





Marine phytoplankton resilience may moderate oligotrophic ecosystem responses and biogeochemical feedbacks to climate change

Adam C. Martiny ^{1,2*} George I. Hagstrom,³ Tim DeVries,⁴ Robert T. Letscher ⁵ Gregory L. Britten,⁶ Catherine A. Garcia,^{1,7} Eric Galbraith,⁸ David Karl,⁷ Simon A. Levin,³ Michael W. Lomas,⁹ Allison R. Moreno,² David Talmy,¹⁰ Weilei Wang ¹ Katsumi Matsumoto ¹¹

¹Department of Earth System Science, University of California, Irvine, California

²Department of Ecology and Evolutionary Biology, University of California, Irvine, California

³Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey

⁴Department of Geography and Earth System Institute, University of California, Santa Barbara, California

⁵Earth Sciences and Ocean Process Analysis Laboratory, University of New Hampshire, Durham, New Hampshire

⁶Department of Earth, Atmospheric, and Planetary Sciences, MIT, Cambridge, Massachusetts

⁷Daniel K. Inouye Center for Microbial Oceanography: Research and Education, University of Hawaii at Manoa, Honolulu, Hawaii

⁸McGill University, Montreal, Quebec, Canada

⁹Bigelow Laboratory for Ocean Sciences, East Boothbay, Maine

¹⁰Department of Microbiology, University of Tennessee, Knoxville, Tennessee

¹¹Department of Earth and Environmental Sciences, University of Minnesota, Minneapolis, Minnesota

Abstract

Are the oceans turning into deserts? Rising temperature, increasing surface stratification, and decreasing vertical inputs of nutrients are expected to cause an expansion of warm, nutrient depleted ecosystems. Such an expansion is predicted to negatively affect a trio of key ocean biogeochemical features: phytoplankton biomass, primary productivity, and carbon export. However, phytoplankton communities are complex adaptive systems with immense diversity that could render them at least partially resilient to global changes. This can be illustrated by the biology of the *Prochlorococcus* “collective.” Adaptations to counter stress, use of alternative nutrient sources, and frugal resource allocation can allow *Prochlorococcus* to buffer climate-driven changes in nutrient availability. In contrast, cell physiology is more sensitive to temperature changes. Here, we argue that biogeochemical models need to consider the adaptive potential of diverse phytoplankton communities. However, a full understanding of phytoplankton resilience to future ocean changes is hampered by a lack of global biogeographic observations to test theories. We propose that the resilience may in fact be greater in oligotrophic waters than currently considered with implications for future predictions of phytoplankton biomass, primary productivity, and carbon export.

The biogeochemical ocean modules in Earth System Models have traditionally been designed with the intent of predicting the carbon export flux to depth and the associated ocean capacity for carbon storage. However, Earth System Models are increasingly being tasked with simulating a broad palette of marine ecosystem responses (Lotze et al. 2019). Reduced mixing of the water column, the most widely expected physical consequence of ocean warming, is predicted to limit

nutrient supply to the surface. In turn, this stratification effect is expected to trigger a trio of negative ecosystem outcomes, namely, global declines in phytoplankton stock, primary productivity, and carbon export (Bopp et al. 2013). These ecosystem declines are expected to have widespread effects on marine life, as they imply lower food stocks and flux to higher trophic levels (Hoegh-Guldberg and Bruno 2010; Moore et al. 2018), while diminished carbon export could weaken the oceanic uptake of atmospheric CO₂ (Bopp et al. 2001). All Earth System Models from the Coupled Model Intercomparison Project Phase 5 agree on these predictions and suggest that there will be a 2–16% decline in NPP and a 7–18% decline in carbon export by 2100 (Bopp et al. 2013; Fu et al. 2016). However, many field observations suggest that the adaptive capacity and resiliency

*Correspondence: amartiny@uci.edu

Author Contribution Statement: A.C.M. designed the study. A.C.M., G.I.H., D.K., S.A.L., and K.M. wrote the manuscript. G.I.H., T.D., and R.T.L. did model analyses. C.A.G., E.G., M.W.L., A.R.M., D.T., and W.W. contributed ideas and edited the manuscript. A.C.M. approved the final submitted manuscript.

of marine communities can moderate the negative impacts of stratification and nutrient stress. Below, we will expand on these lines of evidence and propose that oligotrophic marine ecosystems may be more resilient to future environmental changes than currently assumed.

Phytoplankton resilience

Resilience to environmental changes can be expressed at multiple levels of biological organization. Physiologically, a microorganism will adjust growth to specific temperatures. At the same time, communities consisting of organisms with unique temperature optima assemble differently along a temperature gradient. The integration of physiological and biodiversity changes controls the impact of environmental changes in temperature, nutrient availability, and the like on an ecosystem function (Allison and Martiny 2008). Hence, the impact of an environmental change is likely to be stronger on organisms in isolation, as often observed in controlled settings, than in a diverse community, which is more challenging to measure.

The physiology of diverse genotypes within *Prochlorococcus*—the most abundant phytoplankton in the ocean—provides detailed empirical data for how biodiversity can contribute to resilience to future ocean changes. This can be illustrated by two different transects in the North Pacific and North Atlantic Oceans (Kent et al. 2019). In a cruise from Hawaii to the equator, there is little change in cell abundance (Fig. 1A). The surface temperature is nearly constant, but there is a sharp gradient in phosphate (and nitrate) (Fig. 1C). The gradient in macronutrient availability leads to a shift in *Prochlorococcus* ecotype diversity, but the overall abundance of *Prochlorococcus* is unaffected. In an Atlantic Ocean transect, there is a gradual increase in *Prochlorococcus* abundance from 50°N to 32°N (Fig. 1B). This follows an increase in temperature but a decrease in nutrient availability (Fig. 1D). Again, there is also a clear shift between low and high temperature-adapted *Prochlorococcus* ecotypes (Fig. 1B), but the overall abundance follows the temperature but not nutrient gradient. The example shows a much stronger effect of temperature compared to nutrient availability on the abundance of *Prochlorococcus*.

Prochlorococcus biodiversity modulates the impact of environmental changes on growth and facilitates resilience. *Prochlorococcus* can adapt to very low nutrient concentrations via gene gain and losses leading to improved uptake, lower requirements, or the utilization of alternative forms (Martiny et al. 2019b; Ustick et al. 2021). Hence, some populations can acquire P sufficient for a cell division per day or more at concentrations as low as 2 nM phosphate (Fig. 1E). It is rare that phosphate drops below this concentration across the ocean (Martiny et al. 2019a). Cells can also shift to using alternative phosphate sources (Casey et al. 2009). Other populations are well adapted to low nitrogen or iron concentrations (Rusch et al. 2010; Berube et al. 2015). As a result, *Prochlorococcus* genotypes well-adapted to local environments can provide a

buffer against nutrient stress and enabling the collective to maintain biomass or growth.

While *Prochlorococcus* are thus quite capable of adapting to nutrient perturbations, the same does not hold true for temperature perturbations. Global field observations reveal that *Prochlorococcus* abundance is very sensitive to warming (Fig. 1B) (Flombaum et al. 2013). Individual *Prochlorococcus* strains have a unique but narrow temperature range for growth but shifts in biodiversity allow the lineage to proliferate over a wide temperature range (Zinser et al. 2007). However, thermodynamic constraints on protein kinetics appear to exert a strong effect on division rates leading to an overall temperature control of phytoplankton abundance and growth across a broad swath of biodiversity (Eppley 1972). As an example, Ribalet and coworkers quantified *Prochlorococcus* growth rates along an eastern Pacific Ocean transect from cooler, nutrient-rich to very warm, nutrient-poor conditions (Ribalet et al. 2015) (Fig. 1F). Here, *Prochlorococcus* growth rates increased rapidly and were strongly tied to temperature. Thus, *Prochlorococcus* is more resilient to nutrient compared to temperature stress.

