other times of the year. Better to sustain a modest concentration throughout the year, as most phytoplankton species do, and thus decrease targeted grazing and viral and pathogen attack.

Given the above arguments, we need to search for an alternative explanation for why certain species have a tendency to bloom. Blooming must convey a significant evolutionary advantage because the ability to bloom is associated with specific physiological inventions (see How and When to Bloom, above). Morphological adaptations (e.g., specific armament features) may also be associated with blooming (Smetacek 2001), but even in diatoms this link is not so clear as features such as spines or cell size do not distinguish bloom-forming species from nonblooming species (e.g., Villareal et al. 2012, Leblanc et al. 2018). One might argue that the evolution of bloom-forming physiologies is simply a “selfish gene” phenomenon, allowing a disproportionate acquisition of resources at the expense of other species. But given the above considerations, this explanation seems weak, because the generated biomass will be rapidly consumed...
and regenerated for use by other species and because of the
viiral and pathogen threat. One might counter this
argument by suggesting that the generation of a large
number of individuals increases the likelihood of muta-
tions and thus continued evolution of a species, but it is
not clear why a brief period of high abundance followed
by a prolonged period of very low abundance would be
advantageous for speciation compared to simply sus-
taining a modest abundance and division rate through-
out the year. For bloom-forming diatom species,
however, perhaps a related argument can still be made.
We earlier proposed that a key element in the overall
success of diatoms is their enhanced requirement for sex-
ual reproduction, which (along with being diplontic)
enables rapid speciation as an advantage in the perpet-
ual arms race of the plankton. We add to that here by
suggesting that a bloom-forming tendency also has
advantages for sexual reproduction and thus evolution
of a species. By reaching a high concentration, the likel-
hood of successful sexual reproduction increases, and in
particular the potential for cross-fertilization of gametes
between distantly related individuals (i.e., some diatom
clones produce self-compatible sperm [from smaller
cells] and eggs [from larger cells]; Koester et al. 2007,
which is beneficial when sexual reproduction is required
at low abundances). In other words, the evolution of
physiological attributes that allow a given diatom spe-
cies to sustain accelerations in division rate for a suffi-
cient duration to achieve high concentrations may be
based on improvements in sexual reproduction success
that enhance genetic invention. If this is the case, then
this advantage will be enhanced if sexual reproduction
of a population is coordinated and especially if it is com-
municated or triggered once the population has achieved
its critical density (Edlund and Stoermer 1997, Sterner
and Elser 2002, Moore et al. 2017). Recently, it was
shown that sexual division in the diatom, *Thalassiosira
pseudonana*, can be experimentally triggered by high
concentrations of ammonium, but only after reaching
maximal cell density (Moore et al. 2017). Chemically
coordinated synchronization of sexual reproduction has
also been indicated in other diatom species, along with
the exudation of chemotactic pheromones that may be
involved in optimizing encounter rates between eggs and
sperm (Koester et al. 2007, Amin et al. 2012). Clearly,
the success of this approach increases as population
number increases. Interesting observation in cultures
show that growth rates of *Thalassiosira weisflogii*
increased with decreasing cell size until the threshold for
sperm induction was reached (Von Dassow et al. 2006)
and that growth rates of cells of *T. cf. gravida* that
underwent significant cell size reductions were higher
than growth rates of their sexual products (Lyczkowski
and Karp-Boss 2014).
If the evolution of bloom-forming diatoms is linked to
sexual reproduction, this does not mean that every time a
given species blooms it will necessarily result in a sexual
cycle. As noted above, the requirement for sex in diatoms
is enhanced because frustule replication results in a tem-
poral diminishing of the population size distribution (not-
ing that larger diatom species can tolerate greater size
reductions than smaller species before sexual reproduc-
tion is required: [Round et al. 1990], which is perhaps
another reason why highest $\mu_{\text{max}}$ values are found in
smaller diatom species). However, if the coordinated sex-
ual reproduction just discussed occurs for a population,
its required time interval based on mean population size
dimination may be significantly longer (e.g., many years)
than the repeat cycle of blooming (annual or shorter).
Indeed, sexual cycles in some diatoms (auxospore to aux-
ospore) can be separated by up to 20 yr or more (Round
et al. 1990). In such cases, it might seem conceptually
advantageous to bloom only during those years when
coordinated sex is required, but such a strategy would be
evolutionarily complicated. In contrast, developing a
physiology targeting specific environmental conditions
that are roughly replicated during each annual cycle
would result in predictable blooms, only some of which
are associated with coordinated sexual reproduction. One
might expect that the value of coordinated sex is particu-
larly acute in the pelagic. In benthic species, coordination
may have little value and, indeed, Round et al. (1990)
noted that one can almost always find sexual cells in ben-
thetic populations, although they are rare.
The above considerations may be related to another
interesting phenomenon in diatoms: mass sinking
events. As discussed above, diatoms of all sizes have
minimal sinking rates under favorable growth condi-
tions. However, sinking losses of diatoms often become
significant when concentrations become elevated. One
simple explanation for such events is that high abun-
dance leads to more cells “bumping into each other”
(i.e., higher encounter), creating sinking aggregates
(Kiorboe 1993, Jackson 2001). Although aggregate for-
mation is an undeniable physical process at high concen-
trations, mass sinking events in diatoms appear to be
more of a coordinated phenomenon than a random one.
For example, during the 2008 North Atlantic Bloom
Experiment (NABE08), a massive export event was doc-
umented where diatoms contributed 99% of the mea-
sured sinking flux (Rynearson et al. 2013). What was
interesting about this event was that 35%–90% of the
flux was attributable to a *Chaetoceros* species that only
comprised 1%–5% of the surface diatom community
and these *Chaetoceros* cells left the surface photic layer
(many in the form of high-density resting spores) while
inorganic nitrogen and silicic acid concentrations were
still replete (see also Allredge et al. 1995). In other
words, something triggered a relatively rare species to
terminate buoyancy regulation and exit the photic zone.
Another characteristic of the event was elevated levels of
transparent exopolymer particles (TEP), which has the
general (i.e., nonspecific) effect of increasing the forma-
tion of sinking aggregates.
Mass sinking in pelagic diatoms at first appears a
counterintuitive sequel to a bloom. One potential
explanation for mass sinking is that it coincides with cells near the surface becoming physiologically stressed and simply losing the ability to maintain buoyancy, which is a response to stress that has been experimentally demonstrated (Eppley et al. 1967, Smayda 1970, Walsby and Reynolds 1980, Richardson and Cullen 1995, Waite et al. 1997). Extension of this concept has led to the proposal that, under postbloom conditions, diatoms sink below the euphotic zone to essentially create a seed population that will be re-entrained into the mixed layer along with elevated nutrients during the winter and thus act as the starting population for a bloom the following year (Smetacek 1985). However, there are two issues with this concept. First, the sinking diatoms would have to re-establish neutral buoyancy once they reach the sub-euphotic depth at which they will reside until deep winter mixing. Unfortunately, buoyancy regulation is energy dependent and, below the euphotic zone, the cells would soon deplete energy reserves and once again start sinking. Furthermore, if the sinking flux is largely in the form of resting spores (e.g., NAB08), buoyancy regulation is unlikely. Second, it has never been demonstrated in pelagic systems that subeuphotic seed populations constitute an abundance that is comparable, for a given species, to that which still resides and is actively growing in the euphotic zone (implying that the seed population is inconsequential to subsequent blooming).

