

Environmental control of open-ocean phytoplankton groups: Now and in the future

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Abstract

Climate change will alter concurrently many environmental factors that exert control over oceanic phytoplankton. Recent laboratory culture work, shipboard experiments, and field surveys reveal many remaining unknowns about the bottom-up controls for five globally important algal groups. Increasing uncertainties exist, respectively, for picocyanobacteria, diatoms, *Phaeocystis* spp., N₂-fixing cyanobacteria, and coccolithophores. This missing information about current environmental controls will hinder progress in modeling how these phytoplankton will be influenced by climate change. A review of conceptual approaches used to elucidate the relationship between environmental controls and phytoplankton dominance, from Margalef's mandala to functional traits, uncovered limitations regarding their application to climate-change scenarios. For example, these previous approaches have insufficient scope or dimensions to take into account the confounding effects of synergistic and antagonistic interactions of multiple environmental change variables. A new approach is needed that considers all of the different environmental properties altered by climate change and their interactions while at the same time permitting a subset of the most significant controls for a specific phytoplankton group to be isolated and evaluated in factorial matrix perturbation experiments. We advocate three new interlinked approaches, including environmental clusters that incorporate all factors (temperature, CO₂, light, nutrients, and trace metals), which both exert control over present-day floristics and will be altered by climate change. By carefully linking a holistic conceptual approach to a reductionist experimental design, the future responses of open-ocean phytoplankton groups to a complex, rapidly changing environment can be better predicted.

The last decade has seen increasing awareness of the relationship between key phytoplankton groups and their pivotal roles in the biogeochemical cycles of a range of elements. To cite one example, *Phaeocystis* spp. are crucially important players in ocean sulfur and carbon (C) biogeochemistry (Arrigo et al. 1999; Kettle et al. 1999). Other groups with critical biogeochemical linkages include diatoms, coccolithophores, nitrogen (N₂)-fixing cyanobacteria, and picocyanobacteria. Before we can ascertain the effects of climate change on these biogeochemically and ecologically important phytoplankton functional groups, we must first determine what sets the biogeographical boundaries of each group and, hence, their present-day regional distributions; develop a mechanistic understanding of what environmental factors set their dominance within a biome; and ascertain how climate-driven changes in each factor will alter phytoplankton dynamics both individually and interactively (i.e., antagonisms and synergisms between factors that may lead to diminution or amplification of climate-change signals). Insight into all three of these topics is needed to determine how anthropogenic change will alter phytoplankton community structure in the open ocean and to predict the likely sign and magnitude of any feedbacks resulting from climate-change-mediated floristic shifts.

Developments in remote sensing and ship-based surveys now provide a clearer demarcation of the biomes occupied by each algal group—for example, coccolithophores (Merico et al. 2003; Balch et al. 2005), N₂ fixers (Westberry and Siegel 2006), and picocyanobacteria (Johnson et al.

2006). Moreover, there has been an increasing appreciation of both the diversity of open-ocean N₂ fixers (Zehr et al. 2001; Langois et al. 2005) and the growing threat of decreasing ocean pH to phytoplankton, especially calcifiers such as coccolithophores (Raven et al. 2005). However, the environmental factors that determine bottom-up control on most of these important phytoplankton groups are still relatively uncertain (Zondervan et al. 2007; Van Leeuwe et al. 2007; Cullen and Boyd 2008). Hence, there is a clear need to address the following fundamental question: What do we know about the environmental control of phytoplankton groups in the present day, and how will these modes of control be altered in the future?

In this review we selected diatoms, *Phaeocystis* spp., coccolithophores, N₂ fixers, and picocyanobacteria, since these five algal groups exert major influences on the biogeochemical cycles of a range of elements. All of these groups are competitively successful and ecologically prominent, the first four as major bloom formers and the latter as the dominant group in the low-latitude ocean. We address in turn the following issues: our current understanding of environmental control of each phytoplankton group; reappraisal of the conceptual frameworks used to represent how both individual environmental factors and their interplay (i.e., synergisms and antagonisms) may control the dominance of different phytoplankton groups; and development of new ways in which to represent shifts in modes of environmental control on phytoplankton in future decades. The latter will stem from the concurrent influence of seasonal gradients, climate variability, and climate change on oceanic properties. In this review, as a result of space limitations we are deliberately neglecting

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top-down control on phytoplankton groups, but we realize that herbivory can be equally as influential as bottom-up control (Verity and Smetacek 1996; Legendre and Rivkin 2005; Sommer et al. 2007). The five algal groups that we consider here either form massive blooms (Arrigo et al. 1999; Balch et al. 2005; Westberry and Siegel 2006) and/or are regionally dominant (Johnson et al. 2006), indicating that all are able to escape strong grazing control of their standing stock to some extent. However, we recognize that top-down control, as well as competitive interactions with other potentially important algal groups such as cryptophytes, pelagophytes, and dinoflagellates, will also eventually need to be fully integrated with a framework of bottom-up controlling factors on each group.

One key to understanding the responses of these algal groups to bottom-up controls is consideration of the interactive effects of multiple factors. Simultaneous limitation by two or more factors is often referred to as co-limitation in the literature. Saito et al. (2008) defined three different types of nutrient co-limitation: independent; that influenced by biochemical substitution; and biochemically dependent. Although Saito et al. (2008) report potential co-limitation by multiple nutrients (e.g., iron [Fe] and nitrate) or by nutrients and light, it is evident from the experiments discussed in this review that attempt to mimic altered climatic conditions that other types of environmental factors will also exert control over phytoplankton groups. So in addition to nutrient co-limitation, we must also consider similar co-limiting relationships involving temperature and increased CO₂ concentrations in surface waters.

Our examination of the literature in the following sections strongly indicates that a range of unknowns, from major to minor, remain in our understanding of controls on each of these five phytoplankton functional groups. This evaluation of the state of our knowledge is therefore less positive than that offered by Hood et al. (2006). We present our overview of these five groups, commencing with picocyanobacteria, for which environmental control factors are arguably best understood, and then present the other groups in descending order down to the coccolithophores, the group whose controls are probably most poorly understood.

Throughout this review of environmental controls on each group we attempt to rank these factors from most important to least important (Table 1). Although such a hierarchy of control factors necessarily involves a certain degree of subjectivity, in many cases the relative importance of particular environmental controls for each group has been fairly well documented. Thus, such a ranking system provides a useful framework for discussing how these individual environmental factors and their mutual interactions may affect important phytoplankton groups in the future ocean. We conclude this review by summarizing the challenges that lie ahead in this research area and how they can be addressed.

A multi-stranded approach to environmental controls on phytoplankton

Longhurst (1998) states that “marine pelagic biogeography should provide a framework to better understand the

distribution of individual planktonic organisms, and their interplay with other species to form ecosystems under the regional environmental conditions that typify ocean waters.” Such information should enable biogeographical distributions and—in time—oceanic biogeographical provinces or biomes to be documented (Longhurst 1998). Biogeographical distributions integrate the cumulative effects of environmental control on different algal groups, and, thus, any recently observed changes in algal biogeography are often attributed to holistic changes in ecosystem properties, such as climate change. However, correlative analyses of environmental factors and distributions of algal groups—for example, along oceanic transects—are often inconclusive (Tyrrell et al. 2003; Leblanc et al. 2009; but see also Martiny et al. 2009). Hence, perturbation experiments using either cultures in the laboratory (Hoffmann et al. 2008) or natural assemblages in the field (Boyd et al. 2007; Hare et al. 2007; Feng et al. 2009) are probably the most powerful tool to probe effects of environmental control upon algal groups.

The majority of the data presented in this review are from laboratory culture studies of single species or ecotypes and shipboard manipulation experiments of natural assemblages. Although the environmental relevance of both field and culture experiments has been questioned (Lakeman et al. 2009), the adoption of a multi-stranded approach consisting of shipboard and satellite ocean surveys, perturbation experiments (from single-species lab flasks to mesoscale experiments that encompass ecosystems and upper-ocean physics), and detailed process studies (Boyd and Doney 2002) can be used to provide robust tests of environmental relevance across a range of temporal and spatial scales.

Taken together, biogeographical data and the findings from lab and/or field experiments provide confidence in relating experimental data to the open-ocean environment. For example, the dominance of algal stocks by a particular *Prochlorococcus* ecotype over much of the low-latitude Atlantic (Johnson et al. 2006) reveals its ability to out-compete both other algal groups and *Prochlorococcus* ecotypes as well as its ability to dominate algal stocks in spite of grazing pressure. Moreover, these data provide a biogeographical context for lab culture studies on this ecotype, which in turn reveal the physiological reasons—in this case temperature optima for growth—for its meridional distribution (Johnson et al. 2006). In a recent metagenomic study, Hewson et al. (2009) also emphasized the parallels between population biogeography and the characteristics of corresponding culture isolates: “Ecotypes of dominant cyanobacteria (*Prochlorococcus* and *Synechococcus*) had distinct distributions congruent with their physiological characteristics in cultivation” Other examples include the findings from mesoscale open-ocean Fe enrichments, which reveal that the outcome of bottom-up influences (including ocean physics and cell sinking rates), algal inter-specific competition, and top-down control is a diatom bloom (Boyd et al. 2005).

In this review, most of the data presented come from lab culture studies or shipboard experiments. The lab studies were all conducted with recent phytoplankton isolates

Table 1. Environmental control factors for each major phytoplankton group, with a postulated ranking of each factor based on evidence in the literature, from most important (1) to least important (5). Factors that share the same number denote equal importance for that algal group. Controls that are deemed not significant for each group are marked as n.s., and factors whose relative importance remains controversial or unresolved are marked with a question mark (?). Factors that share a superscripted letter have been demonstrated to have significant interactive effects for that functional group, including co-limitations, synergisms, or antagonisms.

Algal group	Temperature	PAR	Nitrogen	Phosphorus	Silicon	Iron	CO ₂
Diatoms	? ^a	4 ^{bc}	1 ^d	n.s.	3 ^e	2 ^{abcde}	5 ^c
<i>Phaeocystis antarctica</i>	?	1 ^f	n.s.	n.s.	n.s.	2 ^f	3
Coccolithophores	1 ^g	2 ?	3 ? ^h	3 ? ^h	n.s.	n.s.	4 ? ^g
N ₂ fixers	1	2 ⁱ	n.s.	3 ^{jk}	n.s.	3 ^{ikl}	? ^{jl}
Picocyanobacteria							
<i>Prochlorococcus</i>	1	1	2 ^m	n.s.	n.s.	? ⁿ	?
<i>Synechococcus</i>	3 ^o ?	1 ?	2 ?	2 ?	n.s.	? ⁿ	4 ? ^o

^a Temperature and iron have been shown to have marked synergisms on diatom abundance in the Ross Sea (Fig. 1C; Rose et al. 2009).

^b Numerous laboratory and field studies have demonstrated co-limitation of diatoms by light and iron (Sunda and Huntsman 1998; Maldonado et al. 1999; Fig. 5).

^c CO₂, light, and iron have a three-way interactive effect on diatom community structure in the Ross Sea (Feng et al. 2010).

^d Nitrogen and iron are also potentially co-limiting for diatoms (Price et al. 1991; DiTullio et al. 1993).

^e Silicon and iron requirements are antagonistic in diatoms (Hutchins and Bruland 1998).

^f Light and iron have synergistic effects on the abundance of colonial *Phaeocystis antarctica* (Fig. 1D; Feng et al. 2010).

^g Coccolithophore abundance in the North Atlantic spring bloom is synergistically affected by both temperature and CO₂ (Fig. 3C; Feng et al. 2009). In general, such interactions between multiple variables may be especially important for this group, making a hierarchical ranking especially problematic for coccolithophores (uncertainties indicated by the question marks after each number).

^h The ratio of nitrogen to phosphorus has been suggested to be a significant control on coccolithophore blooms (Tyrrell and Taylor 1996).

ⁱ The high iron and light requirements of nitrogen fixers may make them especially vulnerable to iron and light co-limitation.

^j Co-limitation of *Trichodesmium* by phosphorus and CO₂ has been reported (Hutchins et al. 2007).

^k Iron and phosphorus co-limitation of N₂ fixation has been demonstrated in the North Atlantic (Mills et al. 2004).