The resilience to different environmental changes may—or may not—be mirrored in other organisms and whole communities. In *Synechococcus*, seasonal increases in growth rates were tied to temperature changes with little sensitivity to nutrient concentrations (Hunter-Cevera et al. 2016). There is also substantial variation in the nutrient quotas among eukaryotic phytoplankton (Garcia et al. 2018). The resilience is imprinted on the whole community, whereby total chlorophyll concentrations or net primary production are only suppressed below 15 nM phosphate (Martiny et al. 2019a). We also see signs of whole community resilience to temperature changes, whereby single strains have a higher temperature sensitivity (e.g., parameterized by Q_{10}) than the whole community (Chisholm 1992; Sherman et al. 2016) (Fig. 1F). However, temperature still exerts a strong control with a roughly 50% increase in phytoplankton community growth rate every 10°C (Sherman et al. 2016) (Fig. 1F). Phytoplankton resilience to specific environmental factors varies, but understanding resilience is central for predicting marine ecosystem responses to future warming and stratification.

Resilience of phytoplankton biomass to climate change

One of the main model predictions under global warming is that stratification and nutrient limitation will lead to lower photosynthetic biomass in many regions (Irwin and Oliver 2009; Boyce et al. 2010). However, it is not fully understood what factors or sequence of events control phytoplankton biomass levels in the ocean. Armstrong (1994) uses a simple ecosystem-in-a-box model to illustrate these different views. In perhaps the simplest, bottom-up controlled ecosystem, the vertical nutrient supply can control phytoplankton biomass in

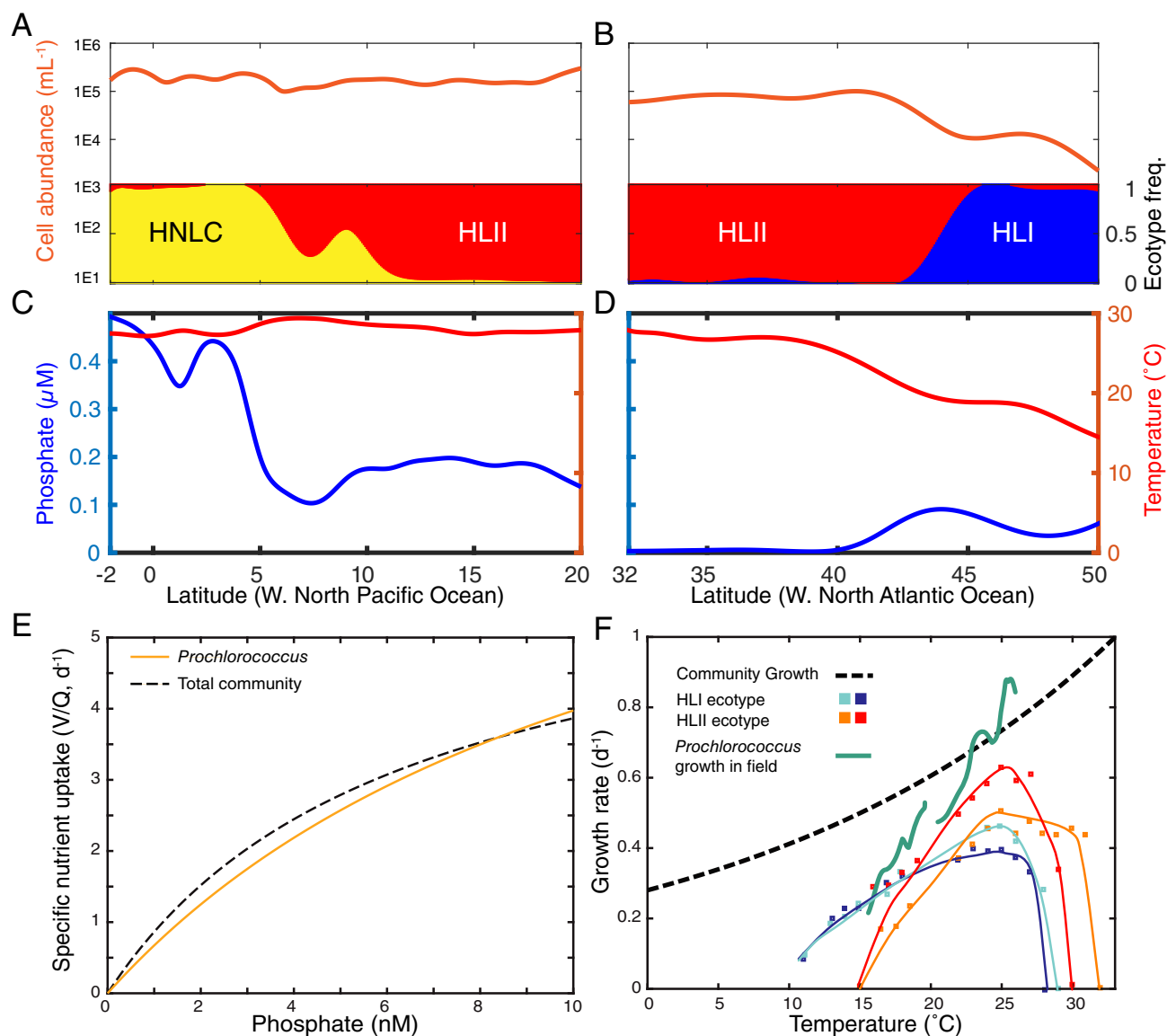
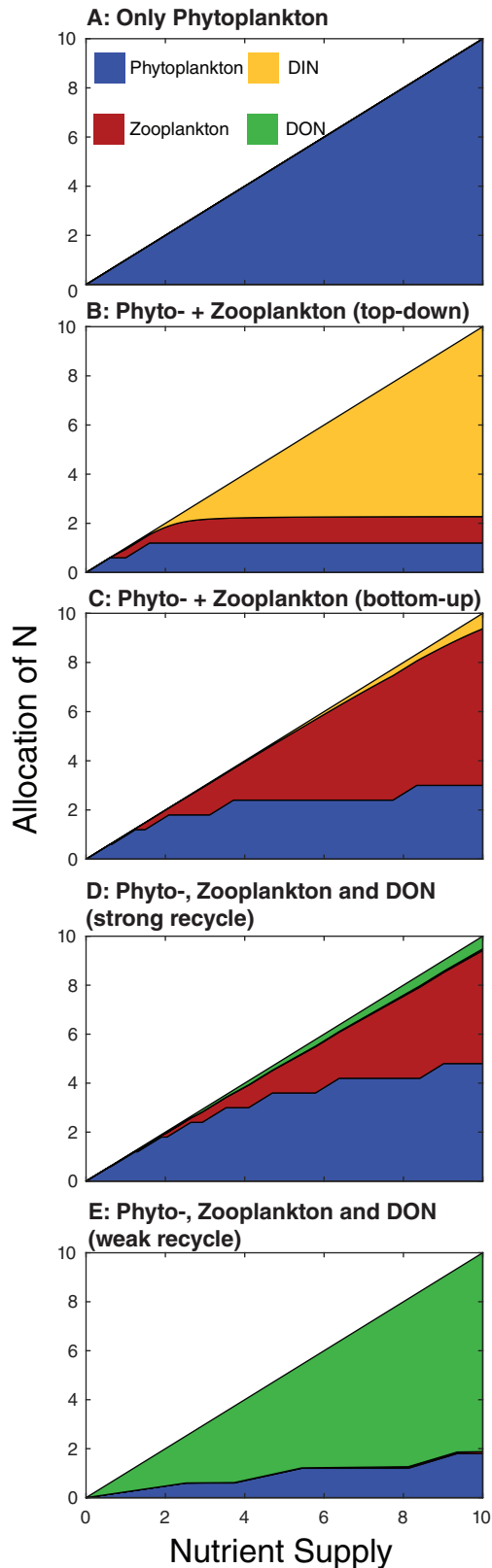