Raven and Waite (2004) alternatively suggested that sinking was a mechanism that improved population success by removing infected or otherwise compromised cells and that, in fact, this function may have been the original basis for silica metabolism in diatoms. Specifically, they proposed that pathogen or virally infected cells would lose the capability for active (energy-demanding) buoyancy control, experience a significant increase in proplast density, and thereby effectively remove themselves from the remaining healthy cells. A challenge to this concept, however, is that it is not easily reconciled with what at times appear to be population-coordinated sinking events (e.g., the NABE08 Chaetoceros event), as opposed to a slow and continuous raining of infected cells over time. It also entails an element of altruism that is difficult to justify, although Kooistra et al. (2007) proposed that such behavior may be envisioned in populations largely composed of directly related daughter cells.

A third possibility, and one that we propose here, is that mass sinking is yet another element linked to diatom sex. Above we suggest that bloom-forming diatom species have evolved specific physiologies that allow the attainment of high cell concentrations to improve the likelihood of successful cross-fertilization of gametes. We also note that attaining bloom concentrations has the adverse consequence of increasing grazer populations and the spread of disease. Accordingly, one effective means to reduce losses of progeny (or the weakly silicified auxospores; Raven and Waite 2004) following sexual reproduction would be simultaneous triggering for the remaining cells to sink (Karl et al. 2012). A simultaneous increase in aggregate formation through TEP production would also contribute to this end. Although triggered sinking following sexual reproduction has never been shown in the laboratory or field (it has never been looked for), this behavior would be far from altruistic, as it would aim to enhance survivorship of sexually produced offspring at the expense of other individuals by rapidly reducing both targeted grazing and the density-dependent spread of pathogens. Phenomenologically, such a strategy can help reconcile observations of strongly species-dependent sinking events under favorable growth conditions, such as observed during NABE08. It is noteworthy here that, in the experimentally triggered study on Thalassiosira pseudonana (Moore et al. 2017), sexual reproduction was accompanied by a high level of TEP production (K.H. Halsey, personal observation). Crawford (1995) also provided strong evidence of coordinated sexual reproduction in the centric diatom, Corethron criophilum, during a bloom climax in the Southern Ocean.

Up to this point, we have largely been considering the counterintuitive occurrence of mass sinking events under pelagic conditions where the water column is far deeper than the annual maximum mixing depth. For neritic environments where resuspension of the sediments is far more likely, sinking can play another important role. Earlier, we related the phenomenon of blooming to the acceleration of division rate. For the pelagic, annual minima in bulk phytoplankton biomass appears to be relatively constrained (although greater variability may exist at the species level) and independent of maximum mixing depth (Behrenfeld 2014), leading to the hypothesis that this annual minimum is related to thresholds for grazing (Reeve and Walter 1977). Under conditions of relatively uniform initial population abundances in the pelagic, the magnitude of a given species’ bloom will thus be largely determined by the difference between the annual minimum and maximum division rates and the degree of coupling with loss rates. Accordingly, one might expect blooms in the pelagic to achieve modest climax concentrations generally. By contrast, diatoms in shallow neritic environments can, postclimax, sink to the sediments and even encyst, thereby creating a resilient seed population (Pitcher 1990, Lewis et al. 1999, Broman et al. 2017) of an abundance significantly greater than that (for a given species) of individuals that reside throughout the year within the water column. If resuspended during the blooming phase, this seed population adds another dimension to the properties defining bloom climax concentration. Specifically, a large resuspended seed population can be an important element to the commonly observed larger blooms found in coastal environments compared to strictly deep pelagic regions. Chlorophytes, dinoflagellates, and prasinophytes also commonly form resting cysts and can be common in coastal picoplankton assemblages (Heiskanen 1993, Kooistra et al. 2007).
Pigments and Blooming

Absorption by water has a spectral minimum at ~440 nm and then increases at both longer and shorter wavelengths (Kirk 1994). In open ocean regions, phytoplankton typically experience light intensities that are subsaturating (i.e., limiting) and blue at most depths within the euphotic layer and during most times of the day. Under these conditions, the most energetically efficient photoacclimation strategy is to invest in chlorophyll molecules, and the green algal (chlorophyte) lineage of the original primary endosymbiotic event has largely followed this strategy. Diatoms, on the other hand, inherited a red-line plastid and have light-harvesting antennae for photosynthesis with strong contributions from fucoxanthin, which absorbs in the blue–green to yellow–green part of the visible spectrum (~450–540 nm). The production of fucoxanthin appears to have arisen from a series of gene duplication events where protein function was modified to produce a pigment absorption at green and yellow wavelengths (G. Peers, personal observation). Integrating fucoxanthin in the light-harvesting antenna involved distinct changes in the conformation of the pigments within the membrane-bound fucoxanthin binding proteins (FCPs, which also bind chlorophylls a and c). These changes allow for efficient toggling between light harvesting and excess light quenching states (Nagao et al. 2019, Pi et al. 2019).

Given the “blue nature” of most pelagic underwater light environments, what advantage might the evolution of fucoxanthin pigments convey? If we consider our earlier proposed evolution of large nonbuoyant species, it may be envisioned that the spectrally broad absorption of diatoms can be advantageous, as it remains today, for colonizing benthic or neritic environments where concentrations of colored dissolved organic matter (which absorbs strongly at blue wavelengths) in the water column can be high. But what might be the advantage for pelagic bloom-forming diatoms? As discussed above, bloom-forming species benefit from high CBB cycle capacities and this advantage is realized near the surface where the incident light spectrum is still broad, so a broad pigment absorption spectrum that depletes the underwater light field more slowly as biomass increases compared to predominantly chlorophyll-based taxa and an ability to continue nutrient uptake in the dark, which improves resource economy by decoupling nutrient acquisition from the highly variable rate of photosynthesis. With regard to blooming attribute (3) above, it appears that significant constraints exist (but are not well understood) on the minimal biomass of pelagic species prior to blooming (Behrenfeld 2014), whereas in neritic systems a large seed population of resting stages in the surface sediments prior to blooming can significantly enhance the magnitude of blooms once favorable growth conditions ensue.