^l Iron limitation has an antagonistic effect on stimulation of *Crocospaera* by increasing CO₂ (Fig. 3A,B; Fu et al. 2008).

^m Some strains of *Prochlorococcus* cannot use nitrate and so must rely on reduced nitrogen sources, including ammonium and nitrite (Rocap et al. 2003).

ⁿ Picocyanobacterial stocks have exhibited transient increases following iron supply during mesoscale iron enrichments in polar, subpolar, and tropical HNLC waters (Boyd et al. 2005).

^o CO₂ and temperature synergisms have been reported for *Synechococcus* (Fu et al. 2007).

cultured in our labs, from regions in which we have background data on the environmental relevance of the isolates, such as Southern Ocean diatoms. In each section on the various algal groups we have interspersed data from such lab and field experiments with correlative information from oceanic surveys to ensure a wider multi-stranded environmental context.

Review of the current understanding of environmental control

Picocyanobacteria and ocean biogeochemistry—The dominance of the two unicellular picocyanobacteria genera *Prochlorococcus* and *Synechococcus*, particularly in the oligotrophic gyres, means that they play an important role in microbial food webs, the ocean N cycle, and global C biogeochemistry. *Prochlorococcus* alone can contribute 13–48% of net primary production in the central gyres (Campbell et al. 1997; Liu et al. 1997; DuRand et al. 2001). In general, the abundance of *Synechococcus* is probably 100 times lower than *Prochlorococcus* where they co-occur. Together, though, both groups of picocyanobacteria may contribute up to 50% of total fixed C in low-latitude waters (Partensky et al. 1999) and may also play a significant role in downward export flux in some oceanic regions (Richardson and Jackson 2008).

Environmental control of Prochlorococcus—The interplay of factors that control *Prochlorococcus* distributions is

probably understood better than that for any other major oceanic algal group (Table 1). *Prochlorococcus* is abundant only in subtropical and tropical regimes, being virtually absent from subpolar or polar waters (Partensky et al. 1999; Johnson et al. 2006). Explanations for these meridional distributions include temperature restrictions, with those below 15–18°C limiting the growth of *Prochlorococcus* (Olson et al. 1990; Cavender-Bares et al. 2001), and also an inverse relationship with nutrient availability (Follows et al. 2007). This genus dominates in both the oligotrophic gyres and in warm-water mesotrophic areas such as the high-nitrate, low-chlorophyll (HNLC) Equatorial Pacific (Binder et al. 1996), indicating that temperature, rather than other co-variables, such as nutrient availability, directly controls its distribution. Field and laboratory data indicate a strong positive relationship between increasing temperature and light intensities and the abundance of *Prochlorococcus* (Zinser et al. 2007). This conclusion is supported by a recent environmental correlative analysis by Martiny et al. (2009), which indicates that light and then temperature are the two most significant factors influencing the overall distribution of *Prochlorococcus* (Table 1).

Prochlorococcus has been classified into two general ecotypes, as defined by their irradiance niches. One possesses a high light requirement for growth and is abundant in near-surface waters (Moore et al. 1998; Johnson et al. 2006). The other ecotype is adapted to the low light conditions at the base of the euphotic zone

(Moore et al. 1995; Johnson and Lin 2009). These two broad ecotypes are further divided into at least six genetically distinct clades, two high-light and four low-light clades (Rocap et al. 2002), which may be adapted to different ecological niches. Martiny et al. (2009) differentiate the roles of light and temperature on *Prochlorococcus* and report that light is the most important factor explaining the distribution of two clades, while temperature is the most significant factor differentiating two others.

Nutrient and trace metal availability are deemed to be less influential as environmental controls on *Prochlorococcus* (Table 1). Cultured strains of *Prochlorococcus* cannot utilize nitrate, which is explained by the lack of the nitrate reductase gene (Dufresene et al. 2003; Rocap et al. 2003). However, there is recent evidence for nitrate utilization in uncultivated subtropical Atlantic populations (Casey et al. 2007), and nitrate concentrations explain a small but significant proportion of the variability of *Prochlorococcus* abundance is usually decoupled from nitrate concentration (Partensky et al. 1999; Fuller et al. 2005; Johnson et al. 2006), and there is also no clear correlation between *Prochlorococcus* biomass and phosphate concentrations (Cavender-Bares et al. 2001; Johnson et al. 2006; Martiny et al. 2009).

The availability of reduced sources of N, including ammonium and nitrite, is likely to be an influential factor in the distribution and abundance of at least some *Prochlorococcus* strains. The nitrite maximum in the lower euphotic zone coincides with the depth of greatest abundance of the low light-adapted ecotypes, which are thought to be the only ones that can utilize nitrite (Moore et al. 2002). With the exception of copper and Fe, there is little evidence that trace metal availability plays an influential role on *Prochlorococcus* abundances. Two studies (Brand et al. 1986; Moffett and Brand 1996) have reported that their growth rate may be inhibited at naturally occurring concentrations of free copper ion (Cu^{2+}). There is also indirect evidence for Fe limitation from mesoscale Fe enrichment studies, since picocyanobacteria exhibit transient increases in abundance before being grazed by microzooplankton (Boyd et al. 2005).

A major uncertainty regarding the environmental control of *Prochlorococcus* is that little is known about the responses of the picocyanobacteria to changes in pCO_2 or about the interactive effects between different environmental factors (i.e., co-limitation) (Table 1). Cyanobacteria utilize C concentrating mechanisms (CCMs) such as active HCO_3^- and CO_2 transporters to facilitate CO_2 fixation, thus helping them maintain optimal growth rates at low external dissolved inorganic carbon (DIC) concentrations. Because CCMs involve substantial energetic and metabolic costs, direct increases in the carboxylation efficiency of Rubisco with future increased CO_2 availability should reduce the need for CCM activity and, hence, reduce the resource costs of C acquisition (Burkhardt et al. 2001; Beardall and Giordano 2002). Despite this potential high CO_2 subsidy, a culture study with *Prochlorococcus* found that acclimation to increased CO_2 levels (76 Pa) did not result in any alteration of growth rate (Fu et al. 2007).

Increased pCO_2 and temperature, either alone or together, also did not affect photosynthesis vs. irradiance parameters in *Prochlorococcus* (Fig. 1A).

Environmental control of Synechococcus—In contrast to *Prochlorococcus*, the environmental controls on *Synechococcus* are less well understood (Table 1). Phosphate and nitrate, as well as light, are likely to be the most important factors affecting the abundance and distribution of *Synechococcus*, while temperature probably plays only a modest role in controlling its growth (Partensky et al. 1999; Table 1). Zinser et al. (2007) found that *Synechococcus* distributions in the field were not correlated with temperature. *Synechococcus* is often more prominent in nutrient-rich waters than in oligotrophic areas and can be abundant even in subpolar waters with blooms recorded at temperatures as low as 6–8°C (reviewed in Partensky et al. 1999). Although *Synechococcus* has at least 10 distinct genetic clades (Fuller et al. 2003), much less is known about their possible ecological niches than for *Prochlorococcus*. *Synechococcus* abundance usually exhibits a surface maximum and decreases markedly with depth, indicating that this organism has a higher light requirement than *Prochlorococcus* (Partensky et al. 1999; Moore et al. 2002). Indeed, laboratory work by Moore et al. (1995) shows that *Synechococcus* has a higher light compensation point than *Prochlorococcus*.

Nutrient utilization is another distinguishing factor between the two genera. *Synechococcus* utilizes a full range of N sources, including nitrate, nitrite, ammonium, urea, and amino acids (Moore et al. 2002). As a result of its N-rich phycobilisomes, *Synechococcus* also requires more N compared to *Prochlorococcus* (Moore et al. 2002; Haldal et al. 2003). Expression of the *ntcA* gene, an indicator of N stress, indicates that natural populations of *Synechococcus* may be limited by N (Lindell and Post 2001), and high biomass of this genus is linked with nitrate concentrations in the North Atlantic Ocean (Johnson et al. 2006).

Phosphorus (P) limitation also appears to be a potential issue for *Synechococcus*, with perturbation experiments using natural populations in the Red Sea and Mediterranean Sea pointing to potential phosphate limitation (Vaulot et al. 1996; Li et al. 1998). Moreover, dissolved inorganic phosphorus (DIP) concentrations also appear to regulate the abundance of *Synechococcus* in the Sargasso Sea and the Gulf of Aqaba (DuRand et al. 2001; Fuller et al. 2005). It has been hypothesized that DIP stress results in a seasonal decline in *Synechococcus* abundance, as evidenced by the expression of the phosphate-binding protein PstS, which is induced when phosphate concentrations fall below 50 nmol L^{-1} (Scanlan et al. 1997). Half-saturation constants of *Synechococcus* cultures growing on phosphate are too high to support observed growth rates of natural populations at the nanomolar concentrations found in most oligotrophic regimes, so they probably rely primarily on dissolved organic P (Fu et al. 2006).

Both copper and Fe are trace metals that may potentially exert environmental control over *Synechococcus*, and little is known about the responses of *Synechococcus* to changes in pCO_2 (Table 1). Genetic analysis indicates that there are

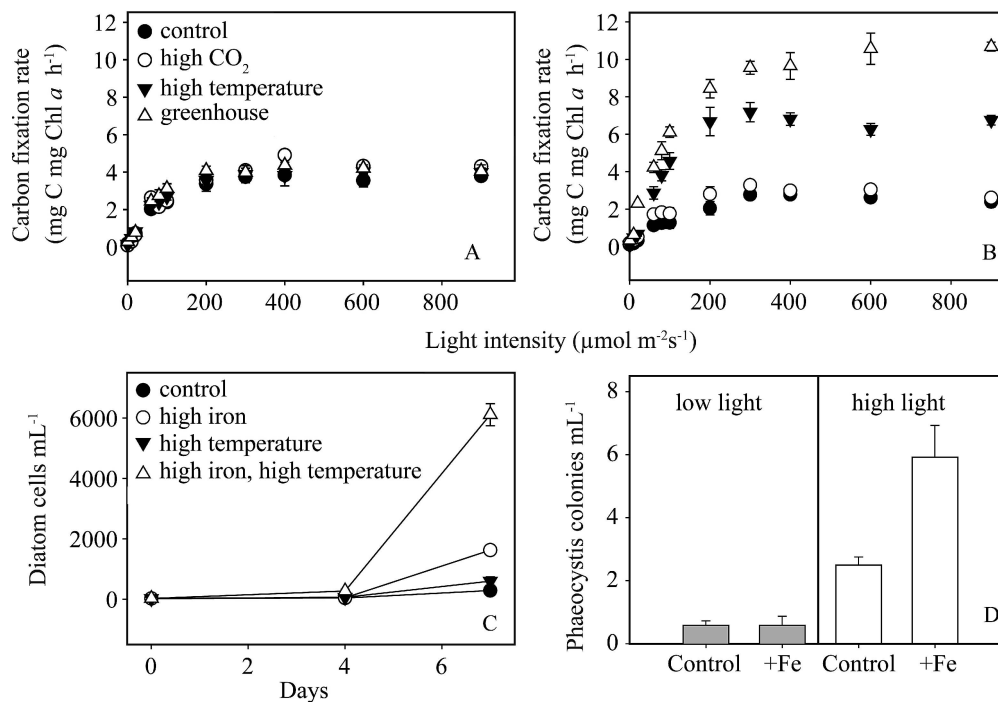


Fig. 1. (A) Photosynthesis vs. irradiance (P/E) curve for a *Prochlorococcus* isolate grown under four CO₂ and temperature conditions (ambient control, high-CO₂ alone, high-temperature alone, and high-CO₂ and high-temperature “greenhouse” treatments; Fu et al. 2007); (B) P/E curve for a *Synechococcus* isolate under the same four CO₂ and temperature conditions as in (A) (Fu et al. 2007); (C) Synergistic response of Ross Sea diatom abundance to increasing iron and temperature together (Rose et al. 2009); and (D) *Phaeocystis antarctica* colony abundance in a four-treatment light and Fe experiment, showing that elevating both Fe and light together is necessary to produce a colonial bloom (Feng et al. 2010). For technical details on the methods employed to obtain the data presented in all figures please see the articles indicated.

differences between these two cyanobacterial groups; *Prochlorococcus* may rely on HCO₃⁻ transport as the sole source of DIC because it lacks the *ndh* genes that are required for active CO₂ uptake in many other cyanobacteria, including *Synechococcus* (Badger et al. 2006). A culture study with both *Synechococcus* and *Prochlorococcus* found that acclimation to increased CO₂ levels (76 Pa) resulted in only a slight, non-significant increase in growth rates of *Synechococcus* (Fu et al. 2007). A mesocosm field study also showed that the abundance of *Synechococcus* was not affected by either decreasing or increasing pCO₂ (Engel et al. 2005). Paulino et al. (2008) observed a different response in another field study, in that the abundance of *Synechococcus* decreased with increasing CO₂ by the end of the 24-d experiment. Hence, in two out of three cases, increasing CO₂ alone appears not to have obvious effects on growth and dominance of this genus.