Fig. 1. *Prochlorococcus* “collective” resilience to changes in nutrient concentrations and temperature. The distribution of *Prochlorococcus* cells and ecotypes along transects in the (A) North Pacific Ocean and (B) North Atlantic Ocean. (C) Variation in surface phosphate and temperature at the transect to the North Pacific Ocean and (D) the North Atlantic Ocean (Kent et al. 2019). (E) Population and community specific phosphate uptake (i.e., uptake normalized to cellular phosphate) as a function of phosphate concentrations. These data are from phytoplankton populations or communities growing in the Western North Atlantic Ocean (Lomas et al. 2014). (F) Phytoplankton strain, population, and community growth as a function of temperature. The squares represent the growth of individual *Prochlorococcus* strains at low to intermediate light levels and a nonlinear interpolation (Zinser et al. 2007). The solid line represents in situ growth rates of *Prochlorococcus* populations from a transect between San Diego, California (122°W) and Hawaii (155°W) (Ribalet et al. 2015). The dashed line represents the globally averaged growth of phytoplankton communities along a temperature gradient (Sherman et al. 2016). The presented ecotypes are the high-light adapted 1 (HLI), high-light adapted 2 (HLII), and the high nutrient, low chlorophyll ecotypes (HNLC, also called HLIII and HLIV).

stratified regions leading to a strong relationship between supply and biomass (Fig. 2A). However, there are other, more complex ecosystem designs, especially with the introduction of grazers, where the link between nutrient supply and biomass is less obvious. Depending on the degree of coupling between grazing and phytoplankton growth rate, the outcome can range from a strong (Fig. 2A), to no (Fig. 2B), or to a weak relationship

(Fig. 2C) between nutrient supply and biomass. Finally, some of the supplied nutrients accumulate as dissolved organic nutrients. Dissolved organic matter (DOM) may be quickly recycled, advected out (Fig. 2D), or accumulate (Fig. 2E). Under some scenarios, the nutrient supply plays a strong role in regulating phytoplankton biomass, but there are many cases where biological dynamics weaken or completely ameliorate such a



(Figure legend continues on next page.)

relationship. Thus, one cannot simply assume a theoretic link between nutrient supply and phytoplankton biomass.

The varying complexity of plankton ecosystems, combined with variation in phytoplankton physiological traits, can lead to biomass resilience in the face of warming and stratification. First, phytoplankton may reduce their quota of the limiting nutrient. For example, cells use fewer P-rich ribosomes for growth at higher temperature, substitute P-containing lipids, or reduce N-containing storage molecules (Van Mooy et al. 2009; Toseland et al. 2013; Mouginot et al. 2015). Second, small phytoplankton may stay suspended or be efficiently recycled, and thereby elevate the lifetime of nutrients in the upper ocean (Marsay et al. 2015). Thirdly, the large stock of organically bound nutrients in DOM in oligotrophic waters can support additional biomass if accessible (Fig. 2D vs. 2E—same nutrient supply but very different plankton biomass stocks). The ratio of dissolved organic nitrogen to particulate organic nitrogen is very high in low latitude ecosystems (Fig. 3A). Phytoplankton may conceivably have improved access to DOM nutrient pools at higher temperature (if enzymatic breakdown is thermodynamically or kinetically more favorable) and thus shift the balance between DOM and biomass/particulate organic matter (POM) (Christian and Karl 1995; Gillooly et al. 2001). We currently have a poor empirical understanding of the environmental sensitivity of marine POM or DOM recycling but this process has repeatedly been shown to be temperature dependent in terrestrial ecosystems (Liu et al. 2017). Fourth, the balance between phytoplankton growth and death (via top-down processes) may shift with temperature and thus alter the standing stock of plankton (Fig. 2B). Physiological, adaptive, and ecosystem responses could all result in previously uncharacterized relationships between stratification, temperature, and the biomass of phytoplankton.

A careful biogeographic quantification of phytoplankton biomass would greatly improve our understanding of the current and future environmental regulation of the biomass. Ocean phytoplankton biomass is almost exclusively estimated using chlorophyll as a proxy. Chlorophyll-based estimates are sensitive to phytoplankton chlorophyll : biomass ratios, but there is high variability in this ratio in both laboratory and

(Figure legend continued from previous page.)

Fig. 2. Allocation of N as a function of the supply into different pools depending on the ecosystem dynamics. **(A)** A community with only phytoplankton. **(B)** A community with strong top-down control from zooplankton. **(C)** A community with weak zooplankton control. **(D)** A phyto- and zooplankton community with DOM production but strong recycle rates. **(E)** A phyto- and zooplankton community with DOM production but weak recycle rates. The simulations are from the “Armstrong” ecosystem model (Armstrong 1994). DIN, dissolved inorganic nitrogen; DON, dissolved organic nitrogen.

field studies (Laws and Bannister 1980; Behrenfeld et al. 2015). Thus, the global distribution of carbon-based biomass is quite uncertain. However, improved instrumentation for the high-throughput quantification of plankton biomass is being developed (Lombard et al. 2019). Analytical approaches for measuring phytoplankton biomass include the use of optical scattering of individual cells (Casey et al. 2013; Graff et al. 2015; Freitas et al. 2020), cell-sorting and elemental analysis of chlorophyll containing cells (Graff et al. 2012), imaging (Sosik and Olson 2007), or biovolume conversions (Menden-Deuer and Lessard 2000; McQuatters-Gollop et al. 2011). We need to scale-up such methodologies to the global ocean to improve our understanding and predictive capability of future changes.

Regulation of growth and net primary production

Another prediction is that future lower nutrient availability leads to declining photosynthetic activity as represented by primary productivity. It is important to recognize and separate that productivity is the product of phytoplankton biomass and growth. The limitation of growth is encoded by the nutrient affinity and generally follows a Michaelis–Menten shape with parameters that can be estimated from culture studies (Moore et al. 2004). Phytoplankton growth may show resilience in several ways, including improved uptake at low concentrations, less requirement, or access to alternative nutrient forms. Field data suggest that it is nearly impossible to restrict growth in *Prochlorococcus* by phosphate depletion (Lomas et al. 2014) (Fig. 1E). To our knowledge, no one has yet quantified the picophytoplankton in situ uptake affinity for any nitrogen compounds. However, the half-saturation constant for nitrogen compounds in larger phytoplankton cultures is ~ 20 nM (Caperon and Meyer 1972), so N-stressed

picophytoplankton likely have a lower value. Unfortunately, we have a weak understanding of the actual nutrient distribution in many oligotrophic regions (Martiny et al. 2019a). So the absence of a clear understanding of the uptake kinetics as well as the standing stock of nutrients makes it challenging to identify where and when nutrients limit growth.