Since the early, net-based studies of phytoplankton annual cycles, it has been noted that diatoms are commonly dominant biomass contributors to the bloom climax. This correlation is often attributed to the protection from predation afforded by a frustule (Smetacek 2001), and in some cases even certain structures of specific frustules (Smetacek 1985). Although protection is certainly important, it does not seem that attributes of a frustule are central to diatom success during blooms. More specifically, all extant diatoms have frustules, yet only a limited number of species bloom and, while bloom-forming species often have notable structural grazing deterrents such as large size, chain formation, and spines (Smetacek 1985), blooms of single-celled small or spineless species have also been recorded (e.g., Villareal et al. 2012, Léblanc et al. 2018). That being said, the striking morphological diversity of diatoms must clearly be linked to fitness. Chain morphologies in particular have been of considerable interest and are viewed as balancing trade-offs between grazing pressures and metabolic constraints. Although individual cells in a chain can remain small, the chain structure
increases effective size and thus influences size-selective predation (Smetacek et al. 2004, Bergkvist et al. 2012), encounter volumes (Karp-Boss and Jumars 1998), and the frequency of collisions between chains, with consequences for sexual reproduction (Kooistra et al. 2007). Although this life form is not unique to diatoms, it appears more prevalent among diatoms and appears to have been acquired independently by several lineages (Kooistra et al. 2007).

Here we have asked a question about diatom blooms that is not common in the literature: Why do it? By recognizing the significant drawbacks of achieving high concentrations, this question leads us to the proposition that blooming (as well as synchronized mass sinking) is largely a strategy linked to sexual reproduction and evolved in specific taxa (rather than diatoms as a whole) through unique physiological attributes. This conclusion then begs the question of when these bloom-forming physiologies emerged in the history of diatoms.

**DIATOMS OVER GEOLOGICAL TIME**

Today, diatoms are seasonally prominent (in terms of biomass) in the nutrient-enriched and colder waters of coastal upwelling systems and higher latitudes. However, these are not the conditions under which diatoms largely evolved. An emergence date between 190 and 240 Ma places the rise of diatoms in the warm middle Triassic to lower Jurassic periods (Fig. 6). Continued diversification and habitat expansion continued through the warm Cretaceous period, with the first massive diatomaceous deposits of benthic, epiphytic, and neritic species being formed from roughly the Albian (115–100 Ma) to Maastrichtian (72–66 Ma) ages (Fig. 6; Gersonde and Harwood 1990, Harwood and Gersonde 1990, Nikolaev and Harwood 1997, Sims et al. 2006). Throughout the Mesozoic Era (Triassic, Jurassic, Cretaceous), it is thought that a two-cell Hadley circulation existed with nearly uniform temperatures over the surface of the Earth (Tozzi et al. 2004). The resultant weak latitudinal thermogradients would have been associated with dampened winds and mixing (Huber et al. 1995) and likely more stratified and nutrient deficient pelagic mixed layers. Accordingly, large open ocean diatom blooms would have been rare, consistent with an absence of significant diatomaceous deposits from pelagic sites during this period (Racki 1999, Ikeda et al. 2017), but a background presence of pelagic diatoms may have existed, as it does in today’s oligotrophic regions (Malviya et al. 2016).

Major innovations in morphology, ecology, and life cycle (e.g., multipolar centrics, araphid and raphid pennates) appeared to have occurred in benthic diatoms and it has been proposed that these populations provided diverse innovations to be “tried out” in the pelagic (Kooistra et al. 2007). In the pelagic domain, it was earlier thought that rapid diversification occurred in the early Miocene (Falkowski et al. 2004a,b), but subsequent sample-standardization analyses have revealed that a rapid rise in diatom diversity occurred between 35 and 40 Ma during the Eocene Epoch (Rabosky and Sorhannus 2009), which we propose might correspond to the evolution of buoyancy regulation (Fig. 6). The Earth’s climate was still warm at this time, but during the Eocene-Oligocene transition (~35 Ma), the climate began to cool and ocean conditions became progressively more...
turbulent (Chandler et al. 1992, Barron et al. 1995). By the beginning of the Miocene around 23 Ma, the Drake Passage was fully opened, extensive permanent ice existed at the poles, and Earth had fully entered into its current state of glacial–interglacial periods driven by Milankovitch Cycles (Fig. 6). For the diatoms, which had evolved for >150 million years under warm conditions (Kooistra and Medlin 1996, Medlin et al. 1996), the Eocene–Oligocene transition was a major event and corresponded to an ~50% reduction in pelagic species diversity by the beginning of the Miocene, from which diversity has never fully recovered (Rabosky and Sorhannus 2009). However, as evidenced by the comparable diversity of diatoms in modern high latitude and oligotrophic waters (Malviya et al. 2016), this drop in diversity should not be taken as a proxy for productivity (counter to the assumption of Rabosky and Sorhannus 2009).

After the establishment of polar ice caps, the Hadley circulation changed dramatically (Crowley and North 1991), yielding more intense thermohaline circulation, greater wind speeds, decreased upper ocean stability (Chandler et al. 1992, Barron et al. 1995), and increased nutrient availability (Follini 1996). Compared to pre-Oligocene times, these conditions would equate to more extreme event-scale to seasonal oscillations in phytoplankton division rates. In other words, $\mu_{\min} - \mu_{\max}$ differences within nutrient-replete mixed layers would have increased, providing new opportunities for the proliferation of diatoms with the bloom-forming physiologies discussed above. Thus, we propose that despite the Eocene–Oligocene transition causing a major decrease in diatom diversity, it simultaneously enabled the first basin-scale pelagic blooms of a subset of diatom species with the necessary physiological adaptations to capitalize on strong temporal changes in mixed layer light conditions. The coincident expansion of savannah and grassland habitats may have contributed to the prominence of pelagic blooms by increasing ocean soluble silicon to meet the demands for enhanced diatom biomass (Fig. 6; Retallack 2001, Falkowski et al. 2004a,b). A link between upper ocean stability and mixing during the latter half of the Cenozoic Era is further supported by opal deposition records. Interglacial periods correspond to lower average wind speeds, stronger upper ocean stratification, and weaker thermal gradients between the equator and poles than during glacial periods (Huber et al. 1995, Tozzi et al. 2004). Accordingly, temporal changes in division rates will be constrained during interglacial times and, thus, opportunities for pelagic bloom-forming diatoms to proliferate are more limited (particularly for large diatoms; Fig. 5). Sediment records show that opal deposition rates are reduced during interglacial and enhanced during glacial periods.

**DIATOMS IN THE MODERN WORLD**

We currently do not have a robust estimate for the contribution of diatoms to global ocean annual net primary production (NPP). Publications by Nelson et al. (1995), Mann (1999), and Smetacek (1999) are commonly cited in the literature for indicating that diatoms contribute 30% to 45% of total ocean NPP (e.g., Litchman et al. 2007, 2009, Rynearson et al. 2013, Hansen and Visser 2019), but inspection of the two latter publications reveals that neither study attempted a quantitative assessment of diatom production. The study of Nelson et al. (1995), on the other hand, did use two independent approaches to quantify diatom productivity, but the first of these was based on what is now outdated estimates of global ocean NPP and the second was based on a model of nutrient transport and biogenic particle flux applied to field data on silica production and dissolution, with an overall uncertainty that is difficult to quantify. More recently, Uitz et al. (2010) used global satellite data to partition surface chlorophyll concentrations into three size classes (micro-, nano-, pico-phytoplankton), propagate group-specific chlorophyll with depth, and apply group-specific physiological properties to determine size-dependent fractional contributions to global total NPP. Their analysis indicated that 32% of global production could be assigned to the microphytoplankton, of which a currently unknown fraction can be specifically attributed to diatoms. Thus, although additional work is still needed to refine such assessments, it appears that the actual contribution of diatoms to global ocean productivity is likely less than 25% at best. The importance of diatoms to ocean carbon cycling, however, is underrepresented by this statistic as diatom-dominated populations are particularly efficient at transferring carbon from the surface ocean to depth (Scharek et al. 1999, Karl et al. 2012, Rynearson et al. 2013), with recent estimates suggesting that diatoms are responsible for ~40% of carbon exported to depth as part of the biological pump (Jin et al. 2006, Treguer et al. 2018).