Few studies have investigated whether co-limitation is an important control on *Synechococcus*. In one recent study, Fu et al. (2007) showed that *Synechococcus* growth rates increased synergistically in a treatment coupling high CO₂ with high temperature, compared to the control or to treatments in which either parameter was increased alone. They also observed that increasing CO₂ alone did not increase maximum light-saturated photosynthetic rates (P_{Bmax}), but increasing temperature alone (by 4°C) nearly doubled P_{Bmax} relative to the control. When both pCO₂ and temperature were increased together in the “green-

house” treatment, though, P_{Bmax} went up by a fourfold measure relative to the control (Fig. 1B). This single study comparing two *Synechococcus* and *Prochlorococcus* isolates indicates that differential responses to increasing CO₂ and temperature together could potentially influence future competition between particular picocyanobacterial ecotypes, but more field and culture studies with a wider variety of strains are needed to make confident generalizations (Fu et al. 2007).

Diatoms and ocean biogeochemistry—This group exerts a major influence upon the biogeochemical cycles of C, silicon (Si), N, and Fe in the open ocean. Si is required for the synthesis of diatom frustules, and in regions such as the polar Southern Ocean, the sediments contain large silica accumulations that testify to the importance of diatom bloom export for the biogeochemical cycle of Si (Tréguer et al. 1995). The ability of some species to form chains with built-in silica ballast and to produce large fast-sinking aggregates during the declining phase of blooms (Lampitt 1985) means that they are key vectors in exporting and sequestering particulate organic carbon (POC) to the deep ocean. Sarthou et al. (2005) reported that diatoms may contribute up to 40% of oceanic primary productivity. Diatoms also use mainly new N (i.e., nitrate) and so are important in setting levels of new production (Dugdale 1967) and in determining the *f* ratio (Eppley and Peterson 1979). Although diatoms have physiological Fe require-

Environmental forcing	J	A	S	O	N	D	J	F	M	A	M	J
A) Irradiance	■	■	■	■	■	■			■	■	■	■
Iron				■	■	■	■	■	■			
Silicic acid								■	■			
B) Irradiance	■	■	■	■					■	■	■	■
Iron				■	■	■	■	■	■			
Others?			■	■								

Fig. 2. Seasonality of environmental controls on phytoplankton (redrawn from Boyd 2002). The putative seasonal progression of factor(s) limiting or co-limiting phytoplankton processes. (A) Represents the scheme originally proposed for diatoms in subpolar waters by Boyd et al. (1999). This scheme can also be related to polar diatoms; however, the period of silicate limitation will be shorter or nonexistent (Nelson et al. 2001). Note that the period over which limitation by irradiance, Fe, or silicate occurs will vary with basin and latitude and from year to year. (B) Depicts a seasonal scheme for *Phaeocystis antarctica* in the Ross Sea or polar diatoms in the Southern Ocean. As a result of several uncertainties outlined in the text this scheme is more speculative, and it is possible that factors other than irradiance and Fe may be exerting environmental control (Tortell et al. 2002; Table 1).

ments that are lower than most algal groups (Ho et al. 2003), their ability to rapidly outcompete other algae and form blooms following natural or purposeful Fe enrichments results in an influential role in Fe biogeochemistry (Boyd et al. 2007).

Environmental control of diatoms—Unlike the four other algal groups considered here, diatoms are cosmopolitan. Although diatoms are ubiquitous, there is a wide range of morphologies, ranging from large, heavily silicified chain-forming species such as *Fragillariopsis kerguelensis* in polar waters (Nodder and Waite 2000) to small, lightly silicified and often unicellular diatoms in tropical waters (Cavender-Bares et al. 1999; Scharek et al. 1999). In a review of diatom growth physiology, Sarthou et al. (2005) emphasize the importance of cell size in explaining many physiological properties in diatoms, from growth rates to settling velocities.

As a result of their cosmopolitan nature, the environmental controls on diatoms vary regionally. For example, perturbation experiments reveal that Fe availability controls diatom growth rates in the HNLC waters of the tropical, subpolar, and polar oceans (Price et al. 1991; Boyd et al. 2007), whereas diatom growth in some low-latitude oligotrophic waters is co-limited by both nitrate and Fe (DiTullio et al. 1993). Based on a modeling study by Moore et al. (2002), the main controls on diatoms for different parts of the world ocean during summer are nitrate (50%; mainly low-latitude oligotrophic gyres), Fe (39%; HNLC waters), and silicate (11%; northern subantarctic and northwest Atlantic). Hence, N, Fe, and Si are given the highest rankings in Table 1. The Moore et al. (2002) modeling study did not consider the spring period, when

regions in both hemispheres are characterized by large diatom blooms (Lochte et al. 1993; Moore and Abbott 2000) fueled by the concurrent availability of nutrients, trace elements, and high light levels.

The ecological dominance of diatoms in mid- and high-latitude waters means that unlike many low-latitude algal groups, seasonality in environmental controls on diatoms is often as influential as the individual control factors themselves (Fig. 2). For example, in subantarctic waters diatom growth is limited by light in winter and early spring and then subsequently by Fe supply when light levels increase later in the year. However, this seasonal progression of limiting factors is complicated by co-limitation of diatom growth in spring (light and Fe), summer (Fe and silicate), and early fall (Fe, light, and silicate). These interactions lead to a complex seasonal cycle of environmental control in these subantarctic waters (Fig. 2A), which were termed high-nitrate, low-silicate, low-chlorophyll (HNLSiLC) waters by Dugdale and Wilkerson (1998). In contrast, the seasonal progression of environmental control is less complex in polar Southern Ocean waters, where silicate limitation is seldom observed (Nelson et al. 2001; Fig. 2B).

Fe and light and Fe and Si interactions of diatoms may be classified as biochemically dependent co-limitations (Saito et al. 2008). Silicate requirements (and hence availability) are dependent upon Fe supply, since there is an antagonistic relationship between these environmental controls (Hutchins and Bruland 1998; Firme et al. 2003). In the case of Fe, light and silicate co-limitation of diatoms, use of the two-factor classification scheme of Saito et al. (2008) is problematic, as evidenced by the findings of Hoffmann et al. (2008), who reported species-specific

effects that are driven by the interactions between all three of these controlling factors. Other co-limiting factors that may influence diatom physiology include Fe and vitamin B12, Fe and zinc, and Fe and cobalt (all classified as independent co-limitation; Saito et al. 2008), and recent experiments provide evidence for such co-limitations (Bertrand et al. 2008).

In addition to nutrient and light co-limitation, as reviewed by Saito et al. (2008), we must also consider the interactive effects of temperature and factors such as Fe and CO₂ concentrations on diatoms. Temperature affects some cellular processes (enzyme-catalyzed reactions such as C fixation) but not others (light harvesting and electron transfer), leading to cellular energy imbalances (Raven and Geider 1988). This selective effect of temperature on cellular biochemical pathways has implications for co-limitation. Thus, temperature often interacts synergistically or antagonistically with other environmental controls, such as light and nutrient supply (Raven and Geider 1988; Sunda and Huntsman 1995; Rose et al. 2009). A field study in the Atlantic sector of the Southern Ocean reported that in addition to low dissolved Fe concentrations, low temperatures contributed to low growth rates in resident diatom assemblages (Feller et al. 2001). Hare et al. (2007) found that elevated temperature and CO₂ concentrations shifted a Bering Sea community from diatom dominance to nanophytoplankton dominance and that temperature played the major role in this floristic shift.

There is now recent evidence of how interactive changes in temperature, CO₂, Fe, and irradiance may alter the growth rate of diatom assemblages, as well as differentially affecting the growth rates of particular diatom groups or species within the same community. Here, we provide examples of synergistic effects of multiple environmental controls on diatoms. Figure 1C presents striking evidence of a marked increase in diatom abundance when both Fe supply and temperature are increased together in an experiment on a resident population from the Ross Sea (Rose et al. 2009). A major floristic shift from the small pennate diatom *Cylindrotheca* to the large chain-forming centric diatom *Chaetoceros* occurred in an incubated Ross Sea diatom assemblage in treatments in which CO₂ was increased, especially when irradiance and Fe were also increased simultaneously (Feng et al. 2010). Tortell et al. (2008b) also reported a similar diatom community shift in this region during perturbation experiments in which only pCO₂ was increased. Significantly, these trends are based on effects of just two (Fe and temperature, Fig. 1C; Rose et al. 2009) or three (CO₂, Fe, and light; Feng et al. 2010) of the many environmental properties projected to be altered as a result of climate change (Sarmiento et al. 2004; Doney 2006).

Phaeocystis spp. and ocean biogeochemistry—*Phaeocystis* spp. form large blooms in high-latitude waters of both hemispheres (Schoemann et al. 2005) and, thus, significantly influence the biogeochemical cycles of C, sulfur, N, and P. For example, the large blooms of *Phaeocystis antarctica* in the Ross Sea result in a marked drawdown in atmospheric CO₂ (Arrigo et al. 1999; Sweeney et al. 2002).

Equally large blooms of *Phaeocystis pouchetii* are reported in the Barents and Greenland Seas (Schoemann et al. 2005), but this species does not make a significant contribution to downward C export (Wassmann et al. 2008).

There is little consensus on the fate of these high-latitude *Phaeocystis* blooms, with reports of direct export, grazing, and indirect export of the mucilage from the colonies (DiTullio et al. 2000; Schoemann et al. 2005). Arrigo et al. (1999) reported that in the Ross Sea, *P. antarctica* blooms fix more C per unit N or P than diatom blooms and hence may have a pronounced effect on upper-ocean N, P, and C inventories. *P. antarctica* blooms in the Ross Sea also have a marked effect on dimethyl sulfide (DMS) production (Kettle et al. 1999), equivalent to 5–10% of the global DMS flux (Schoemann et al. 2005). The Charlson Lovelock Andreae Warren hypothesis, although controversial (Ayers and Caine 2007), suggests that DMS fluxes from the surface ocean act as cloud condensation nuclei and thus help to regulate net incoming solar radiation and global temperatures (Charlson et al. 1987). We point the reader to useful reviews of the biogeochemistry of *Phaeocystis* spp. by Verity et al. (2007) and Schoemann et al. (2005).

Environmental control of Phaeocystis spp.—A striking feature of the three main *Phaeocystis* spp. (*globosa*, *antarctica*, and *pouchetii*) is their complex life cycle (Beardall et al. 2008) that encompasses alternating phases between free-living cells (< 10 μm) and large colonies (> 2–3 mm) that are mucilaginous (Schoemann et al. 2005). Both laboratory and field studies have investigated the environmental controls on both of these phases, revealing striking differences in many parameters, including Fe requirements (higher levels required for colony formation; Boyd et al. 2008). Consequently, it is important to compare findings specifically for either the colonial or single-celled forms. In addition, the majority of recent research into environmental controls has focused on *P. antarctica* (DiTullio et al. 2007; Sedwick et al. 2007; Van Leeuwe and Stefels 2007) rather than on other *Phaeocystis* species.

In contemporary discussions of environmental control on phytoplankton the role of temperature is often overlooked, with studies focusing on factors such as trace metals, light, and nutrients. Surveys of the regional and global distributions of algal groups reveal that not everything is everywhere (Finlay 2002), and temperature plays a fundamental role in setting the biogeographical distributions of phytoplankton groups such as *Phaeocystis* species. *Phaeocystis* spp. are mainly dominant at high latitudes (e.g., *P. pouchetii* in the subarctic and Arctic; Schoemann et al. 2005). Despite being confined to high latitudes, each *Phaeocystis* species has different optimal temperature ranges for growth (Schoemann et al. 2005).