Many lineages can supplement inorganic nutrients with alternative forms of broadly defined as dissolved organic nutrients. The ratio of dissolved organic nitrogen to dissolved inorganic nitrogen approaches a thousand in oligotrophic gyres (Fig. 3) (Letscher et al. 2013), and similar high ratios can be observed for dissolved organic phosphorus to dissolved inorganic phosphorus ratios in the P-stressed western North Atlantic Ocean (Lomas et al. 2010). An Earth System Model simulation with and without DOM cycling suggests that the temporal and spatial decoupling between DOM production and consumption can greatly alter spatial patterns of marine productivity, with the recycling of organic nutrients ultimately enhancing global primary production by 10% (Fig. 3C). The utilization was highest in the oligotrophic gyres ($> 150\%$) supporting the notion that lateral DOM transport and its (re)cycling is critical to the functioning of low latitude ecosystem (Letscher et al. 2016). Future warming may increase the bioavailability of dissolved organic nutrients due to thermodynamically and kinetically more favorable conditions for DOM breakdown at warmer temperatures (Lønborg et al. 2018). It is an open question, if a temperature-driven increased recycling rate of DOM can compensate for a possible 10% decline in productivity. In sum, we propose that possible adaptations for increased nutrient uptake, reduced need, or increased recycling all can facilitate resilience against future stratification.

Multiple observations support that phytoplankton growth is resilient to stratification and nutrient stress. First, primary production in the North Pacific Subtropical Gyre is highest during

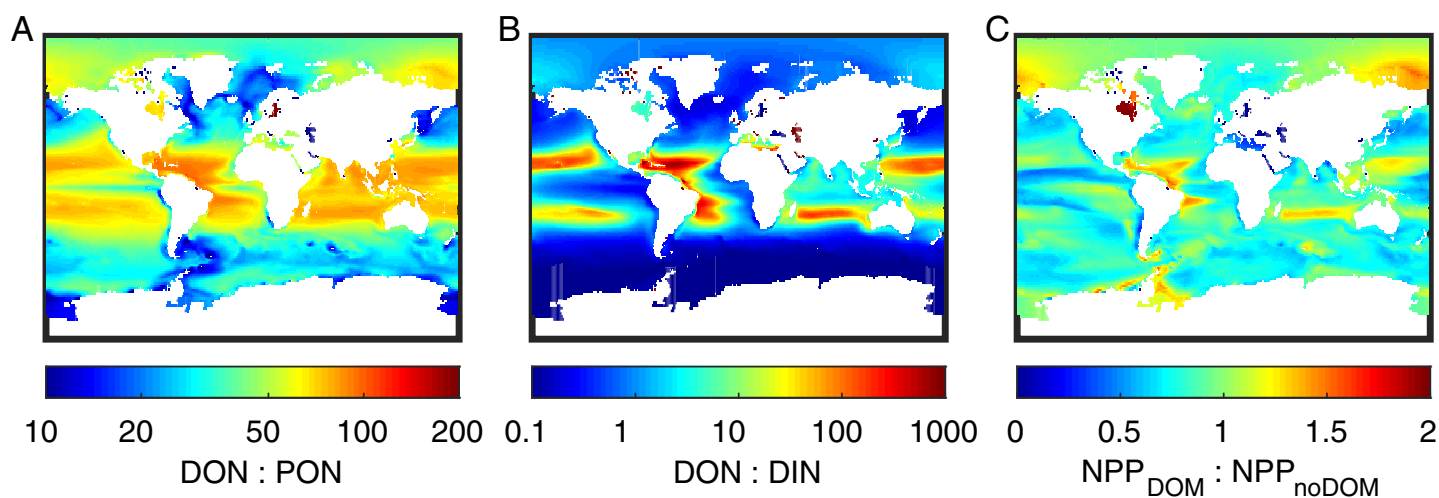


Fig. 3. The distribution and biogeochemical impacts of dissolved organic nutrients. **(A)** The ratio of DON to PON. **(B)** The ratio of DON to DIN. **(C)** The ratio of ocean primary productivity with and without DOM representation (Letscher and Moore 2015).

the most stratified period (Dave and Lozier 2010). Second, in situ measures of primary production show a weak regulation by nutrient concentrations, whereas Earth System Models show a strong regulation (Martiny et al. 2019a). Third, *Prochlorococcus* showed substantially lower growth rates ($\sim 0.3 \text{ d}^{-1}$) in the nutrient rich but cooler California Current waters and progressively higher rates (up to 0.9 d^{-1}) in warmer but oligotrophic water in the North Pacific Subtropical Gyre (Ribalet et al. 2015) (Fig. 1D). Fourth, temperature was the primary control on *Synechococcus* growth rates in coastal waters off Martha's Vineyard (Hunter-Cevera et al. 2016). These results suggest that phytoplankton growth and primary production can be stimulated by higher temperature but resilient to nutrient stress. In support, Taucher and Oschlies (2011) showed that future ocean changes could either lead to depressed or increased NPP depending on the exact (but uncertain) ecosystem description.

A careful biogeographic quantification of phytoplankton productivity would greatly improve our understanding of the current and future regulation of net primary production. Issues that need further clarification include possible losses to heterotrophic processes during the incubation period (Karl et al. 1998) and the release of newly fixed carbon as DOC (Nagata 2008). Measurements performed using oxygen rather than particulate carbon as the metric for primary production find substantially higher primary production rates in oligotrophic regions (Ferrón et al. 2015). Finally, more recent analytical techniques like flow cytometry analysis of picophytoplankton cell cycles can offer alternative estimates of growth and thus help us further understand the environmental regulation of productivity.

Regulation of carbon export

The third prediction we consider is that warming leads to declining carbon export to deeper parts of the ocean. Such a decline in the downward carbon flux has large implications for carbon sequestration as well as energy availability for meso- and bathypelagic communities. If one again considers the surface ocean as a water parcel box and a constant elemental composition (carbon : nitrogen : phosphorus) of particles—*a.k.a.* the Redfield Ratio (Redfield 1958; Dugdale and Goering 1967)—then mass balance dictates that maximum carbon export equals the influx of new nutrients times a carbon-to-nutrient ratio. From this perspective, the nutrient influx sets a hard limit on carbon export and only ecosystems with residual (commonly termed preformed) nutrients can support increasing carbon export (Sarmiento and Toggweiler 1984).

Phytoplankton adaptation offers several pathways that can lead to a more resilient carbon export response to future warming and stratification. Phytoplankton can reduce their cell quota under severe nutrient stress (Moreno and Martiny 2018), use less nutrient-rich enzymes when growing at high temperature (Toseland et al. 2013), or become more carbon rich at high $p\text{CO}_2$ (Fu et al. 2007). Marine phytoplankton biomass C : P and

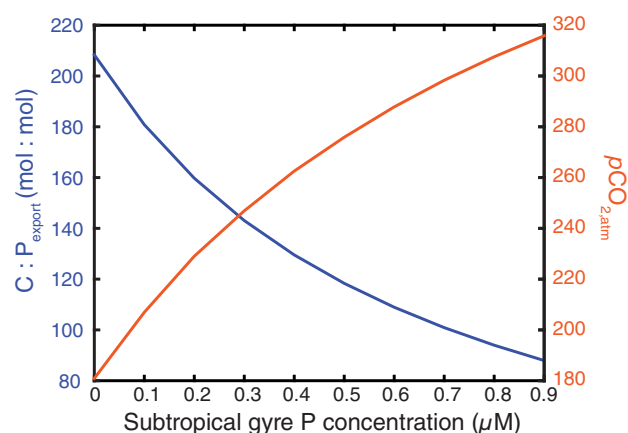


Fig. 4. Regulation of carbon export by the elemental stoichiometry and DOM production. Linking subtropical gyre nutrient availability, the elemental composition of surface particles and export flux, and atmospheric CO_2 . To a first order, the C : P elemental composition of surface ocean particles can be linked to nutrient availability (Martiny et al. 2013a). Based on this relationship, a simplified box-model simulation demonstrates how varying C : P of exported material from low latitude regions can lead to substantial long-term changes in atmospheric CO_2 (Galbraith and Martiny 2015).