Contributions to global NPP and carbon export are two metrics of success, but the statistics reported above predominantly reflect contributions of a subgroup of pelagic and neritic diatoms that periodically bloom, rather than diatoms as a whole. More specifically, the important role of diatoms in the modern ocean can, at a very basic level, be attributed to the simple fact that some diatom species of modest to large cell diameter have evolved physiologies that allow them to transiently attain modest cell numbers, such that the cytoplasmic volume of these cells significantly exceeds that of the far more numerous smaller-diameter phytoplankton species. If not for these bloom-forming species, diatoms would not be viewed as particularly successful against the metrics of NPP and export. Similarly, if number abundance is taken as the standard for success, even the bloom-forming diatoms are less than impressive (e.g., Marañón et al. 2015). Instead, the most successful phytoplankton would be the prokaryotes and picoeukaryotes (Marañón et al. 2001). With respect to the latter group, it is not yet clear whether these small eukaryotes are dominated by red-line or
green-line plastids an alternative metric of success, as discussed above (Setting the Stage), is species diversity. Here, diatoms as a group have been very successful, not only in terms of the number of species but also the rate of speciation (Nakov et al. 2019). We have proposed that this shared success can be traced to two unique attributes of diatoms (the fortuitous consequence of the frustule enhancing requirements for sexual reproduction and diploidy) and that the bloom-forming habit (and mass sinking) of some species largely evolved to enhance successful reproductive further. We suggest that, for a given size class of diatoms, a hallmark of bloom-forming species is a relatively elevated \( \mu_{\text{max}} \) and that the significance of this attribute is that it corresponds to an enhanced CBB cycle capacity that counterintuitively conveys an advantage in a generally light-limited surface mixed layer. One thing that is not clear is when the bloom-forming physiology emerged in the diatoms. A bulk of diatom evolution occurred under the greenhouse climate of the Mesozoic Era and into the Cenozoic Era where pelagic regions were likely strongly stratified, nutrient depleted, and not conducive to significant phytoplankton blooms. Perhaps bloom-forming species during these times were specialists confined to specific, perhaps near-shore or lagoon, habitats. In the modern glacial–interglacial ocean, bloom-forming diatom species have occupied prominent pelagic and coastal niches. We propose that within these regions, predator–prey dynamics have governed size-dependent differences in physiology that in turn predicate the temporal succession of bloom-forming species, such that smaller diatoms precede larger species because of the tighter coupling between division and loss rates with decreasing size.

Our physiological explanation for size-dependent succession during diatom blooms brings us back to the first paragraph of the manuscript. Why did we not observe a phytoplankton bloom climax during NAAMES that was dominated by large diatoms? Perhaps a key element in the answer to this question resides in the physics of the subarctic Atlantic basin and the history of biological oceanography studies. In general, winter mixed layer depths are significantly deeper in the eastern subarctic Atlantic than in the west (Behrenfeld et al. 2013, Behrenfeld 2014). What this means is that winter division rates in the west will tend to be higher than in the east (Barron, E. J., P. J. Fawcett, W. H. Peterson, D. Pollard, and S. M. Pratt, 2011). As summer mixed layer depths are similar east to west across the basin, the winter differences imply that the annual \( \mu_{\text{min}}–\mu_{\text{max}} \) ranges will be smaller in the west. Under such conditions, smaller diatoms that accelerate division rapidly during the spring would still be able to achieve significant abundances in the west, whereas larger species may not. During the western Atlantic NAAMES study, we did observe abundant small diatoms during the bloom climax, just not large diatoms. Historically, much of the early work on phytoplankton blooms was conducted using nets with relatively large mesh sizes and by marine laboratories in Europe (Mills 2012) where surrounding waters may experience more extreme differences in winter–late spring growth conditions. Here, vernal changes within the mixed layer may afford the larger diatoms, with their lower \( \mu_{\text{max}} \) but longer temporal lag between division and loss rates, an opportunity to realize their advantage and ultimately dominate late-bloom climax biomass. Thus, perhaps the surprise of the NAAMES experience was founded on a concept of diatom succession with roots in the historical eastern Atlantic net-tow studies of European plankton ecologists.

**Acknowledgments**

This work was supported by the North Atlantic Aerosol and Marine Ecosystem Study (NAAMES) (grant NNX15AF30G), an interdisciplinary project funded by the NASA Earth Venture Suborbital program.

**Literature Cited**

Agutter, P. S., and D. N. Wheatley. 2004. Metabolic scaling: consensus or controversy? Theoretical Biology and Medical Modelling 1:1–11.

Aitken, Z. H., S. Luo, S. N. Reynolds, C. Thauelow, and J. R. Greer. 2016. Microstructure provides insights into evolutionary design and resilience of *Coscinodiscus* sp. frustule. Proceedings of the National Academy of Science of the United States of America 113:2017–2022.

Allen, A. E., et al. 2011. Evolution and metabolic significance of the urea cycle in photosynthetic diatoms. Nature 473:203–207.

Allredge, A. L., C. Gotschalk, U. Passow, and U. Riebesell. 1995. Mass aggregation of diatom blooms: Insights from a mesocosm study. Deep-Sea Research Part II 42:9–27.

Amin, S. A., M. S. Parker, and E. V. Armbrust. 2012. Interactions between diatoms and bacteria. Microbiology and Molecular Biology Reviews 76:667–684.

Anderson, D. M., A. D. Cembella, and G. M. Hallegraeff. 2012. Progress in understanding harmful algal blooms: paradigm shifts and new technologies for research, monitoring, and management. Annual Review of Marine Science 4:143–176.

Anderson, L. W., and B. M. Sweeney. 1978. Role of inorganic ions in controlling sedimentation rate of a marine centric diatom *Ditylum brightwellii*. Journal of Phycolgy 14:204–214.

Anning, T., H. L. Machntyre, S. M. Pratt, P. J. Sammes, S. Gibb, and R. J. Geider. 2000. Photosynthesis in the marine diatom *Skeletonema costatum*. Limnology and Oceanography 45:1807–1817.

Bailleul, B., et al. 2015. Energetic coupling between plastids and mitochondria drives CO₂ assimilation in diatoms. Nature 524:366–369.

Bakun, A. 1997. Patterns in the ocean: ocean processes and marine population dynamics. Oceanographic Literature Review 5:530.

Banse, K. 1982. Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. Limnology and Oceanography 27:1059–1071.