A significant difference between the southern and northern hemisphere *Phaeocystis* species is the general absence of Fe limitation in northern high-latitude waters, where blooms are often reported in neritic waters such as fjords (Verity et al. 2007) and where macronutrient concentrations generally control bloom development (Veldhuis et al. 1991). Fe addition has, however, been reported to increase *Phaeocystis* colony abundance in shipboard

experiments in the Peru Upwelling and Humboldt Current (Hutchins et al. 2002). There is a sole report of increased *Phaeocystis* spp. abundance (species not known, as the authors relied only on algal pigments) due to increased CO₂ during a perturbation experiment in Equatorial Pacific waters (Tortell et al. 2002). As a result of this paucity of information on northern hemisphere waters, we will focus mainly on the environmental controls of *P. antarctica*.

In the Southern Ocean, the main environmental controls on *P. antarctica* are reported to be irradiance and Fe (Table 1; Arrigo et al. 2003; Arrigo and Tagliabue 2005; Arrigo 2007). *Phaeocystis* blooms, comprising mainly colonies, usually occur prior to those of diatoms in the Ross Sea, possibly as a result of their ability to better adapt to low irradiance levels early in spring (Arrigo et al. 2003; Fig. 2B). At this time, dissolved Fe is present at concentrations that are not limiting the *Phaeocystis* blooms, indicating that bloom development is controlled by irradiance (Sedwick et al. 2007). Presumably the bloom is terminated as a result of Fe limitation (Smith et al. 2000; Fig. 2B) and/or an inability to grow under high-irradiance conditions later in the season. Modeling studies (Tagliabue and Arrigo 2006) have suggested that irradiance may favor *Phaeocystis* over diatoms in spring in the Ross Sea by controlling Fe speciation and photo-physiology.

Nutrients appear to have little influence on *P. antarctica*, as nitrate and phosphate remain at relatively high concentrations over the annual cycle in the Ross Sea (Boyd et al. 2008). Field experiments have found negligible effects of changing CO₂ concentrations on either solitary or colonial *P. antarctica* (Feng et al. 2010), perhaps because this species has been reported to have an efficient inorganic CCM (Tortell et al. 2008a). Hence, we have ranked nutrients and CO₂ as insignificant in controlling *P. antarctica* (Table 1). Relatively few studies have investigated temperature effects on this species, and so we have ranked the effect of this variable as unknown, although a maximum temperature of about 10°C for its growth has been reported (Buma et al. 1991).

The nature of the interplay between Fe and light as environmental controls on *P. antarctica* also requires discussion. It has been reported that at low irradiances the Fe requirement of phytoplankton species such as polar flagellates increases as a result of their need to increase harvest lighting via chlorophyll synthesis (Van Leeuwe and de Baar 2000). This observation points to an antagonistic relationship between Fe supply and irradiance. Sedwick et al. (2007) found that colonial *P. antarctica* cultured under low irradiances ($< 70 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) have high Fe requirements, results that were interpreted by Verity et al. (2007) as evidence of this antagonistic relationship. However, the marked differences between the Fe requirements of the unicellular and colonial forms (Boyd et al. 2008) may complicate such an interpretation. It is clear that even if only Fe and light are the main drivers during the growth season (Fig. 2B), the environmental controls on *P. antarctica* are complex and insufficiently resolved. Contrary to current hypotheses about this species being low-light adapted and less prone to Fe limitation than diatoms, new experimental work indicates that both high light and

Fe are necessary to produce a colonial *P. antarctica* bloom in the Ross Sea (Fig. 1D; Feng et al. 2010). Thus, as for many diatoms, Fe and light co-limitation could be an important control for this species.

N₂ fixers and ocean biogeochemistry—This prokaryotic phytoplankton group plays an essential role in the N cycle by supplying 100–200 Tg N of new fixed N annually to oligotrophic waters (Mulholland 2007). Early studies considered the filamentous cyanobacterium *Trichodesmium* to be the dominant global N₂ fixer (Capone et al. 1997). Indeed, *Trichodesmium* is believed to fix 60–80 Tg N yr⁻¹ and supports almost 50% of new production in the nutrient-poor waters of the tropical and subtropical oceans (Mulholland 2007).

We now know that unicellular cyanobacteria are also major N₂ fixers in areas such as the tropical North Atlantic and subtropical North Pacific Oceans (Zehr et al. 2001). Worldwide, *Crocospaera* probably fixes an amount of N that is comparable to *Trichodesmium* and may be responsible for up to 10% of global new production (Montoya et al. 2004). Intracellular symbiotic cyanobacteria associated with diatoms (diatom and diazotroph associations), dinoflagellates, or protozoan zooplankton also make a large but poorly quantified contribution to global N₂ fixation (Carpenter et al. 1999; Foster et al. 2006). The diazotrophs perform a single clearly defined biogeochemical function but are diverse taxonomically, although only cyanobacteria will be considered further here. A three to four order-of-magnitude range in cell sizes, from macroscopic colonies of *Trichodesmium* to picoplanktonic unicells, means they can have widely divergent ecological roles in marine food webs.

Environmental control of N₂ fixers—Despite the morphological and ecological diversity of N₂ fixers, it is possible to make some broad generalizations about their environmental niche in the ocean. Temperature appears to be a primary control on their global distribution (Table 1), and some culture studies indicate that it exerts a direct control on their growth, rather than acting through other potential environmental co-variables such as light and nutrients (Falcon et al. 2005; Breitbarth et al. 2007). Like picocyanobacteria, the N₂ fixers are by far most prominent in the oligotrophic central gyres. *Trichodesmium* spp. are common worldwide throughout the tropical and subtropical oceans, where their range is relatively easily defined based on both anecdotal observations of blooms and remote sensing data (Westberry and Siegel 2006). The lower thermal boundary for *Trichodesmium* growth is around 20°C (Breitbarth et al. 2007), so significant accumulations of biomass occur only between 20°N and 20°S in the Atlantic and eastern Pacific Oceans, with somewhat broader latitudinal ranges in the Indian and western Pacific Oceans (Westberry and Siegel 2006). Unicellular diazotrophic cyanobacteria such as *Crocospaera* appear to be similarly subject to strong temperature constraints, with some strains unable to grow below 25°C (Falcon et al. 2005). It has been suggested (Stal 2009) that warm seawater directly favors non-heterocystous N₂ fixers such as *Trichodesmium* and *Crocospaera*, since the resulting lower

gas solubility of O₂ and higher cellular respiration rates both help to protect their nitrogenase enzymes from inactivation by oxygen. Despite this, recent evidence indicates the presence of previously unrecognized N₂ fixers in cooler waters, such as the central gyre, as far north as 40°N, although rates of N₂ fixation here seem to be relatively modest (Needoba et al. 2007; Rees et al. 2009).

Other than temperature, though, environmental controls on diazotrophs are still relatively difficult to rank with confidence, with contradictory findings reported for the role of irradiance, Fe, P, and CO₂ and for co-limitation between these (Table 1). Irradiance is a potentially limiting factor, since N₂ fixation is extremely energy-intensive (Capone et al. 1997). Sañudo-Wilhelmy et al. (2001) found an inverse correlation between *Trichodesmium* N₂ fixation rates and mixed layer depth in the subtropical Atlantic, indicative of light limitation. However, *Trichodesmium* can regulate its buoyancy and so position itself vertically to optimize the light regime for maximum growth (Bell and Fu 2005). A field photo-physiology study showed that *Trichodesmium* requires a high light environment and can tolerate irradiances of > 1000 μmol quanta m⁻² s⁻¹ without photoinhibition (Carpenter and Roenneberg 1995). Some laboratory photo-physiology studies support this lack of photoinhibition but indicate a better ability to grow at low irradiances (Breitbarth et al. 2008). The latter is consistent with observations that the maximum abundances of *Trichodesmium* are often localized at 20–40 m (Capone et al. 1997). Little is known about the photo-physiology of *Crocospaera*, but the few available data indicate its photosynthetic parameters do not differ substantially (despite lacking buoyancy regulation) from those of *Trichodesmium* (Fu et al. 2008).

P and Fe are the two nutrients most often believed to limit the growth and fixation rates of N₂ fixers, but their relative importance remains controversial (Hutchins and Fu 2008). Support for the P limitation hypothesis comes from a correlation between the P quotas of natural *Trichodesmium* colonies in the North Atlantic and their N₂ fixation rates (Sañudo-Wilhelmy et al. 2001) and from P kinetic determinations of collected colonies from this region, which demonstrated that *Trichodesmium* are strongly P-limited (Sohm et al. 2008). A laboratory P kinetics study using two strains showed that it is unlikely that *Trichodesmium* can rely solely on DIP for growth at nanomolar concentrations (Fu et al. 2005) and so must rely largely on dissolved organic phosphorus (DOP) sources in nature (Dyrman et al. 2006).

The possible role of Fe, an essential cofactor of the nitrogenase enzyme, as a limiting micronutrient for N₂ fixers like *Trichodesmium* was first suggested by Rueter (1988). Moreover, these cyanobacteria have a very high photosystem I:photosystem II ratio, resulting in Fe requirements that are two- to fivefold greater than in NH₄⁺-assimilating phytoplankton (Kustka et al. 2003). Some fieldwork also supports the importance of Fe in the environmental control of *Trichodesmium*. A bloom was observed north of Bermuda, where the Fe concentration per colony increased approximately threefold following a dust deposition event (Orcutt et al. 2001). Sohm et al.

(2008) suggested that natural populations of *Trichodesmium* in areas of the North Pacific and waters north of Australia are most likely Fe-limited. However, the role of Fe has been questioned for the central Atlantic after *Trichodesmium* N₂ fixation rates were shown to be independent of dissolved Fe concentrations and colonial Fe content (Sañudo-Wilhelmy et al. 2001).

The possible role of P or Fe as a limiting factor for the growth and N₂ fixation of unicellular cyanobacteria such as *Crocospaera* remains uncertain, with few data available. Fe:C ratios of *Cyanothece* (Berman-Frank et al. 2007) and *Crocospaera* (Fu et al. 2008) are significantly lower than for *Trichodesmium*, indicating less potential for Fe limitation for these unicells. The P half-saturation constant for growth of *Crocospaera* (Falcon et al. 2005) is similar to typical phosphate concentrations in oligotrophic waters (Wu et al. 2000), indicating that they are not significantly P-limited in situ.

CO₂ limitation is another factor that may control N₂ fixers. Several recent culture studies using *Trichodesmium* (Barcelos e Ramos et al. 2007; Hutchins et al. 2007; Levitan et al. 2007) and *Crocospaera* (Fu et al. 2008) demonstrated that CO₂ availability can strongly control their N₂ and C fixation rates and elemental ratios. Both of these groups of diazotrophic cyanobacteria appear to be C-limited at present-day CO₂ levels, adding a new twist to the controversy over limiting factors for N₂ fixation.

The interplay between these potentially limiting factors and their combined effects on N₂ fixers are particularly poorly understood at present. A tropical Atlantic study revealed that both phosphate and Fe had to be added to stimulate N₂ fixation and C fixation in 200 μm-screened (i.e., excluding most *Trichodesmium*) water samples (Mills et al. 2004). Therefore, this study indicates closely balanced co-limitation of unicellular N₂ fixers by both Fe and P; relatively small changes in the stoichiometric ratios of these two nutrients under future climate regimes could thus have large consequences for their diazotrophic growth. However, Moore et al. (2009) more recently suggested that large-scale patterns of N₂ fixation in the north and south Atlantic correlate primarily with Fe availability alone. In contrast, Bonnet et al. (2008) observed no response to Fe and P additions in the southern subtropical Pacific Gyre, and Mackie et al. (2008) reported no response by *Trichodesmium* to the largest dust storm in 30 yr in subtropical southwest Pacific waters, which are characterized by very high phosphate concentrations, relative to nitrate (Moutin et al. 2008).