C : N vary significantly between ocean regions and are highest in oligotrophic gyres (Weber and Deutsch 2010; Martiny et al. 2013a,b; Teng et al. 2014; Lee et al. 2021). Model simulations support that variable stoichiometry at least partially buffers the impact of lower nutrient supply on carbon export. Thus, a 10% upshift in C : P or C : N can potentially fully compensate for stratification effects on C export (Tanioka and Matsumoto 2017) and have a substantial impact on long-term future changes in atmospheric CO_2 level (Fig. 4) (Galbraith and Martiny 2015). In support, Earth System Models with a temperature and nutrient stress control on plankton elemental stoichiometry have smaller changes in C export than expected assuming constant elemental composition under past (Matsumoto et al. 2020) and future conditions (Bopp et al. 2013; Kwiatkowski et al. 2018; Wang et al. 2019; Matsumoto and Tanioka 2020). These predictions are supported by studies using different metabolite mass balances or inverse models showing little variation in export rates across biomes (Richardson and Jackson 2007; Emerson 2014; Teng et al. 2014). A decoupling between C export and “new” nutrients from depth combined with a slowing overturning circulation could instead increase C sequestration (Kwon et al. 2009). However, such a resilience of C export processes may bring about major changes to the meso-pelagic oxygen levels and denitrification. Thus, resilience for one biogeochemical process may increase the sensitivity of others with yet-to-be explored outcomes.

Modeling resilience using a complex adaptive systems framework

How can we incorporate resilience into predictions of future biogeochemical cycles? Marine ecosystems can be

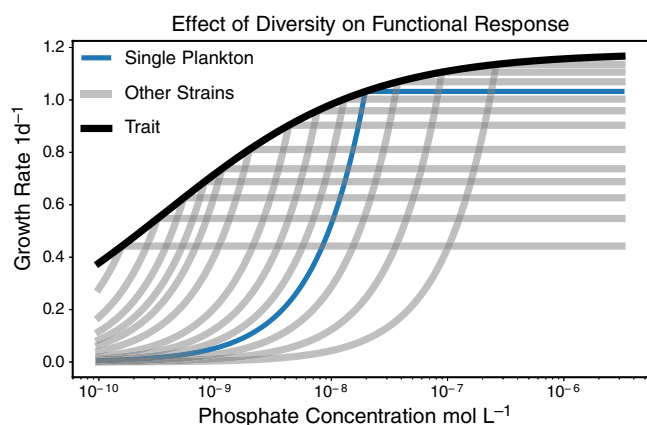


Fig. 5. Diversity and ecosystem function. Growth trait response to phosphate at constant light and temperature of a high-diversity plankton community (black) and for single species (red and blue). A simple model simulation shows how the diverse community contain resilience over a broad range of phosphate concentrations compared to single species.

considered complex adaptive systems (Hagstrom and Levin 2017), which are multi-scale systems in which macroscopic properties emerge from the selection and collective dynamics of a diverse pool of genotypes at smaller scales. Earth System Models typically represent the entire plankton community with one or a handful of functional types derived from laboratory studies of single species. As a result, Earth System Models may represent flexibility insufficiently in the relationships between environmental conditions and measures of ecosystem function. Thus, if phytoplankton diversity and adaptation were represented more holistically, we may well find that the community-level functional responses are more resilient to future environmental conditions such as nutrient limitation. With a complex-adaptive-system framework such as shown in Fig. 5, we can describe how phytoplankton can sustain rapid growth rates over four orders of magnitude of nutrient concentrations.

One approach is to use a trait-based framework capturing the growth and physiological trade-offs of many lineages simultaneously (Litchman and Klausmeier 2008). Trait-based models have been most widely adopted in the study of terrestrial plants, where they have been particularly successful at capturing the functional effect of diversity and the response of ecosystems to climate change (Lavorel and Garnier 2002). In marine ecosystems, trait-based models have provided a mechanistic explanation for the environmental drivers of phytoplankton C : N : P stoichiometry and export production (Toseland et al. 2013; Daines et al. 2014; Moreno et al. 2018). Trait-based approaches can also use trait covariance to reduce the complexity of the model. For example, there is a strong mechanistic link between cell size, many nutrient acquisition traits, and grazing that can be incorporated into an ecosystem model (Edwards et al. 2012; Ward et al. 2012). Trait-based models enable the modeling of diverse ecosystems but are too

complex for global-scale Earth System Models. Fortunately, several computational and theoretical tools allow trait-based models with thousands of types to be reduced to low-dimensional models, while still capturing the high-diversity functional responses of real ecosystems. These techniques range from Monte-Carlo methods (Follows et al. 2007), moment-closure derivations of equations for the mean and variance of the trait distribution (Norberg et al. 2001), adaptive dynamics (Dieckmann 2002), and optimality (Lan Smith and Yamanaka 2007).

The relationship between phosphate concentrations and uptake is an example of the importance of phytoplankton adaptive dynamics for an ecosystem process (Lomas et al. 2014). Phosphate acquisition is normally parameterized with a Michaelis–Menten-style hyperbolic shape seen in laboratory studies. However, a field study across a nutrient gradient and diverse picophytoplankton populations in the North Atlantic Ocean revealed a linear relationship between phosphate concentrations and in situ uptake (Lomas et al. 2014). An adaptive dynamics framework supported how adaptation to local nutrient conditions resulted in dampened uptake response and resilience to nutrient stress (Fig. 5). These observations suggest that alternative parameterizations derived from trait-based models facilitate the integration of complex adaptive systems and resilience into Earth System Models.

We propose a two-pronged approach to quantify the resilience of key ocean biogeochemical processes. First, we need a greatly expanded empirical biogeographic description of phytoplankton carbon biomass, productivity, and export flux. Such data will greatly constrain how core biogeochemical processes are affected by warming and stratification. Many of the observations described here are linked to marine Cyanobacteria that are abundant in low latitude ecosystems. However, we have less information about trait variations among especially picoeukaryotic phytoplankton that constitute an important part of both biomass, growth, and export in many regions (Fawcett et al. 2011; Demory et al. 2018; Flombaum et al. 2020). Second, we need to understand how ecosystem processes vary at extreme nutrient concentrations or temperature and describe such conditions with more specificity than the generic term “oligotrophic conditions.” Here, we propose that our efforts be focused on the uptake affinity, growth, cellular stoichiometry, and cycling of organic forms and done in situ across diverse environments. Substantial variation in these processes can occur during subtle shifts at nanomolar concentrations (Hashihama et al. 2021) emphasizing the need to accurately measure and simulate low nutrient conditions (Martiny et al. 2019a). Similarly, we have a poor understanding of how small changes in temperature affect cellular physiology and ecosystem processes that takes into account the role of adaptation (Schaum et al. 2017; Barton and Yvon-Durocher 2019). Furthermore, we do not know if there are bounds on adaptation to nutrient stress. For example, phytoplankton grow slowly at extreme C : nutrient ratios

(Klausmeier et al. 2004) and a large fraction of DOM-bound nutrients may be inaccessible even at elevated temperature. Despite a weak observed link between phosphate and NPP, there was still a growth depression at very low phosphate concentrations (Martiny et al. 2019a). Thus, a combination of biogeographic surveys, mechanistic studies, and a model structure that allows for adaptation of diverse communities are needed to understand the resilience of phytoplankton, possible limitations to adaptation, and resulting biogeochemical processes.