Barron, E. J., P. J. Fawcett, W. H. Peterson, D. Pollard, and S. L. Thompson. 1995. A simulation of Midcretaceous climate. Paleocenography 10:953–962.

Beardall, J., and I. Morris. 1976. The concept of light intensity adaptation in marine phytoplankton: some experiments with *Phaeodactylum tricornutum*. Marine Biology 37:377–387.

Behrenfeld, M. J. 2014. Climate-mediated dance of the plankton. Nature Climate Change. 4:880–887.
Behrenfeld, M. J., et al. 2017. Annual boom–bust cycles of polar phytoplankton biomass revealed by space-based lidar. Nature Geoscience 10:118–122.

Behrenfeld, M. J., et al. 2019. The North Atlantic Aerosol and Marine Ecosystem Study (NAAMES): Science motive and mission overview. Frontiers in Marine Science 6:122.

Behrenfeld, M. J., and E. S. Boss. 2014. Resurrecting the ecological underpinnings of ocean plankton blooms. Annual Review of Marine Science 6:167–194.

Behrenfeld, M. J., and E. S. Boss. 2018. Student’s tutorial on bloom hypotheses in the context of phytoplankton annual cycles. Global Change Biology 24:55–77.

Behrenfeld, M. J., S. C. Doney, I. Lima, E. S. Boss, and D. A. Siegel. 2013. Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom. Global Biogeochemical Cycles 27:526–540.

Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42:1–20.

Behrenfeld, M. J., K. Halsey, and A. Milligan. 2008. Evolved physiological responses of phytoplankton to their integrated growth environment. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2687–2703.

Bergkvist, J., I. Klawonn, M. J. Whitehouse, G. Lavik, V. Sachpazidou, M. Dopson, and S. Hylander. 2019. Annual boom during spring in coastal sediments. Proceedings of the Royal Society B 286:20171617.

Boyd, C., and D. Gradmann. 2002. Impact of osmolytes on the buoyancy of marine phytoplankton. Marine Biology 141:605–618.

Broddrick, J. T., et al. 2019. Cross-compartment metabolic coupling enables flexible photoprotective mechanisms in the diatom Phaeodactylum tricornutum. New Phytologist 222:1364–1379.

Broman, E., V. Sachpazidou, M. Dopson, and S. Hylander. 2017. Diatoms dominate the eukaryotic metatranscriptome during spring in coastal ‘dead zone’ sediments. Proceedings of the Royal Society B 284:20171617.

Buick, R. 2008. When did oxygenic photosynthesis evolve? Philosophical Transactions of the Royal Society B 363:2731–2743.

Chan, A. T. 1978. Comparative physiological study of marine diatoms and dinoflagellates in relation to irradiance and cell size I. Growth under continuous light. Journal of Phycology 14:396–402.

Chan, A. T. 1980. Comparative physiological study of marine diatoms and dinoflagellates in relation to irradiance and cell size. II. Relationship between photosynthesis, growth, and carbon/chlorophyll a ratio. Journal of Phycology 16:428–432.

Chandler, M. A., D. Rind, and R. Ruedy. 1992. Pangaea climate during the Early Jurassic: GCM simulations and the sedimentary record of paleoclimate. Geological Society of America Bulletin 104:543–559.

Chepurinov, V. A., D. G. Mann, K. Sabbe, and W. Vyverman. 2004. Experimental studies on sexual reproduction in diatoms. International Review of Cytology 237:91–154.

Chisholm, S. W. 1992. Phytoplankton size. Pages 213–237 in P. G. Falkowski, and A. D. Woodhead, editors. Primary productivity and biogeochemical cycles in the sea. Springer, Boston, Massachusetts, USA.

Clark, D. R., K. J. Flynn, and N. J. Owens. 2002. The large capacity for dark nitrate-assimilation in diatoms may overcome nitrate limitation of growth. New Phytologist 155:101–108.

Crawford, R. M. 1995. The role of sex in the sedimentation of a marine diatom bloom. Limnology and Oceanography 40:200–204.

Crow, J. F., and M. Kimura. 1965. Evolution in sexual and asexual populations. American Naturalist 99:439–450.

Crowley, T., and G. North. 1991. Paleoclimatology. Oxford University Press, New York, New York, USA.

Cullen, J. J., and J. G. MacIntyre. 1998. Behavior, physiology and the niche of depth-regulating phytoplankton. NATO ASI Series G Ecological Sciences 41:559–580.

Davis, A., R. Abbbriano, S. R. Smith, and M. Hildebrand. 2017. Clarification of photosensory processes and the role of malic enzyme in diatoms. Protist 168:134–153.

de Vargas, C., M. P. Aubry, I. A. N. Probert, and J. Young. 2007. Origin and evolution of coccolithophores: from coastal hunters to oceanic farmers. Pages 251–285 in P. Falkowski, and A. H. Knoll, editors. Evolution of primary producers in the sea. Academic Press, London, UK.

Delwiche, C. F. 2007. The origin and evolution of dinoflagellates. Pages 191–205 in P. Falkowski, and A. H. Knoll, editors. Evolution of primary producers in the sea. Academic Press, London, UK.

Dortch, Q. 1982. Effect of growth conditions on accumulation of internal nitrate, ammonium, amino acids, and protein in three marine diatoms. Journal of Experimental Marine Biology and Ecology 62:263–264.

Dortch, Q., J. R. Clayton, S. S. Thoresen, and S. I. Ahmed. 1984. Species differences in accumulation of nitrogen pools in phytoplankton. Marine Biology 81:237–240.

Du Clos, K. T., L. Karp-Boss, T. A. Villareal, and B. J. Gemmell. 2019. Coscinodiscus wailesii mutes unsteady sinking in dark conditions. Biology Letters 15:20180816.

Edlund, M. B., and E. F. Stoermer. 1997. Ecological, evolutionary, and systematic significance of diatom life histories. Journal of Phycology 33:897–918.

Eppley, R. W. 1977. The growth and culture of diatoms. Pages 24–64 in D. Werner, editor. The biology of diatoms, Volume 13. Botanical monographs. University of California Press, Berkeley, California, USA.

Eppley, R. W., R. W. Holmes, and J. D. Strickland. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. Journal of Experimental Marine Biology and Ecology 1:191–208.

Falkowski, P. G., M. E. Katz, A. Knoll, A. Quigg, J. A. Raven, O. Schofield, and F. J. R. Taylor. 2004a. The evolution of modern eukaryotic phytoplankton. Science 305:354–360.

Falkowski, P. G., O. Schofield, M. E. Katz, B. Van de Schot-brugge, and A. H. Knoll. 2004b. Why is the land green and the ocean red? Pages 429–453 in H. R. Thierstein and J. R.
sequestration in the North Pacific Ocean supported by symbiotic nitrogen fixation. Proceedings of the National Academy of Science 109:1842–1849.

Karp-Boss, L., and P. A. Jumars. 1998. Motion of diatom chains in a steady shear flow. Limnology and Oceanography 43:1767–1773.