Hutchins et al. (2007) examined the interactions between CO₂ and P limitation in *Trichodesmium* and found that even severely P-limited cultures showed enhanced N₂ fixation rates at high pCO₂. Since either CO₂ or P additions would result in N₂ fixation increases, *Trichodesmium*, which are apparently P-limited at present-day pCO₂, may be co-limited by both P and C. In contrast, *Crocospaera* N₂ fixation rates are increased by elevated CO₂ levels in Fe-replete cultures (Fig. 3A), but not in Fe-limited ones (Fig. 3B), and cellular Fe:C ratios also respond to changing CO₂ only when Fe is available (Fu et al. 2008). Thus, it appears that P limitation and Fe limitation could

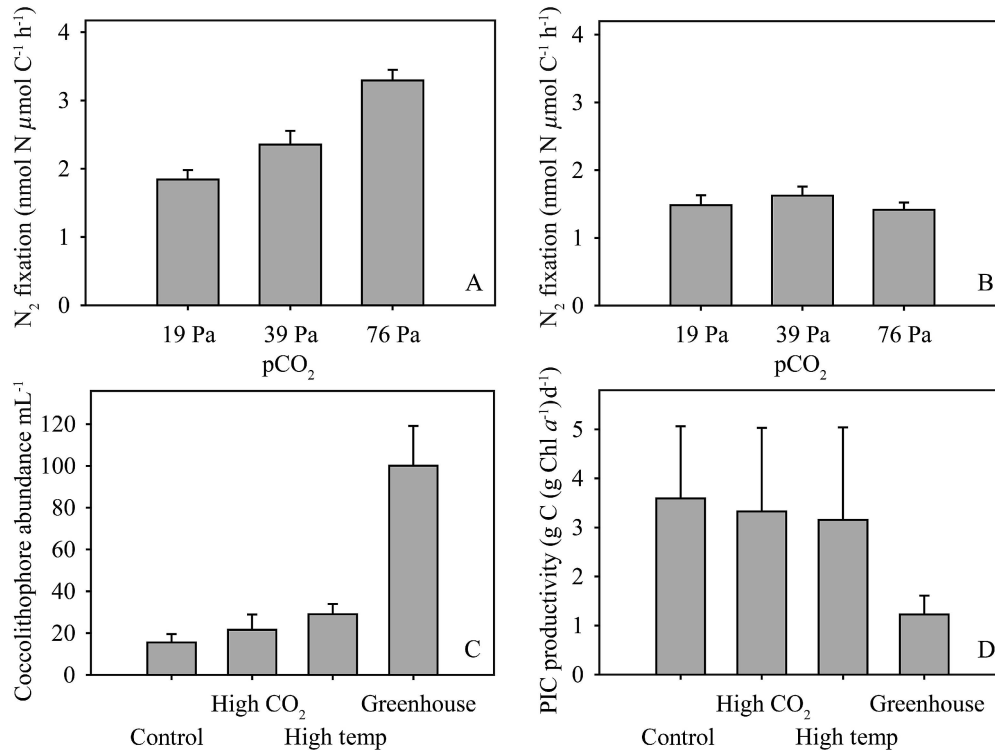


Fig. 3. (A) N₂ fixation rates of Fe-replete *Crocospaera* cultures increase with pCO₂ (Fu et al. 2008); (B) N₂ fixation rates of Fe-limited *Crocospaera* cultures are not affected by changing pCO₂ (Fu et al. 2008); (C) Coccolithophore abundance increases synergistically in a North Atlantic spring bloom CO₂ and temperature matrix perturbation experiment in the high-CO₂ and high-temperature greenhouse treatment (Feng et al. 2009); and (D) Particulate inorganic carbon (PIC or calcite) production decreases antagonistically in the high-CO₂ and high-temperature greenhouse treatment in the same North Atlantic spring bloom experiment (Feng et al. 2009), indicating denser blooms of less calcified cells in the future.

interact in very different ways with CO₂ to control cyanobacterial N₂ fixation rates (Hutchins et al. 2009).

Coccolithophores and ocean biogeochemistry—Coccolithophores occupy a pivotal position in the C cycle by the conversion of dissolved inorganic C to both POC and particulate inorganic (PIC or calcite) forms. As for all phytoplankton, their C fixation will draw down CO₂, but coccolithophore calcification results in the conversion of 2 mols of HCO₃⁻ to 1 mol each of CO₂ and CaCO₃. Consequently, uncertainties exist over whether coccolithophore blooms are net sinks or sources of CO₂ to the atmosphere (Boyd and Trull 2007). Calcite may also influence the marine C cycle indirectly by contributing to mineral ballasting of marine aggregates, thus facilitating rapid and efficient C export (Armstrong et al. 2002; Ziveri et al. 2007). Coccolithophores may also influence global climate, since like *Phaeocystis*, they are a major DMS source (Malin et al. 1993).

Environmental control of coccolithophores—Despite a long-standing research focus on coccolithophores, there is little consensus about the relative importance of environmental controls on their growth (Table 1). Coccolithophores have cosmopolitan distributions from tropical to

temperate waters, but this group is virtually absent in polar waters. In recent years this group has apparently extended its latitudinal range into both northern and southern subpolar waters (Merico et al. 2003; Cubillos et al. 2007), which these studies have indicated could be due to climate warming trends. Thus, temperature appears to be a primary control factor setting the boundaries of their biome, and so is ranked highly in Table 1.

High irradiances (i.e., > 500 μmol quanta m⁻² s⁻¹) have often been suggested (Nanninga and Tyrrell 1996; Paasche 2002; Zondervan 2007) to favor coccolithophores over diatoms and other algal taxa, and coccolithophore blooms frequently occur under shallow-mixed layer, high-light conditions. However, blooms have also been observed under low irradiances (< 200 μmol quanta m⁻² s⁻¹), and cultured cells grow quite well at low light levels (Zondervan 2007).

Nutrient availability and dissolved nutrient stoichiometric ratios have also been reported to control coccolithophore growth rates. Observations (Sieracki et al. 1993; Leblanc et al. 2009) indicate that the transition from diatoms to coccolithophores observed during the latter stages of the North Atlantic bloom is driven by depletion of silicate before nitrate. High dissolved N:P ratios have also been found to favor coccolithophore dominance (Table 1).

Emiliana huxleyi may have an unusually high affinity for phosphate uptake and also can use alkaline phosphatase to access DOP sources (Riegmann et al. 2000). Although coccolithophore blooms frequently occur under conditions of high dissolved inorganic N:P ratios, there are also numerous exceptions to this trend (Lessard et al. 2005). Trace metal availability is another possible influence on coccolithophore growth. Most studies of coccolithophore Fe requirements report relatively low Fe:C ratios and/or very high affinity for Fe (Sunda and Huntsman 1995; Muggli and Harrison 1996); therefore, they appear unlikely to be constrained by Fe limitation, compared to other groups such as diatoms. Although zinc has been implicated as a possible limiting micronutrient for coccolithophore growth and calcification (Crawford et al. 2003; Schulz et al. 2004), evidence for trace metal limitation in coccolithophores remains sparse (Ellwood and van den Berg 2001).

CO₂ and carbonate saturation state have received much recent attention with regard to environmental control of coccolithophores. C fixation by this group appears to be under-saturated at present-day pCO₂ (Rost et al. 2003; Feng et al. 2008, 2009), so coccolithophores may be truly C-limited in today's ocean. In contrast to C fixation, numerous laboratory and field experiments have shown that calcification is reduced at high pCO₂ (reviewed in Zondervan 2007). A recent study (Iglesias-Rodriguez et al. 2008) presented evidence for increased calcification in *E. huxleyi* at elevated CO₂, although their findings are disputed (Riebesell et al. 2009). Different coccolithophore species and even strains may exhibit variable responses to pCO₂ changes, so generalizations should be made cautiously (Zondervan 2007; Langer et al. 2009).

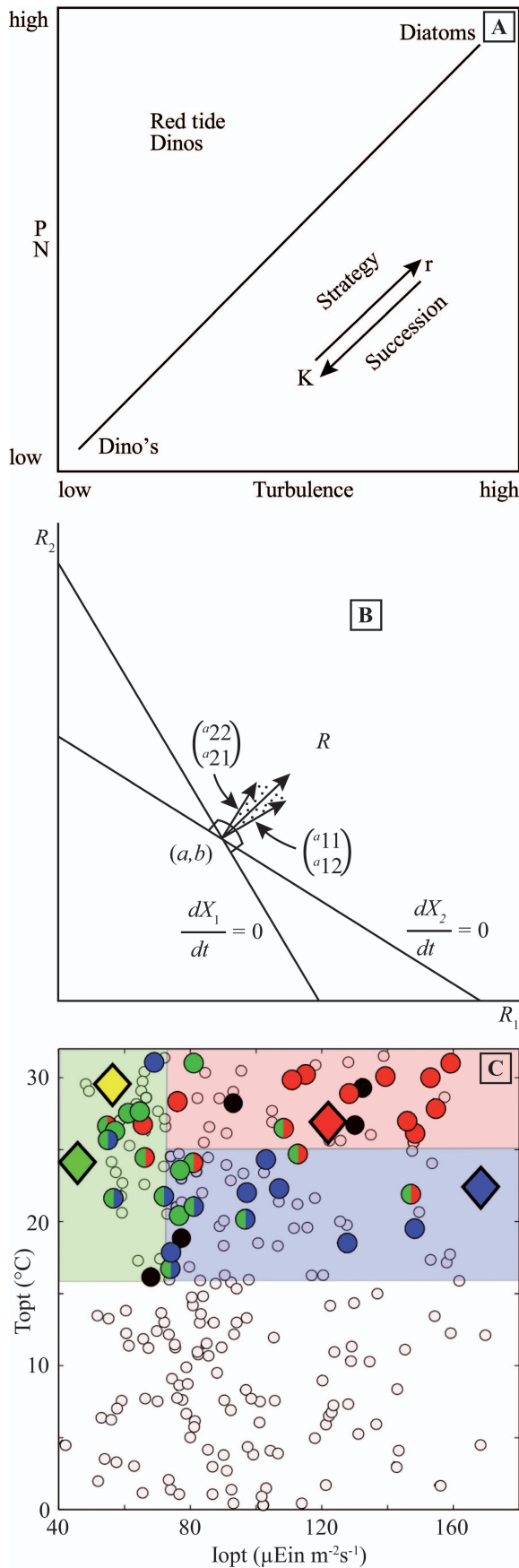
Research into the effects of co-limitation of coccolithophore physiology is also fraught with uncertainties. In a review, Zondervan (2007) collated studies reporting temperature effects on coccolithophore light responses. In addition, other effects of co-limitation show that light and nutrient availability may modulate the physiological effects of changing pCO₂. Feng et al. (2008) found that in cultures of *E. huxleyi*, elevated CO₂ reduced cellular calcification, but only under saturating irradiances. In an experiment using a natural North Atlantic bloom community, Feng et al. (2009) found that coccolithophore abundances increased dramatically in a combined high-pCO₂ (~76-Pa) and high-temperature (ambient plus 4°C) treatment, whereas no effect on abundance was seen from increases in either pCO₂ or temperature alone (Fig. 3C). In a seemingly paradoxical situation, calcite production was simultaneously greatly decreased in this experiment, but again only in the combined high-CO₂, high-temperature treatment (Fig. 3D). This indicates that elevated CO₂ and temperature may favor more intense coccolithophore blooms by relieving C limitation of photosynthesis, but at the same time these rapidly growing cells may be very lightly calcified. Reciprocal interactions between changing pCO₂, temperature, irradiance, and major and micronutrient availability may be more significant than the individual effects of any of these variables alone, and coccolithophores seem poised to be one of the algal groups most affected by such interactions.

Theoretical frameworks of environmental control on phytoplankton

In light of our discussion of the relative importance and interplay of environmental control factors for phytoplankton groups, we summarize here four theoretical frameworks that have been widely applied to these issues. The first approach is conceptual and includes Margalef's Mandala (Margalef 1978), Reynolds Intaglio (Reynolds 1987), and Resource Ratio Theory (RRT; MacArthur 1972; Tilman 1977, 1982). The second approach is mathematical modeling, in which simulations explore the controls on the biogeography of different phytoplankton groups (Moore et al. 2002). We also consider two studies (Anderson 2005; Hood et al. 2006) that appraise and critique this modeling approach. The third framework is an alternative modeling approach in which dominant phytoplankton groups emerge based on a stochastic determination of their physiological traits, rather than being prescribed (Follows et al. 2007). Finally, the fourth framework builds on prior concepts (Margalef 1978; Reynolds 1987) and uses functional traits to explore organization within phytoplankton communities (Litchman and Klausmeier 2008). We use the data presented and issues raised in our review to probe the efficacy and potential of each approach in the context of phytoplankton and climate change.