Outlook

Will climate change lead to ocean desertification? There is great uncertainty in how well our current ocean measurements, concepts, and models can capture resilience in key biological responses and their associated biogeochemical impacts in oligotrophic ecosystems. Phytoplankton can be resilient to changes in nutrient availability leading to a more muted biogeochemical response to climate change than previously thought. Imagine a scenario with rapid birth and death of phytoplankton due to high temperature, very effective recycling of nutrients, high cellular C : nutrient ratio, cellular release of fixed carbon as DOC in the surface ocean, and particulate and dissolved organic material with high carbon-to-nutrient ratios. Such an ecosystem could potentially support large populations of small phytoplankton with very rapid rates of (short-lived) primary production and increased energy transfer to zooplankton and higher trophic levels. The effective stripping and recycling of nutrients would leave highly carbon-enriched residual pools of DOM and POM and at least partially decouple C export from nutrient inputs. The presented ideas are very different from a scenario with strong connections between the upward flux of nutrient and nutrient-stressed biomass, growth, and export productivity. The more recent CMIP6 includes models with some of these adaptive mechanisms for nutrient use. Here, it is much more uncertain if NPP will decline with warming and stratification (Kwiatkowski et al. 2020; Tagliabue et al. 2021), but it is yet unclear if a muted response is linked to the mechanisms we have discussed. At this point, it is impossible to say which of these scenarios are correct. Thus, we suggest a combination of new global measurements and models that allow for adaptive responses are needed to accurately constrain and predict future changes to ocean ecosystems and biogeochemical cycles.

References

- Allison, S. D., and J. B. H. Martiny. 2008. Colloquium paper: Resistance, resilience, and redundancy in microbial communities. *Proc. Natl. Acad. Sci. USA* **105**: 11512–11519. doi:10.1073/pnas.0801925105
- Armstrong, R. A. 1994. Grazing limitation and nutrient limitation in marine ecosystems: Steady state solutions of an ecosystem model with multiple food chains. *Limnol. Oceanogr.* **39**: 597–608. doi:10.4319/lo.1994.39.3.0597
- Barton, S., and G. Yvon-Durocher. 2019. Quantifying the temperature dependence of growth rate in marine phytoplankton within and across species. *Limnol. Oceanogr.* **64**: 2081–2091. doi:10.1002/lno.11170
- Behrenfeld, M. J., and others. 2015. Reevaluating ocean warming impacts on global phytoplankton. *Nat. Clim. Change* **6**: 323–330. doi:10.1038/nclimate2838
- Berube, P. M., and others. 2015. Physiology and evolution of nitrate acquisition in *Prochlorococcus*. *ISME J.* **9**: 1195–1207. doi:10.1038/ismej.2014.211
- Bopp, L., P. Monfray, O. Aumont, J. L. Dufresne, H. Le Treut, G. Madec, L. Terray, and J. C. Orr. 2001. Potential impact of climate change on marine export production. *Global Biogeochem. Cycles* **15**: 81–99. doi:10.1029/1999GB001256
- Bopp, L., and others. 2013. Multiple stressors of ocean ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences* **10**: 6225–6245. doi:10.5194/bg-10-6225-2013
- Boyce, D. G., M. R. Lewis, and B. Worm. 2010. Global phytoplankton decline over the past century. *Nature* **466**: 591–596. doi:10.1038/nature09268
- Caperon, J., and J. Meyer. 1972. Nitrogen-limited growth of marine phytoplankton-II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. *Deep-Sea Res.* **19**: 619–632. doi:10.1016/0011-7471(72)90090-3
- Casey, J. R., J. P. Aucan, S. R. Goldberg, and M. W. Lomas. 2013. Changes in partitioning of carbon amongst photosynthetic pico- and nano-plankton groups in the Sargasso Sea in response to changes in the North Atlantic Oscillation. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **93**: 58–70. doi:10.1016/j.dsr2.2013.02.002
- Casey, J. R., M. W. Lomas, V. K. Michelou, S. T. Dyhrman, E. D. Orchard, J. W. Ammerman, and J. B. Sylvan. 2009. Phytoplankton taxon-specific orthophosphate (Pi) and ATP utilization in the western subtropical North Atlantic. *Aquat. Microb. Ecol.* **58**: 31–44. doi:10.3354/ame01348
- Chisholm, S. W. 1992. Phytoplankton size, p. 213–237. *In* P. G. Falkowski and A. D. Woodhead [eds.], *Primary productivity and biogeochemical cycles in the sea*. Plenum Press.
- Christian, J. R., and D. M. Karl. 1995. Bacterial ectoenzymes in marine waters: Activity ratios and temperature responses in three oceanographic provinces. *Limnol. Oceanogr.* **40**: 1042–1049. doi:10.4319/lo.1995.40.6.1042
- Daines, S. J., J. R. Clark, and T. M. Lenton. 2014. Multiple environmental controls on phytoplankton growth strategies determine adaptive responses of the N : P ratio. *Ecol. Lett.* **17**: 414–425. doi:10.1111/ele.12239
- Dave, A. C., and M. S. Lozier. 2010. Local stratification control of marine productivity in the subtropical North Pacific. *J. Geophys. Res. Oceans* **115**: C12. doi:10.1029/2010JC006507