Katz, M. E., Z. V. Finkel, D. Grzebyk, A. H. Knoll, and P. G. Falkowski. 2004. Evolutionary trajectories and biogeochemical impacts of marine eukaryotic phytoplankton. Annual Review of Ecology, Evolution, and Systematics 35:523–556.

Keeling, P. J. 2013. The number, speed, and impact of plastid gene transfers in eukaryotic evolution. Nature Reviews Genetics 9:605–618.

Kemp, A. E., and T. A. Villareal. 2018. The case of the diatoms among bloom-forming diatoms. Proceedings of the National Academy of Science 115:E12275–E12284.

Koester, J. A., S. H. Brawley, L. Karp-Boss, and D. G. Mann. 1998. Motion of diatom producers in the sea. Academic Press, London, UK.

Koestler, J. A., S. H. Brawley, L. Karp-Boss, and D. G. Mann. 1998. Sexual reproduction in the marine centric diatom Ditylum brightwellii (Bacillariophyta). European Journal of Phycology 42:351–366.

Kooistra, W. H., R. Gersonde, L. K. Medlin, and D. G. Mann. 2007. The origin and evolution of the diatoms: their adaptation to a planktonic existence. Pages 207–249 in P. Falkowski, and A. H. Knoll, editors. Evolution of primary producers in the sea. Academic Press, London, UK.

Kooistra, W. H. C. F., and L. K. Medlin. 1996. Evolution of the diatoms (Bacillariophyta). IV. A reconstruction of their age from small subunit rRNA coding regions and fossil record. Molecular Phylogenetics and Evolution 6:391–407.

Kranzler, C. F., et al. 2019. Silicon limitation facilitates virus infection and mortality of marine diatoms. Nature Microbiology 4:179–184.

Kroth, P. G., et al. 2008. A model for carbohydrate metabolism in the diatom Phaeodactylum tricornutum deduced from comparative whole genome analysis. PLoS One 3:e1426.

Ku, C., M. Roettger, V. Zinmorski, S. Nelson-Sathi, F. L. Sousa, and W. F. Martin. 2014. Plastid origin: Who, when and why? Acta Societatis Botanicorum Poloniae 83:281–289.

Lacour, T., J. Larivière, and M. Babin. 2017. Growth, Chl a content, photosynthesis, and elemental composition in polar and temperate microalgae. Limnology and Oceanography 62:43–58.

Lampe, R. H., E. L. Mann, N. R. Cohen, C. P. Till, K. Thamatrakoln, M. A. Brzezinski, K. W. Bruland, B. S. Twining, and A. Marchetti. 2018. Different iron storage strategies among bloom-forming diatoms. Proceedings of the National Academy of Science 115:E12275–E12284.

Langdon, C. 1987. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. Part I. A comparative study of the growth-irradiance relationship of three marine phytoplankton species: Skeletonema costatum, Olisthodiscus luteus and Goniasulcus tamarense. Journal of Plankton Research 9:459–482.

Langdon, C. 1988. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. II. General review. Journal of Plankton Research 10:1291–1312.

Lavoie, M., J. A. Raven, and M. Levasseur. 2016. Energy cost and putative benefits of cellular mechanisms modulating buoyancy in a flagellate marine phytoplankton. Journal of Phycology 52:229–251.

Leblanc, K., et al. 2018. Nanoplanktonic diatoms are globally overlooked but play a role in spring blooms and carbon export. Nature Communications 9:1–12.

Lepetit, B., G. Géli, M. Lepetit, S. Sturm, S. Vugrinec, A. Rogato, P. G. Kroth, A. Falcicatore, and J. Lavaud. 2017. The diatom Phaeodactylum tricornutum adjusts nonphotochemical fluorescence quenching capacity in response to dynamic light via fine-tuned Lhcx and xanthophyll cycle pigment synthesis. New Phytologist 214:205–218.

Leu, J. Y., S. L. Chang, J. C. Chao, L. C. Woods, and M. J. McDonald. 2020. Sex alters molecular evolution in diploid experimental populations of S. cerevisiae. Nature Ecology and Evolution 4:453–460.

Lewis, J. A., S. D. Harris, K. J. Jones, and R. L. Edmonds. 1999. Long-term survival of marine planktonic diatoms and dinoflagellates in stored sediment samples. Journal of Plankton Research 21:343–354.

Litchman, E., C. A. Klausmeier, O. M. Schofield, and P. G. Falkowski. 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. Ecology Letters 10:1170–1181.

Litchman, E., C. A. Klausmeier, and K. Yoshijama. 2009. Contrasting size evolution in marine and freshwater diatoms. Proceedings of the National Academy of Science 106:2665–2670.

Liu, H., K. Suzuki, and H. Saito. 2004. Community structure and dynamics of phytoplankton in the western subarctic Pacific Ocean: A synthesis. Journal of Oceanography 60:119–137.

Lomas, M. W., and P. M. Glibert. 2000. Comparisons of nitrate uptake, storage, and reduction in marine diatoms and flagellates. Journal of Phycology 36:903–913.

Lyczkowski, E. R., and L. Karp-Boss. 2014. Allelopathic effects of Alexandrium fundyense (Dinophyceae) on Thalassiosira cf. gravida (Bacillariophyceae): a matter of size. Journal of Phycology 50:376–387.

Maeda, Y., D. Nojima, T. Yoshino, and T. Tanaka. 2017. Structure and properties of oil bodies in diatoms. Philosophical Transactions of the Royal Society B 372:20160408.

Malviya, S., et al. 2016. Insights into global diatom distribution and diversity in the world’s ocean. Proceedings of the National Academy of Science 113:E1516–E1525.

Mann, D. G. 1999. The species concept in diatoms. Phycologia 38:437–495.

Marañón, E., P. Cermenó, M. Latasa, and R. D. Tadonlélé. 2012. Temperature, resources, and phytoplankton size structure in the ocean. Limnology and Oceanography 57:1266–1278.

Marañón, E., P. Cermenó, M. Latasa, and R. D. Tadonlélé. 2015. Resource supply alone explains the variability of marine phytoplankton size structure. Limnology and Oceanography 60:1848–1854.

Marañón, E., P. Cermenó, D. C. López-Sandoval, T. Rodríguez-Ramos, C. Sobrino, M. Huete-Ortega, J. M. Blanco, and J. Rodríguez. 2013. Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use. Ecology Letters 16:371–379.