Conceptual frameworks—Of the early approaches, the Mandala and Intaglio approaches both attempted to explain observed trends in the dominance of algal groups along gradients in both nutrient supply and turbulence in terms of the survival strategies that phytoplankton employ. Hence, Margalef (1978) reported that “r” strategists (diatoms) dominate in high-nutrient and high-turbulence environments, the other end-member being “K” strategists (dinoflagellates) that dominate under low-nutrient and low-turbulence conditions (Fig. 4A). The Intaglio focused on nutrient accessibility and light and mixed layer depth and defined three phytoplankton categories, C (invasive, small size, rapid growth), R (acclimated to well-mixed low-light environments, with intermediate growth rates and size), and S (acquisitive; i.e., for nutrients, large size, slow growing, and motile). Application of the Intaglio to a coastal phytoplankton community resulted in a range of species within each taxonomic group considered (for example, diatoms) being split across C, R, and S categories (Reynolds and Smayda 1998). Smayda and Reynolds (2001) applied both the Mandala and Intaglio models to harmful algal bloom studies in coastal waters. They concluded that the Intaglio was a better model, emphasized that it was a descriptive rather than mechanistic model, and in particular advocated that more attention be paid to the stochastic selection of bloom species (i.e., the importance of the “right time and right place”).

Based on our data sets (Figs. 1, 3, 5), there are problems with applying either approach to the open ocean. In the case of Margalef's Mandala, it has insufficient dimensions to take into account seasonal changes in the multiple limiting and co-limiting factors that control a phytoplank-



ton group (Fig. 2). This is also a problem with the oceanic application of the Intaglio to the phytoplankton groups we examined, since individual species within a phytoplankton group are spread across different categories.

RRT focused on the relative success of different species in competing for available resources. This theory states that the species that can maintain a positive growth rate at the lowest level of a resource (for example, nitrate) will out-compete the others for the same resource (Fig. 4B). This approach has been used primarily in terrestrial and freshwater environments and on both primary producers and primary consumers (see fig. 3 in Miller et al. 2005) to predict the outcome of competition between two or more species as well as the resulting patterns for the planktonic assemblage. RRT has seldom been tested in the marine environment, but Sommer (1985) has been its most avid user, with at least nine publications between 1985 and 1996. For example, Sommer (1994) carried out elaborate laboratory culture competition experiments with up to 11 marine phytoplankton species over a wide range of light intensities and Si:N ratios and three different photoperiods. The outcome of these logistically challenging experiments is a summary of the competitive success of all 11 species, plotted as a series of diagrams (figs. 3–9 in Sommer 1994). In his study, diatoms dominated at high Si:N ratios, and dinoflagellates dominated at low Si:N ratios, as expected. Light had no effect on functional groups but did exert an influence at the species level on this floristic transition along the Si:N gradient (Sommer 1994).

A comparison of the experimental design of Sommer (1994) with the data sets presented here (Figs. 1, 3, 5) raises several issues about the utility of RRT for open-ocean phytoplankton groups. In most oceanic systems phytoplankton community structure is too poorly resolved at the

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Fig. 4. Examples of approaches to represent environmental control of phytoplankton groups (A) Conceptual—Margalef's Mandala (Margalef 1978) to express and explain the dominance of different phytoplankton life forms under different combinations of natural factors; (B) Conceptual—Resource Ratio Theory, as illustrated by a schematic redrawn from MacArthur (1972). Abundances of two living resources are denoted by R_1 and R_2 ; the vector R indicates the combined supply rate of the two resources to the environment. The isoclines define the points at which the growth rates of each of the two species are 0 (i.e., dX_1/dt and dX_2/dt); a_{ij} describes the consumption of resource j by species i ; (C) Modeling—results from a phytoplankton model of emergent biogeography (redrawn from Follows et al. 2007). Results are presented as a property–property plot of optimum temperature and light intensity for phytoplankton growth, T_{opt} and I_{opt} , of all initialized *Prochlorococcus* analogs (all circles) from the ensemble of 10 model integrations. Large circles denote the analogs that exceeded a total biomass of 10^6 mol P along the Atlantic Meridional Transect in the 10th year of the model run. Colors indicate classification into model ecotypes m-e (i.e., red circles, m-e1; blue circles, m-e2; green circles, m-e3). Mixed color and solid black circles denote ambiguity in model-ecotype classification. Bold diamonds indicate real-world *Prochlorococcus* ecotypes (red, eMIT9312; blue, eMED4; green, eNATL2A; and yellow, eMIT9313) (for more details see Follows et al. 2007).

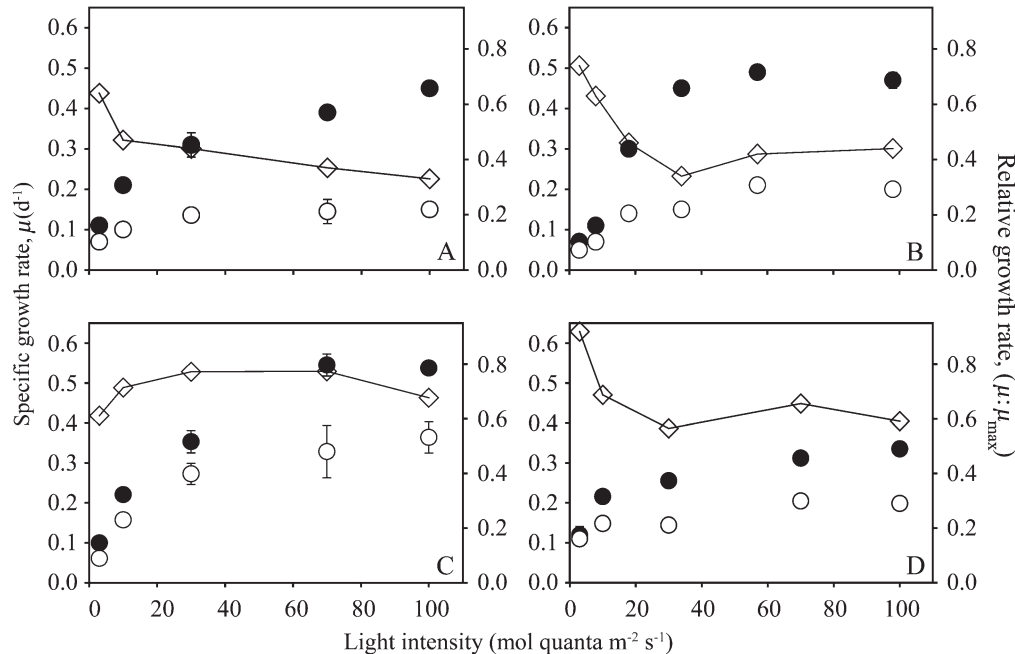


Fig. 5. Steady-state growth rates of four Southern Ocean phytoplankton isolates grown over a range of photon flux densities (PFD). Closed circles are data from Fe-replete cultures; open circles are data from Fe-limited cultures. Fe-limited growth rates (μ) relative to Fe-replete growth rates (μ_{\max}) are plotted as open diamonds. (A) *Phaeocystis antarctica* (clone SX9; colonial). (B) *P. antarctica* (clone AA1; solitary cells). (C) *Proboscia inermis* (diatom). (D) *Eucampia antarctica* (diatom). Error bars represent standard error and are smaller than the symbol when not visible ($n = 3\text{--}16$).

species level (Irigoien et al. 2004; Follows et al. 2007) to rigorously test RRT predictions about the outcome of competition for resources. Our knowledge of the physiology of phytoplankton groups is largely based on laboratory culture studies using model species such as *Trichodesmium erythraeum*, *Thalassiosira oceanica*, or *E. huxleyi* (Hood et al. 2006) that may not be broadly representative of each algal group (Langer et al. 2006). This point is well illustrated by the wide range of responses to altered Fe supply and light climate by closely related Southern Ocean phytoplankton isolates (Fig. 5). These data reveal that alteration of Fe and light conditions can result in a change in growth rate, ranging from negligible to more than twofold, between diatom species and between *Phaeocystis* strains (Fig. 5), making generalizations difficult. This lack of a consistent response to environmental conditions makes representation of algal groups within models difficult. Moreover, RRT has seldom been applied to field studies (Miller et al. 2005), indicating that it is difficult to test such predictions outside of the controls imposed within a laboratory culture flask. Perhaps the major impediment to adopting RRT for oceanic studies is that it requires each species to be limited by a single nutrient to allow predictions to be tested; throughout this review we have presented numerous examples of co-limitation and the resulting non-linearities (amplification, diminution) that occur when there are interactive effects between factors that exert environmental control.

Models of phytoplankton biogeography—The Coupled Ocean Atmosphere Models (COAMs) of Moore et al.

(2002) incorporate both multiple elements (C, P, N, Fe, “dust”) and phytoplankton groups (diatoms, diazotrophs) within “offline” model runs. This approach increased the biological sophistry of such models, which previously had no explicit biology (i.e., nutrient restoration), or of a simple phytoplankton-zooplankton-N-detritus approach (Boyd and Trull 2007). The incorporation of both elements and algal groups permitted exploration of environmental control on phytoplankton. The outcome of such simulations was two-dimensional maps of the world ocean overlaid with predicted biogeographical distributions for each group. These enabled estimates of the areal extent of regions in which phytoplankton are limited by a particular element, such as Fe or silicate.

Such an approach is attractive, as it provides both global maps of biomes and mechanistic links to modes of environmental control. However, Anderson (2005) questioned whether such models could actually predict the global distributions of phytoplankton groups, as opposed to simply reproducing observed trends in distributions. Anderson (2005) illustrates this point by comparing the outputs and parameterizations for two different models and states the following: “Consider, for example, separate models examining the distribution of nitrogen fixers in the subtropical Atlantic and Caribbean by Hood et al. (2004) and Lenos et al. (2005), respectively. Both models broadly reproduced spatial distributions of *Trichodesmium* but used entirely different parameterizations, Hood et al. focusing solely on the effect of light on growth, Lenos et al. including also the effects of limitation by phosphorus and iron. It would be interesting to see how well each parameterization

would perform if supplanted into the other's geographical domain." In our view, this quote from Anderson (2005) highlights some of the potential limitations of this modeling approach rather than pointing to the co-evolution of phytoplankton traits to optimize with regard to several selective pressures (Litchman and Klausmeier 2008).

In another such appraisal, Hood et al. (2006) focused on how models using algal functional groups and coupled biogeochemistry can predict changes in the ocean due to climate change. They raised three key issues in their review: over-reliance on validation data and model simulations for several representative species (e.g., *Trichodesmium*); a potential decrease in the predictive power of models having greater biological complexity; and the need to incorporate more detail at higher trophic levels. On the issue of the response of the biota to climate change, Hood et al. (2006) point out that increased stratification should favor groups like coccolithophores and N₂ fixers (relative to diatoms), but that uncertainties remain over how altered Fe supply or pH will affect these algal groups. Our appraisal of the state of understanding of environmental control on both of these groups (Table 1) is less optimistic than that of Hood et al. (2006), and, thus, we suggest that the functional group modeling approach is of less utility when trying to predict how environmental controls on algal groups will be modified by future climate change.

Modeling emergent phytoplankton biogeography—An alternative approach has been developed by Follows et al. (2007) to circumvent some of the drawbacks of models in which the selection and parameterization of phytoplankton groups are prescriptive. They populated the global ocean model domain with many different phytoplankton that exhibited a wide range of physiological permutations based on published, environmentally reasonable ranges. Simulations were then run, and a biogeographical distribution of the most successful phytoplankton emerged rather than being imposed, as in the work of Moore et al. (2002) or Gregg et al. (2003). The model results showed an encouraging convergence between the simulated biomes of the most successful model phytoplankton group and observed distributions of *Prochlorococcus* ecotypes, as reported by Johnson et al. (2006). What was particularly striking in their property–property space plot of temperature vs. light optima (Fig. 4C) was that two tightly clustered points (akin to nodes) within property–property space captured the dominance of much of the low-latitude Atlantic by two major *Prochlorococcus* ecotypes. Follows et al. (2007) concluded that "... because the ecosystem structure and function are, by design, emergent and not tightly prescribed, this modeling approach is ideally suited for studies of the relations between marine ecosystems, evolution, biogeochemical cycles, and past and future climate change." However, they did not indicate how this might be achieved.