- Demory, D., and others. 2018. Picoeukaryotes of the *Micromonas* genus: Sentinels of a warming ocean. *ISME J.* **13**: 132–146. doi:[10.1038/s41396-018-0248-0](https://doi.org/10.1038/s41396-018-0248-0)
- Dieckmann, U. 2002. Adaptive dynamics of pathogen-host interactions, p. 39–59. *In* U. Dieckmann, J. Metz, M. Sabelis, and K. Sigmund [eds.], *Adaptive dynamics of pathogen–host interactions*. Cambridge Univ. Press.
- Dugdale, R. C., and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* **12**: 196–206. doi:[10.4319/lo.1967.12.2.0196](https://doi.org/10.4319/lo.1967.12.2.0196)
- Edwards, K., M. Thomas, C. A. Klausmeier, and E. Litchman. 2012. Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. *Limnol. Oceanogr.* **57**: 554–566. doi:[10.4319/lo.2012.57.2.0554](https://doi.org/10.4319/lo.2012.57.2.0554)
- Emerson, S. 2014. Annual net community production and the biological carbon flux in the ocean. *Global Biogeochem. Cycles* **28**: 14–28. doi:[10.1002/2013GB004680](https://doi.org/10.1002/2013GB004680)
- Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* **70**: 1063–1085.
- Fawcett, S. E., M. W. Lomas, J. R. Casey, B. B. Ward, and D. M. Sigman. 2011. Assimilation of upwelled nitrate by small eukaryotes in the Sargasso Sea. *Nat. Geosci.* **4**: 717–722. doi:[10.1038/ngeo1265](https://doi.org/10.1038/ngeo1265)
- Ferrón, S., S. T. Wilson, S. Martínez-García, P. D. Quay, and D. M. Karl. 2015. Metabolic balance in the mixed layer of the oligotrophic North Pacific Ocean from diel changes in O₂/Ar saturation ratios. *Geophys. Res. Lett.* **42**: 3421–3430. doi:[10.1002/2015GL063555](https://doi.org/10.1002/2015GL063555)
- Flombaum, P., W.-L. Wang, F. W. Primeau, and A. C. Martiny. 2020. Global picophytoplankton niche partitioning predicts overall positive response to ocean warming. *Nat. Geosci.* **13**: 116–120. doi:[10.1038/s41561-019-0524-2](https://doi.org/10.1038/s41561-019-0524-2)
- Flombaum, P., and others. 2013. Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*. *Proc. Natl. Acad. Sci. USA* **110**: 9824–9829. doi:[10.1073/pnas.1307701110](https://doi.org/10.1073/pnas.1307701110)
- Follows, M. J., S. Dutkiewicz, S. Grant, and S. W. Chisholm. 2007. Emergent biogeography of microbial communities in a model ocean. *Science* **315**: 1843–1846. doi:[10.1126/science.1138544](https://doi.org/10.1126/science.1138544)
- Freitas, F. H., M. Dugenne, F. Ribalet, A. Hynes, B. Barone, D. M. Karl, and A. E. White. 2020. Diel variability of bulk optical properties associated with the growth and division of small phytoplankton in the North Pacific Subtropical Gyre. *Appl. Optics* **59**: 6702–6716. doi:[10.1364/ao.394123](https://doi.org/10.1364/ao.394123)
- Fu, F. X., M. E. Warner, Y. H. Zhang, Y. Y. Feng, and D. A. Hutchins. 2007. Effects of increased temperature and CO₂ on photosynthesis, growth, and elemental ratios in marine *Synechococcus* and *Prochlorococcus* (Cyanobacteria). *J. Phycol.* **43**: 485–496. doi:[10.1111/j.1529-8817.2007.00355.x](https://doi.org/10.1111/j.1529-8817.2007.00355.x)
- Fu, W., J. T. Randerson, and J. K. Moore. 2016. Climate change impacts on net primary production (NPP) and export production (EP) regulated by increasing stratification and phytoplankton community structure in the CMIP5 models. *Biogeosciences* **13**: 5151–5170. doi:[10.5194/bg-13-5151-2016](https://doi.org/10.5194/bg-13-5151-2016)
- Galbraith, E. D., and A. C. Martiny. 2015. A simple nutrient-dependence mechanism for predicting the stoichiometry of marine ecosystems. *Proc. Natl. Acad. Sci. USA* **112**: 8199–8204. doi:[10.1073/pnas.1423917112](https://doi.org/10.1073/pnas.1423917112)
- Garcia, N. S., J. Sexton, T. Riggins, J. Brown, M. W. Lomas, and A. C. Martiny. 2018. High variability in cellular stoichiometry of carbon, nitrogen, and phosphorus within classes of marine eukaryotic phytoplankton under sufficient nutrient conditions. *Front. Microbiol.* **9**: 543. doi:[10.3389/fmicb.2018.00543](https://doi.org/10.3389/fmicb.2018.00543)
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* **293**: 2248–2251. doi:[10.1126/science.1061967](https://doi.org/10.1126/science.1061967)
- Graff, J. R., A. J. Milligan, and M. J. Behrenfeld. 2012. The measurement of phytoplankton biomass using flow-cytometric sorting and elemental analysis of carbon. *Limnol. Oceanogr.: Methods* **10**: 910–920. doi:[10.4319/lom.2012.10.910](https://doi.org/10.4319/lom.2012.10.910)
- Graff, J. R., T. K. Westberry, A. J. Milligan, M. B. Brown, G. Dall’Omo, V. van Dongen-Vogels, K. M. Reifel, and M. J. Behrenfeld. 2015. Analytical phytoplankton carbon measurements spanning diverse ecosystems. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **102**: 16–25. doi:[10.1016/j.dsr.2015.04.006](https://doi.org/10.1016/j.dsr.2015.04.006)
- Hagstrom, G. I., and S. A. Levin. 2017. Marine ecosystems as complex adaptive systems: Emergent patterns, critical transitions, and public goods. *Ecosystems* **20**: 458–476. doi:[10.1007/s10021-017-0114-3](https://doi.org/10.1007/s10021-017-0114-3)
- Hashihama, F., and others. 2021. Nanomolar phosphate supply and its recycling drive net community production in the subtropical North Pacific. *Nat. Commun.* **12**: 1–8. doi:[10.1038/s41467-021-23837-y](https://doi.org/10.1038/s41467-021-23837-y)
- Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the World’s marine ecosystems. *Science* **328**: 1523–1528. doi:[10.1126/science.1189930](https://doi.org/10.1126/science.1189930)
- Hunter-Cevera, K. R., M. G. Neubert, R. J. Olson, A. R. Solow, A. Shalapyonok, and H. M. Sosik. 2016. Physiological and ecological drivers of early spring blooms of a coastal phytoplankton. *Science* **354**: 326–329. doi:[10.1126/science.aaf8536](https://doi.org/10.1126/science.aaf8536)
- Irwin, A. J., and M. J. Oliver. 2009. Are ocean deserts getting larger? *Geophys. Res. Lett.* **36**: L18609. doi:[10.1029/2009GL039883](https://doi.org/10.1029/2009GL039883)
- Karl, D. M., D. V. Hebel, K. Björkman, and R. M. Letelier. 1998. The role of dissolved organic matter release in the productivity of the oligotrophic North Pacific Ocean. *Limnol. Oceanogr.* **43**: 1270–1286. doi:[10.4319/lo.1998.43.6.1270](https://doi.org/10.4319/lo.1998.43.6.1270)