Marañón, E., P. M. Holligan, R. Barciela, N. González, B. Mouriño, M. J. Pazó, and M. Varela. 2001. Patterns of phytoplankton size structure and productivity in contrasting...
open-ocean environments. Marine Ecology Progress Series 216:43–56.
Marchetti, A., M. S. Parker, L. P. Moccia, E. O. Lin, A. L. Arrieta, F. Ribalet, M. E. P. Murphy, M. T. Maldonado, and E. V. Armbrust. 2009. Ferritin is used for iron storage in bloom-forming marine pinnate diatoms. Nature 457:467–470.
Martens, C., K. Vandepoele, and Y. Van de Peer. 2008. Whole-genome analysis reveals molecular innovations and evolutionary transitions in chromalveolate species. Proceedings of the National Academy of Science 105:3427–3432.
Massana, R., V. Balagué, L. Guillou, and C. Pedrós-Alió. 2004. Picoeukaryotic diversity in an oligotrophic coastal site studied by molecular and culturing approaches. FEMS Microbiology Ecology 50:231–243.
Matsuda, Y., and P. G. Kroth. 2014. Carbon fixation in diatoms. Pages 335–362 in M. F. Hohmann-Marriott, editor. The structural basis of biological energy generation. Springer, Dordrecht, The Netherlands.
McDonald, B. A., and C. Linde. 2002. Pathogen population evolutionary transitions in chromalveolate species. Proceedings of the National Academy of Science 105:3427–3432.
Medlin, L. K. 2016. Evolution of the diatoms: major steps in their evolution and a review of the supporting molecular and morphological evidence. Phycology 55:79–103.
Medlin, L. K., W. H. C. F. Kooistra, R. Gersonde, P. A. Sims, and U. Wellbrock. 1997. Is the origin of the diatoms related to the end-Permian mass extinction? Nova Hedwigia 65:1–11.
Medlin, L. K., W. H. Kooistra, R. Gersonde, and U. Wellbrock. 1996. Evolution of the diatoms (Bacillariophyta). II. Nuclear-encoded small-subunit rRNA sequence comparisons confirm a paraphyletic origin for the centric diatoms. Molecular Biology and Evolution 13:67–75.
Menden-Deuer, S., and E. J. Lessard. 2000. Carbon to volume ratios for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45:569–579.
Miklasz, K. A., and M. W. Denny. 2010. Diatom sinking speeds: Improved predictions and insight from a modified Stokes’ law. Limnology and Oceanography 55:2513–2525.
Mills, E. L. 2012. Biological oceanography: An early history, 1870–1960. University of Toronto Press, Toronto, Ontario, Canada.
Miralto, A., et al. 1999. The insidious effect of diatoms on copepod reproduction. Nature 402:173–176.
Mizuno, M. 1991. Influence of cell volume on the growth and size reduction of marine and estuarine diatoms. Journal of Phycology 27:473–478.
Moore, E. R., B. S. Bullington, A. J. Weisberg, Y. Jiang, J. H. Chang, and K. H. Halsey. 2017. Morphological and transcriptomic evidence for ammonium induction of sexual reproduction in Thalassiosira pseudonana and other centric diatoms. PLoS One. https://doi.org/10.1177/1090144667.
Moore, J. K., and T. A. Villareal. 1996. Size-aspect ratio relationships in positively buoyant marine diatoms. Linnlomy and Oceanography 41:1514–1520.
Munk, W. H., and G. A. Riley. 1952. Absorption of nutrients by aquatic plants. Journal of Marine Research 11:215–240.
Nagai, S., Y. Hori, T. Manabe, and I. Imai. 1995. Restoration of cell size by vegetative cell enlargement in Coscinodiscus walessi (Bacillariophyceae). Phycologia 34:533–535.
Nagao, R., et al. 2019. Structural basis for energy harvesting and dissipation in a diatom PSII–FCPII supercomplex. Nature Plants 5:890–901.
Nakov, T., J. M. Beaulieu, and A. J. Alverson. 2018. Accelerated diversification is related to life history and locomotion in a hyperdiverse lineage of microbial eukaryotes (Diatoms, Bacillariophyta). New Phytologist 219:462–473.
Nakov, T., J. M. Beaulieu, and A. J. Alverson. 2019. Diatoms diversify and turn over faster in freshwater than marine environments. Evolution 73:2497–2511.
Nelson, D. M., P. Tréguer, M. A. Brzezinski, A. Leynaert, and B. Quéguiner. 1995. Production and dissolution of biogenic silica in the ocean: revised global estimates, comparison with regional data and relationship to biogenic sedimentation. Global Biogeochemical Cycles 9:359–372.
Nikolaev, V. A., and D. M. Harwood. 1997. New process, genus and family of Lower Cretaceous diatoms from Australia. Diatom Research 12:43–53.
Orellana, M. V., and M. J. Perry. 1992. An immunoprobe to measure Rubisco concentrations and maximal photosynthetic rates of individual phytoplankton cells. Linnlomy and Oceanography 37:478–490.
Otto, S. P., and A. C. Gerstein. 2008. The evolution of haploidy and diplody. Current Biology 18:R1121–R1124.
Otto, S. P., and D. B. Goldstein. 1992. Recombination and the evolution of diplody. Genetics 131:745–751.
Pancic, M., R. R. Torres, R. Almeda, and T. Kröboe. 2019. Silicified cell walls as a defensive trait in diatoms. Proceedings of the Royal Society B: Biological Sciences 286:20190184.
Parré, L. W., D. J. G. Lahr, A. H. Knoll, and L. A. Katz. 2011. Estimating the timing of early eukaryotic diversification with multigene molecular clocks. Proceedings of the National Academy of Science 108:13624–13629.
Penta, B., J. Fox, and K. H. Halsey. 2021. Evidence that episodic mixing-induced phytoplankton growth augments the biological carbon pump. Linnlomy and Oceanography. https://doi.org/10.1002/ino.11728.
Pil, X., S. Zhao, W. Wang, D. Liu, C. Xu, G. Han, T. Kuang, S. F. Sui, and J. R. Shen. 2019. The pigment–protein network of a diatom photosystem II–light-harvesting antenna supercomplex. Science 365:eaax4406.
Pitcher, G. C. 1990. Phytoplankton seed populations of the Cape Peninsula upwelling plume, with particular reference to resting spores of Chaetoceros (Bacillariophyceae) and their role in seeding upwelling waters. Estuarine, Coastal and Shelf Science 31:283–301.
Pollner, G. 2000. Wound-activated chemical defense in unicellular planktonic algae. Angewandte Chemie International Edition 39:4352–4354.
Priez, J. A., J. Ananta, W. R. de Paula, J. F. Allen, L. Tirichine, and C. Bowler. 2012. Chloroplast-mitochondria cross-talk in diatoms. Journal of Experimental Botany 63:1543–1557.
Rabosky, D. L., and U. Sorhannus. 2009. Diversity dynamics of marine planktonic diatoms across the Cenozoic. Nature 457:183–186.
Racki, G. 1999. Silica-secreting biota and mass extinctions: survival patterns and processes. Palaeogeography, Palaeoclimatology, Palaeoecology 154:107–132.
Raven, J. A. 1983. The transport and function of silicon in plants. Biological Reviews 58:179–207.
Raven, J. A. 1984. A cost–benefit analysis of photon absorption by photosynthetic unicells. New Phytologist 98:593–625.
Raven, J. A. 1987. The role of vacuoles. New Phytologist 103:379–386.
Raven, J. A. 1994. Why are there no picoplanktonic O2 evolvers with volumes less than 10⁻¹⁹ m³? Journal of Plankton Research 16:565–580.
Raven, J. A. 1995. Scaling the seas. Plant, Cell and Environment 18:1090–1100.
Raven, J. A. 1998. The twelfth Tansley Lecture. Small is beautiful: the picoplankton. Functional Ecology 12:503–513.