There are several potential issues that need to be overcome prior to applying this modeling approach to climate change. Phytoplankton responses to climate change will likely be driven by the interactions of a range of different environmental controls (Figs. 1, 3, 5), necessitat-

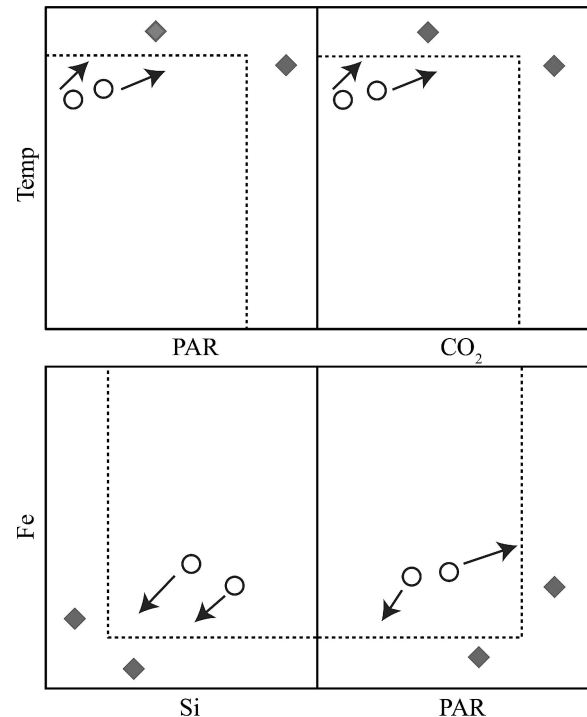


Fig. 6. Schematic of a suite of property–property plots of optima for algal growth illustrating the potential responses to climate change by phytoplankton via long-term (years to decades) adaptation. The plots represent projected changes to upper-ocean environmental properties (from COAMs; Boyd et al. 2008), which also have been demonstrated to have interactive effects on phytoplankton processes (Figs. 1, 3, 5). The dashed line represents the present-day property–property space, which is equivalent to that presented in Fig. 4C. Changes in environmental properties may result in alteration of the property–property space, for example, that due to warming temperatures and higher irradiances, reduced supply of Fe and silicate, or reduced Fe supply and increased irradiances. Natural selection by sustained environmental change may result in phytoplankton groups developing physiological traits for optima that lie outside the current property–property space (depicted by closed diamonds). Alternatively, phytoplankton groups may shift away from present-day nodes (see Fig. 4C) to populate new locations within this space (denoted by the open circles), depending on the relative influence of each property.

ing a suite of multi-dimensional property–property plots. In Fig. 6 we have represented four examples of such plots based on interactions between environmental factors, such as Fe and light or CO₂ and temperature, and phytoplankton processes (Figs. 1, 3, 5). Based on the projections from climate-change models (Sarmiento et al. 1998), the existing property–property space (as represented by Fig. 4C) will be altered to include additional permutations—for example, altered temperature optima due to warming or increased upper-ocean CO₂ concentrations modifying the CO₂ optima for phytoplankton growth.

As natural selection by sustained changes in environmental properties causes algal groups to eventually adapt to climate change (Boyd et al. 2008), they may either display physiological traits outside the present-day property–property space (i.e., beyond the dashed lines in Fig. 6)

or shift from present-day clusters or nodes to populate new locations within the dashed lines (Fig. 6). The greatest attribute of the Follows et al. (2007) model is its emergent nature. Hence, it reveals for the oligotrophic Atlantic Ocean which permutations of temperature and light optima permit species to subsist successfully (nodes) and which will not (anti-nodes). It should therefore be possible to extend the property–property grid by either adding new hypothetical physiological traits to simulate climate-change–altered conditions and new opportunities or to add in novel physiological traits to mimic adaptation and explore where nodes or clusters migrate (Fig. 6).

Phytoplankton physiological traits—The final framework we consider involves the application of physiological traits to explore the structuring of phytoplankton communities along environmental gradients (Litchman and Klausmeier 2008). This approach follows the lineage of Margalef (1978), but Litchman and Klausmeier considerably expand the number of trait types considered (e.g., morphology, physiology, behavior, and life history), which they each cross-reference to ecological function (reproduction, resource acquisition, and predator avoidance—see their fig. 1, Litchman and Klausmeier 2008). This holistic approach may enable one to avoid the constructs of bottom-up vs. top-down control of phytoplankton community structure. In addition, comparison of trait type relative to ecological function permits the exploration of trade-offs. For example, larger cell size may increase resistance to grazing but decrease the ability of a cell to compete for nutrients (Litchman et al. 2007; Litchman and Klausmeier 2008). Litchman and Klausmeier (2008) conclude their comprehensive review by stating “one of the great potential applications of trait-based approaches is to increase our ability to predict community composition and dynamics under rapidly changing conditions.” Their suggestion that traits can change rapidly (within a growing season) is, however, not supported by some longer term experiments (> 1 yr) into the selective pressures of climate change (Collins and Bell 2004, 2006; Bell and Collins 2008).

The study of functional traits is valuable when addressing fundamental questions of phytoplankton cell size, optimization of nutrient uptake stoichiometry, or comparisons of freshwater and marine systems (Klausmeier et al. 2004). However, there are issues with its more specific application to environmental control of different algal groups across a range of oceanographic provinces. For example, several of the trait types summarized by Litchman and Klausmeier (2008), such as colonial morphology, apply broadly across several of the groups considered in our review (N_2 fixers, *Phaeocystis* spp.), and the drivers of coloniality are poorly understood (Beardall et al. 2008). In contrast, other traits are specific to one of the groups we reviewed (such as calcification or N_2 fixation). Hence, the relationship between trait types and phytoplankton groups is complex. Also, as previously mentioned, the paucity of data on species composition and the inter-specific and even inter-strain differences in physiology evident within an algal group (Fig. 5) are problematic for this approach; Litchman and Klausmeier (2008) have advocated the

grouping of species into functional groups that are defined by trait types.

It is not clear how comparable trait-based functional groups would be to other ways of clustering phytoplankton groups, such as taxonomic groupings (this review) or biogeochemical roles (Hood et al. 2006). Indeed, Litchman and Klausmeier (2008) present a succinct summary of the issues surrounding a comparison of traits with environmental conditions. Moreover, given the complex interactive effects (synergisms and antagonisms) between climate-change–influenced environmental factors and phytoplankton groups (Figs. 1, 3, 5), it is uncertain whether traits can be used to predict changes in phytoplankton community structure due to climate change.

Environmental control of phytoplankton in the future

Synthesizing projected changes from models, experiments, and observations—All published modeling experiments using COAMs (Sarmiento et al. 1998; Matear and Hirst 1999) broadly agree that climate change will increase stratification, shoal the surface mixed layer, and warm the upper ocean. There will also be an increase in CO_2 concentrations and, hence, ocean acidification (Caldeira and Wickett 2003). These changes in upper-ocean properties are predicted to manifest themselves in different ways in the low- and high-latitude oceans (Doney 2006): for example, increased stratification and shoaling of the mixed layer may alleviate seasonal light limitation of phytoplankton at high latitudes but accentuate nutrient limitation at low latitudes. On this basis, some modeling studies (Bopp et al. 2001; Behrenfeld et al. 2006) predict that climate change may increase net primary production at high latitudes but decrease it in low-latitude waters.

Such predictions must, however, be placed in the context of major uncertainties over the influence of other future environmental changes on oceanic primary producers. For instance, both the sign and the magnitude of changes in Fe supply are uncertain and may be influenced by many complex factors, including altered dust supplies from climate-driven precipitation changes and/or from shifting patterns of human land use (Tegen and Fung 1995; Mahowald et al. 2005). Similarly, no modeling study has yet attempted to incorporate the effects of anthropogenic CO_2 enrichment on global N_2 fixation, although experimental results (Hutchins et al. 2009) have indicated that new N inputs by *Trichodesmium* and *Crocospheera* could increase by as much as one third to one half by the year 2100. Fewer model studies have probed how climate change will alter floristics, but there are indications of changes in the extent of biomes, such as a greater latitudinal range for N_2 fixers in COAM simulations (Boyd and Doney 2002).

As is evident from our review of present-day knowledge, there are major gaps for each phytoplankton group that require further study in order to ascertain the individual and interactive effects of these environmental factors. These uncertainties are especially large for N_2 fixers and coccolithophores. Although we cannot yet definitively rank the importance of various environmental controls on these two algal groups in the present-day ocean (Table 1), it is

Table 2. Examples of clusters of environmental properties that influence phytoplankton processes and how they are altered concurrently by seasonal, interannual, or decadal climate change. The arrows denote departures from ambient or winter conditions for (a) the winter to summer progression of the algal growth season; (b) an event driven by climate variability due to the la Niña condition in the Equatorial Pacific, when upwelling of colder iron-, nutrient-, and CO₂-rich waters from the Cromwell Undercurrent intensifies (Chavez et al. 1999); (c) altered oceanic conditions resulting from climate variability during a positive Southern Annular Mode (SAM), when higher wind speeds result in deeper surface mixed layers in Southern Ocean waters (Le Quéré et al. 2007); and (d) projected changes due to future climate change (from COAM simulations; Sarmiento et al. 2004; Boyd et al. 2008). For mixed layer depth, ↓ denotes shoaling, NC denotes no change, and ? denotes uncertainty over the sign of the change.

Property	(a) Seasonal	(b) la Niña climate variability	(c) SAM climate variability	(d) Future climate change
Temperature	↑	↓	↓	↑
Iron	↓	↑	↑?	?
Nutrients	↓	↑	↑	↓
Mixed layer depth	↓	↑	↑	↓
CO ₂	↓	↑	↑	↑
Incident irradiance	↑	NC	NC	?

clear from perturbation experiments (Figs. 1, 3) that their growth rates and physiologies will probably be among those most affected by future climate change.

For instance, coccolithophores are apparently extending both latitudinal limits of their biome, with novel blooms reported in the Bering Sea in the 1990s (Merico et al. 2004) and higher abundances found in the high-latitude Southern Ocean over the last decade (Cubillos et al. 2007). These two studies have attributed these latitudinal extensions to increased warming and stratification, while Merico et al. (2006) have pointed out that the unprecedented Bering Sea blooms also correlate reasonably well with higher seawater CO₃²⁻ ion concentrations. However, the ongoing invasion of the surface ocean by anthropogenic CO₂ will force the seawater carbonate system in the opposite direction in the future, with higher pCO₂ and lower CO₃²⁻. Future summertime blooms will therefore be growing at pCO₂ levels that are similar to today's wintertime concentrations (Boyd et al. 2008). Leaving aside the controversy over whether the effects of pCO₂ on coccolithophore calcification are positive or negative, it seems clear that in either case these calcifiers will need to adjust to a complex changing matrix of environmental controls in the future ocean. Hence, present-day models are inadequate to predict how concurrent changes in temperature, nutrient and trace metal supply, light climate, and carbonate chemistry will alter the biogeography and dominance of phytoplankton groups, particularly those for which present-day controls are still enigmatic.

It is also evident from our appraisal of existing conceptual frameworks, designed to reconcile patterns in environmental control and phytoplankton distribution, that most cannot accommodate the large degree of predicted future environmental change. Moreover, no experiments have so far attempted to test the effects of concurrent alteration of this large suite of ocean properties, with perturbation experiments only able to address at most a matrix of three properties (e.g., Fe, light, and silicate, Hoffmann et al. 2008; CO₂, light, and temperature, Feng et al. 2008; CO₂, light, and Fe, Feng et al. 2010). Hence, to make progress we require improved conceptual frameworks

that holistically address this issue of concurrent changes in many environmental conditions. These new approaches must also be sufficiently reductionist (i.e., which of these changes matters most, to which phytoplankton group) to provide realistic guidance to design useful experiments that lie within the bounds of what is logistically feasible and to provide results that can be clearly interpreted.