Raven, J. A., and M. A. Doblin. 2014. Active water transport in unicellular algae: where, why, and how. Journal of Experimental Botany 65:6279–6292.

Raven, J. A., and R. J. Geider. 1988. Temperature and algal growth. New Phytologist 110:441–461.

Raven, J. A., and A. M. Waite. 2004. The evolution of silicification in diatoms: inescapable sinking and sinking as escape? New Phytologist 162:45–61.

Reeve, M. R., and M. A. Walter. 1977. Observations on the existence of lower threshold and upper critical food concentrations for the copepod Acartia tonsa Dana. Journal of Experimental Marine Biology and Ecology 29:211–221.

Reinförder, J. R., A. M. L. Kraepiel, and F. M. M. Morel. 2000. Unicellular C-4 photosynthesis in a marine diatom. Nature 407:996–999.

Reinförder, J. R., A. J. Milligan, and F. M. M. Morel. 2004. The role of the C4 pathway in carbon accumulation and fixation in a marine diatom. Plant Physiology 135:2106–2111.

Retallack, G. J. 2001. Neogene expansion of the North American prairie. Palaeos 12:380–390.

Richardson, K., J. Beardall, and J. A. Raven. 1983. Adaptation of unicellular algae to irradiance: an analysis of strategies. New Phytologist 93:157–191.

Richardson, T. L., A. M. Ciotti, J. J. Cullen, and T. A. Vilareal. 1996. Physiological and optical properties of Rhizosolenia formosa (Bacillariophyceae) in the context of open-ocean vertical migration. Journal of Phycology 32:741–757.

Richardson, T. L., and J. J. Cullen. 1995. Changes in buoyancy and chemical composition during growth of a coastal marine diatom: ecological and biogeochemical consequences. Marine Ecology Progress Series 128:77–90.

Richardson, T. L., J. J. Cullen, D. E. Kelley, and M. R. Lewis. 1998. Potential contributions of vertically migrating Rhizosolenia to nutrient cycling and new production in the open ocean. Journal of Plankton Research 20:219–241.

Rivkin, R. B. 1990. Photoadaptation in marine phytoplankton: Variations in ribulose 1, 5-biphosphate activity. Marine Ecology Progress Series 62:61–72.

Round, F. E., R. M. Crawford, and D. G. Mann. 1990. The diatoms: biology and morphology of the genera. Cambridge University Press, Cambridge, UK.

Rynearson, T. A., K. Richardson, R. S. Lampitt, M. E. Sieracki, A. J. Poulton, M. M. Lyngsgaard, and M. J. Perry. 2013. Major contribution of diatom resting spores to vertical flux in the sub-polar North Atlantic. Deep Sea Research I 82:60–71.

Scharek, R., L. M. Tupas, and D. M. Karl. 1999. Diatom fluxes to the deep sea in the oligotrophic North Pacific gyre at Station ALOHA. Marine Ecology Progress Series 182:55–67.

Shen, C., C. L. Dupont, and B. M. Hopkinson. 2017. The diversity of CO2-concentrating mechanisms in marine diatoms as inferred from their genetic content. Journal of Experimental Botany 68:3937–3948.

Sicko-Goad, L. M., C. L. Schelske, and E. F. Stoermer. 1984. Estimation of intracellular carbon and silica content of diatoms from natural assemblages using morphometric techniques. Limnology and Oceanography 29:1170–1178.

Siegel, D. A. 1998. Resource competition in a discrete environment: Why are plankton distributions paradoxical? Limnology and Oceanography 43:1133–1146.

Sims, P. A., D. G. Mann, and L. K. Medlin. 2006. Evolution of the diatoms: insights from fossil, biological and molecular data. Phycology 45:361–402.

Smyda, T. J. 1970. The suspension and sinking of phytoplankton in the sea. Oceanography and Marine Biology—An Annual Review 8:353–414.

Smyda, T. J. 1980. Phytoplankton species succession. Pages 493–570 in I. Morris, editor. The physiological ecology of phytoplankton. Blackwell Scientific Publications, New York, New York, USA.

Smyda, T. J. 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. Limnology and Oceanography 42:1137–1153.

Smetacek, V. 1999. Diatoms and the ocean carbon cycle. Protist 92:267–281.

Smetacek, V. 2001. A watery arms race. Nature 411:745.

Smetacek, V., P. Assmy, and J. Henjes. 2004. The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. Antarctic Science 16:541–558.

Smith, J. C., T. Platt, and W. G. Harrison. 1983. Photoadaptation of carboxylating enzymes and photosynthesis during a spring bloom. Progress in Oceanography 12:425–459.

Smith, S. R., R. M. Abbriano, and M. Hildebrand. 2012. Comparative analysis of diatom genomes reveals substantial differences in the organization of carbon partitioning pathways. Algal Research 1:2–16.

Snoeijis, P., S. Busse, and M. Potapova. 2002. The importance of diatom cell size in community analysis. Journal of Phycology 38:265–281.

Steinbiss, H., J., and K. Zetsche. 1986. Light and metabolite regulation of the synthesis of ribulose-1, 5-biphosphate carboxylase/oxygenase and the corresponding mRNAs in the unicellular alga Chlorella. Planta 167:575–581.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey, USA.

Stolle, W., and R. Riegm. 1996. A model approach for size-selective competition of marine phytoplankton for fluctuating nitrate and ammonium. Journal of Phycology 32:732–740.

Strathmann, R. R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnology and Oceanography 12:411–418.

Sukenchok, A., J. Bennett, and P. G. Falkowski. 1987. Light-saturated photosynthesis—limitation by electron transport or carbon fixation? Biochimica et Biophysica Acta 919:205–215.

Taddei, L., V. U. Chukhutsina, B. Lepeit, G. R. Stella, R. Bassi, H. van Amerongen, J. P. Bouly, M. Jaubert, G. Finazzi, and A. Falciatore. 2018. Dynamic changes between two LHCl-related energy quenching sites control diatom photoclimination. Plant Physiology 177:953–965.

Tang, E. P. 1995. The alloometry of algal growth rates. Journal of Plankton Research 17:1325–1335.

Thomas, W. H. 1966. Effects of temperature and illumination on cell divisions rates of three species of tropical oceanic phytoplankton. Journal of Phycology 2:17–22.

Tozzi, S., O. Schofield, and P. Falkowski. 2004. Historical climate change and ocean turbulence as selective agents for two key phytoplankton functional groups. Marine Ecology Progress Series 274:123–132.

Tréguer, P., et al. 2018. Influence of diatom diversity on the ocean biological carbon pump. Nature Geoscience 11:27–37.

Trimborn, S., D. Wolf-Gladrow, K.-U. Richter, and B. Rost. 2009. The effect of pCO2 on carbon acquisition and intracellular assimilation in four marine diatoms. Journal of Experimental Marine Biology and Ecology 376:26–36.
Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1457/full