Approaches to represent future shifts in modes of environmental control—Three interlinked approaches are presented that provide holism at the conceptual level while accommodating needed reductionism at the experimental and observational level (note that these approaches must also take into account the transition from present-day environmental controls to those in the future): (1) physiological ranking of environmental controls from ultimate to proximate for each phytoplankton group (Table 1); (2) the incorporation of both seasonality and regional trends in the factors controlling phytoplankton groups (for example, Fig. 2); and (3) the need in the future to consider concurrent changes in all environmental properties due to climate change that are relevant to floristics as being linked using clusters (Table 2).

The aim of the first approach is to facilitate the design of experiments to improve our understanding of environmental control by providing a reductionist approach within a holistic framework. For the second approach, the goal is to overlay a range of different scenarios (in time and space) onto the first approach. The third approach feeds back into the first one by defining the set of concurrent trends in environmental conditions that phytoplankton in different regions will encounter in the future as a result of climate change. These multivariate clusters can then be cautiously pared down to design experiments that target the most important individual controls in a manner that is logistically feasible, but that still includes the context of the other linked environmental changes.

Physiological ranking of environmental factors from ultimate to proximate—We advocate using a ranking

scheme to identify the relative effects of each mode of environmental control (from ultimate to proximate; Cullen 1991) for each phytoplankton group, as we have done throughout the individual phytoplankton group sections for the present day using Table 1. Such an approach requires detailed knowledge about which factors control different algal groups and about how such environmental controls will be altered by climate change. The ranking schemes we have chosen in Table 1 reflect the degree of our current understanding for each algal group. It is evident from the results presented in Table 1 that this approach is necessary to prioritize which factors to include in the design of a factorial matrix perturbation experiment for a specific region or algal group.

Incorporating seasonality in the factors controlling algal function groups—This approach extends that of the physiological ranking scheme by taking into account how such modes of the underlying control of algal distributions vary over the annual cycle in the present day (Figs. 2, 7). This will provide a platform to examine how climate change effects will be superimposed on the current annual cycle of phytoplankton growth and phenology (Edwards and Richardson 2004). This is a prerequisite to designing more realistic perturbation experiments to evaluate the effect of these altered seasonal changes, in particular the effects of co-limitation. In the example used in Fig. 7, this would involve Fe and light; silicate and light and Fe; silicate; and light co-limitation for HNLSiLC regions such as the subantarctic Southern Ocean. The two examples in Fig. 7 show the different seasonal patterns in terms of co-limitation based either on the conventional notion of an antagonistic relationship between Fe and light supply (Sunda and Huntsman 1998; Maldonado et al. 1999) or on the recently emerging view of a synergistic effect between Fe and light supply (R. F. Strzepek unpubl.).

Treating environmental properties as clusters—The third approach is based on the realization that climate change will simultaneously alter many oceanic properties, each of which will exert some degree of environmental control on different phytoplankton groups. Many of these factors will co-vary in more or less predictable directions (e.g., temperature and CO₂ will both increase together, stratification and mixed layer depth shoaling will increase under-water irradiance while decreasing nutrient availability), even if the absolute magnitude of each individual change is not yet known in every case. Although it is not logistically feasible to manipulate all of these factors individually and in all possible permutations during experimental studies, a more tractable approach is possible by recognizing that phytoplankton will be subjected to all of these changes concurrently.

In Table 2 we present four different clusters of such trends in environmental properties. The first of these summarizes seasonal trends in each environmental factor over the algal growth season; the second and third are clusters associated with specific climate variability events for two different regions—the la Niña-induced upwelling from the Cromwell Undercurrent in the Equatorial Pacific

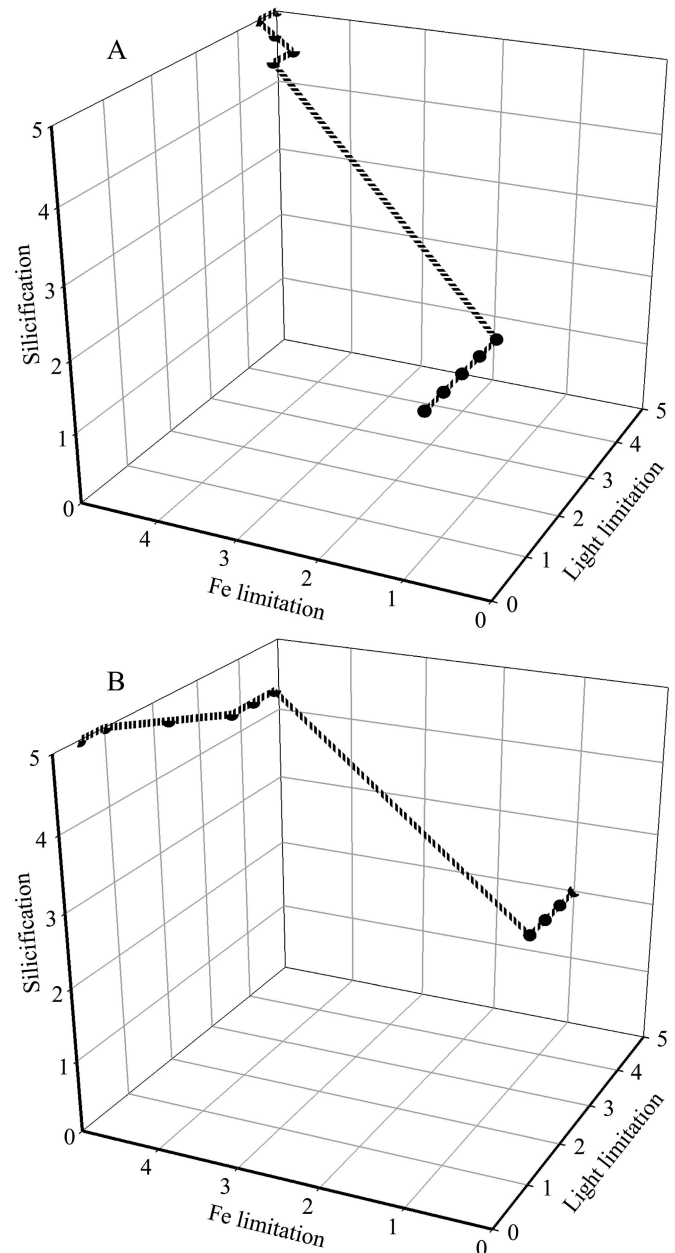


Fig. 7. A three-dimensional representation of the interplay between the degree of light limitation, Fe limitation, and cell silicification of diatoms in HNLSiLC waters. Seasonal changes in light climate, Fe supply, and silicate supply over the annual cycle and their co-limiting effects on diatoms will be captured by this scheme. (A) Depicts the antagonistic relationship between Fe limitation (1 is low, 5 is high) and light limitation (1 is low, 5 is high; Sunda and Huntsman 1997; Maldonado et al. 1999). In turn, increasing Fe limitation increases cell silicification (1 is low, 5 is high; Hutchins and Bruland 1998). (B) Depicts an alternative view of the Fe–light relationship, with Fe limitation increasing with decreasing light limitation (Raven 1990; R. F. Strzepek unpubl.). In both (A, B) we have assumed that physiological thresholds play a role in the non-linear relationships between these environmental controls. Such a scheme can readily be animated to describe the changing interplay of these controlling factors, and it can also be applied to other co-limitation scenarios (Saito et al. 2008).

(Chavez et al. 1999) and increased wind-mixing in the polar Southern Ocean due to a positive Southern Annular Mode (Le Quéré et al. 2007). The fourth cluster is one that broadly summarizes how the upper ocean will be altered as a result of climate change (Doney 2006).

It is evident that when viewed as clusters of environmental variables there are different permutations of control. The seasonal progression cluster is broadly similar to the climate-change signature, with a general trend toward summer conditions (warming, shoaling, higher irradiance, and reduced nutrient supply). This trend is, however, reversed for CO₂, which is projected to increase with climate change toward concentrations that are now more typical of the winter season (Sarmiento et al. 1998). This climate change cluster will thus not have been encountered by present-day phytoplankton, and so the prediction of the outcome of this cumulative change is difficult (Boyd et al. 2008).

In the case of the climate variability clusters there are several significant departures from those in the other clusters in Table 2. Differences in the signs of the controls within this cluster due to the upwelling of colder, nutrient-rich waters include decreased temperature and increased Fe (though uncertainties remain for the Southern Ocean, with mismatches between the depths of the ferricline and nutricline; Ellwood et al. 2008), nutrients, and CO₂. In addition to the sign of the environmental controls in the clusters, the magnitude of the changes is also important, as are the specific responses and environmental controls operating on the resident phytoplankton groups. For example, in the HNLC Equatorial Pacific waters, diatoms bloom during the la Niña condition as Fe supply is increased by sixfold over ambient conditions (Chavez et al. 1999). Fe becomes the ultimate control during this upwelling event in these warm tropical waters, since temperature is not limiting growth rates and because this regime is characterized by high-nutrient concentrations and no phytoplankton community CO₂ limitation (Tortell et al. 2002). Viewing such examples of alteration of multiple environmental controls as holistic clusters can offer insights into the nature of the main controlling factors during such climate variability events. In the case of predicting the effects of climate change, using clusters decreases our ability to evaluate the individual importance of single factors. However, this loss is greatly outweighed by our ability to make more realistic experiments logistically tractable, offering much better predictions by implicitly including all synergisms and antagonisms.

By taking both the first and third approaches, it may be possible to not only consider the effect of climate change on floristics holistically but also to identify the factors that are most likely to alter the role of (for example) diatoms for a specific region and season. Hence, in the case of the HNLC Southern Ocean, factors that may be more influential than increasing CO₂ (all polar diatoms investigated so far have CCMs; Tortell et al. 2008a) or nutrients (these HNLC waters have excess nutrients) probably include warming and stratification (Moline et al. 2004; Montes-Hugo et al. 2009), decreased Fe supply, and increased mean irradiances (Doney 2006; R. F. Strzepek unpubl.). The cluster approach is flexible enough to

design experiments in which multiple treatments of variables with relatively high uncertainty (such as Fe) can be embedded in a cluster matrix of better understood variables, such as temperature and CO₂. A recent Ross Sea study by Feng et al. (2010) using an Fe, light, and CO₂ matrix supports this viewpoint. Hence, we have taken all of the properties within a cluster into consideration and have taken a subset of the most influential factors that is small enough to be considered within a factorial matrix, such as those run by Hoffmann et al. (2008) and Feng et al. (2008, 2010).

Confounding issues on future alteration of modes of environmental control

The set of three interlinked approaches we advocate to represent future shifts in modes of environmental control provides a pragmatic way forward for both designing perturbation experiments and improving model parameterizations and design. Such pragmatism is required to make further progress on this subject in the face of the many complex ramifications of climate change with regard to the ocean. However, we acknowledge that there are other climate-change-mediated issues that cannot presently be accommodated within our set of approaches.

One pressing issue is the likelihood of acclimation and subsequent adaptation to an altered ocean in the future by all phytoplankton groups (Boyd et al. 2008), species, or strains (Langer et al. 2006, 2009). It is likely that different groups, species, or strains will have a differential susceptibility to altered climatic conditions (Boyd et al. 2008), and a range of susceptibilities for planktonic communities have previously been reported as a result of increased ultraviolet radiation exposure attributable to ozone depletion (Boyd and Doney 2003). Thus, major uncertainties exist as to which phytoplankton will either benefit or lose out from climate change, and the phenotypic plasticity and genetic diversity of algal populations may become important factors to consider. Other important issues to consider are how such differential susceptibility will affect planktonic food web trophic interactions (i.e., top-down control on phytoplankton), the qualifications inherent in extrapolating lab culture and shipboard experiments to the open ocean, and the variable degree of uncertainty in current model projections of how climate change will alter the properties of the upper ocean (i.e., from almost certain effect for warming and elevated CO₂ to relatively uncertain effect for changes in Fe supply). Nevertheless, the three approaches we propose may represent a valuable stepping stone in increasing our understanding of how physiological rates, floristics, biomes, and biogeochemical cycles will be altered in the future changing ocean.

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