- Kent, A. G., S. E. Baer, C. Mouginot, J. S. Huang, A. A. Larkin, M. W. Lomas, and A. C. Martiny. 2019. Parallel phylogeography of *Prochlorococcus* and *Synechococcus*. *ISME J.* **13**: 430–441. doi:10.1038/s41396-018-0287-6
- Klausmeier, C. A., E. Litchman, and S. A. Levin. 2004. Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnol. Oceanogr.* **49**: 1463–1470. doi:10.4319/lo.2004.49.4_part_2.1463
- Kwiatkowski, L., O. Aumont, L. Bopp, and P. Ciais. 2018. The impact of variable phytoplankton stoichiometry on projections of primary production, food quality, and carbon uptake in the Global Ocean. *Global Biogeochem. Cycles* **32**: 516–528. doi:10.1002/2017GB005799
- Kwiatkowski, L., and others. 2020. Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. *Biogeosciences* **17**: 3439–3470. doi:10.5194/BG-17-3439-2020
- Kwon, E. Y., F. Primeau, and J. L. Sarmiento. 2009. The impact of remineralization depth on the air-sea carbon balance. *Nat. Geosci.* **2**: 630–635. doi:10.1038/ngeo612
- Lan Smith, S., and Y. Yamanaka. 2007. Optimization-based model of multinutrient uptake kinetics. *Limnol. Oceanogr.* **52**: 1545–1558. doi:10.4319/lo.2007.52.4.1545
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Funct. Ecol.* **16**: 545–556. doi:10.1046/j.1365-2435.2002.00664.x
- Laws, E. A., and T. T. Bannister. 1980. Nutrient- and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. *Limnol. Oceanogr.* **25**: 457–473. doi:10.4319/lo.1980.25.3.0457
- Lee, J. A., C. A. Garcia, A. A. Larkin, B. R. Carter, and A. C. Martiny. 2021. Linking a latitudinal gradient in ocean hydrography and elemental stoichiometry in the eastern Pacific Ocean. *Global Biogeochem. Cycles* **35**: e2020GB006622. doi:10.1029/2020gb006622
- Letscher, R. T., D. A. Hansell, C. A. Carlson, R. Lumpkin, and A. N. Knapp. 2013. Dissolved organic nitrogen in the global surface ocean: Distribution and fate. *Global Biogeochem. Cycles* **27**: 141–153. doi:10.1029/2012gb004449
- Letscher, R. T., and J. K. Moore. 2015. Preferential remineralization of dissolved organic phosphorus and non-Redfield DOM dynamics in the global ocean: Impacts on marine productivity, nitrogen fixation, and carbon export. *Global Biogeochem. Cycles* **29**: 325–340. doi:10.1002/2014GB004904
- Letscher, R. T., F. Primeau, and J. K. Moore. 2016. Nutrient budgets in the subtropical ocean gyres dominated by lateral transport. *Nat. Geosci.* **9**: 815–819. doi:10.1038/ngeo2812
- Litchman, E., and C. A. Klausmeier. 2008. Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Evol. Syst.* **39**: 615–639. doi:10.1146/annurev.ecolsys.39.110707.173549
- Liu, Y., and others. 2017. A global synthesis of the rate and temperature sensitivity of soil nitrogen mineralization: Latitudinal patterns and mechanisms. *Glob. Change Biol.* **23**: 455–464. doi:10.1111/GCB.13372
- Lomas, M. W., J. A. Bonachela, S. A. Levin, and A. C. Martiny. 2014. Impact of ocean phytoplankton diversity on phosphate uptake. *Proc. Natl. Acad. Sci. USA* **111**: 17540–17545. doi:10.1073/pnas.1420760111
- Lomas, M. W., A. L. Burke, D. A. Lomas, D. W. Bell, C. Shen, S. T. Dyhrman, and J. W. Ammerman. 2010. Sargasso Sea phosphorus biogeochemistry: An important role for dissolved organic phosphorus (DOP). *Biogeosciences* **7**: 695–710. doi:10.5194/bg-7-695-2010
- Lombard, F., and others. 2019. Globally consistent quantitative observations of planktonic ecosystems. *Front. Mar. Sci.* **6**: 196. doi:10.3389/fmars.2019.00196
- Lønborg, C., X. A. Álvarez-Salgado, R. T. Letscher, and D. A. Hansell. 2018. Large stimulation of recalcitrant dissolved organic carbon degradation by increasing ocean temperatures. *Front. Mar. Sci.* **4**: 436. doi:10.3389/FMARS.2017.00436/BIBTEX
- Lotze, H. K., and others. 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl. Acad. Sci. USA* **116**: 12907–12912. doi:10.1073/pnas.1900194116
- Marsay, C. M., R. J. Sanders, S. A. Henson, K. Pabortsava, E. P. Achterberg, and R. S. Lampitt. 2015. Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean. *Proc. Natl. Acad. Sci. USA* **112**: 1089–1094. doi:10.1073/pnas.1415311112
- Martiny, A. C., C. T. A. Pham, F. W. Primeau, J. A. Vrugt, J. K. Moore, S. A. Levin, and M. W. Lomas. 2013a. Strong latitudinal patterns in the elemental ratios of marine plankton and organic matter. *Nat. Geosci.* **6**: 279–283. doi:10.1038/ngeo1757
- Martiny, A. C., L. Ustick, C. A. Garcia, and M. W. Lomas. 2019b. Genomic adaptation of marine phytoplankton populations regulates phosphate uptake. *Limnol. Oceanogr.* **65**: S340–S350. doi:10.1002/lno.11252
- Martiny, A. C., J. A. Vrugt, F. W. Primeau, and M. W. Lomas. 2013b. Regional variation in the particulate organic carbon to nitrogen ratio in the surface ocean. *Global Biogeochem. Cycles* **27**: 723–731. doi:10.1002/gbc.20061
- Martiny, A. C., and others. 2019a. Biogeochemical controls of surface ocean phosphate. *Sci. Adv.* **5**: eaax0341. doi:10.1126/sciadv.aax0341
- Matsumoto, K., R. Rickaby, and T. Tanioka. 2020. Carbon export buffering and CO₂ drawdown by flexible phytoplankton C:N:P under glacial conditions. *Paleoceanogr. Paleoclimatol.* **35**: e2019PA003823. doi:10.1029/2019PA003823
- Matsumoto, K., and T. Tanioka. 2020. Shifts in regional production as a driver of future global ocean production stoichiometry. *Environ. Res. Lett.* **15**: 124027. doi:10.1088/1748-9326/abc4b0

- McQuatters-Gollop, A., and others. 2011. Is there a decline in marine phytoplankton? *Nature* **472**: E6–E7. doi:[10.1038/nature09950](https://doi.org/10.1038/nature09950)
- Menden-Deuer, S., and E. J. Lessard. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol. Oceanogr.* **45**: 569–579. doi:[10.4319/lo.2000.45.3.0569](https://doi.org/10.4319/lo.2000.45.3.0569)
- Moore, J. K., S. C. Doney, and K. Lindsay. 2004. Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. *Global Biogeochem. Cycles* **18**: GB4028. doi:[10.1029/2004GB002220](https://doi.org/10.1029/2004GB002220)
- Moore, J. K., and others. 2018. Sustained climate warming drives declining marine biological productivity. *Science* **359**: 1139–1143. doi:[10.1126/science.aao6379](https://doi.org/10.1126/science.aao6379)
- Moreno, A. R., G. I. Hagstrom, F. W. Primeau, S. A. Levin, and A. C. Martiny. 2018. Marine phytoplankton stoichiometry mediates nonlinear interactions between nutrient supply, temperature, and atmospheric CO₂. *Biogeosciences* **15**: 2761–2779. doi:[10.5194/bg-15-2761-2018](https://doi.org/10.5194/bg-15-2761-2018)
- Moreno, A. R., and A. C. Martiny. 2018. Ecological stoichiometry of ocean plankton. *Ann. Rev. Mar. Sci.* **10**: 43–69. doi:[10.1146/annurev-marine-121916-063126](https://doi.org/10.1146/annurev-marine-121916-063126)
- Mouginot, C., A. E. Zimmerman, J. A. Bonachela, H. Fredricks, S. D. Allison, B. A. S. Van Mooy, and A. C. Martiny. 2015. Resource allocation by the marine cyanobacterium *Synechococcus* WH8102 in response to different nutrient supply ratios. *Limnol. Oceanogr.* **60**: 1634–1641. doi:[10.1002/lno.10123](https://doi.org/10.1002/lno.10123)
- Nagata, T. 2008. Organic matter-bacteria interactions in seawater. *Microb. Ecol. Ocean. Second Ed.* **2**: 207–241. doi:[10.1002/9780470281840.ch7](https://doi.org/10.1002/9780470281840.ch7)
- Norberg, J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proc. Natl. Acad. Sci. USA* **98**: 11376–11381. doi:[10.1073/pnas.171315998](https://doi.org/10.1073/pnas.171315998)
- Redfield, A. C. 1958. The biological control of the chemical factors in the environment. *Am. Sci.* **46**: 1–18.
- Ribalet, F., and others. 2015. Light-driven synchrony of *Prochlorococcus* growth and mortality in the subtropical Pacific gyre. *Proc. Natl. Acad. Sci. USA* **112**: 8008–8012. doi:[10.1073/pnas.1424279112](https://doi.org/10.1073/pnas.1424279112)
- Richardson, T. L., and G. A. Jackson. 2007. Small phytoplankton and carbon export from the surface ocean. *Science* **315**: 838–840. doi:[10.1126/science.1133471](https://doi.org/10.1126/science.1133471)
- Rusch, D. B., A. C. Martiny, C. L. Dupont, A. L. Halpern, and J. C. Venter. 2010. Characterization of *Prochlorococcus* clades from iron-depleted oceanic regions. *Proc. Natl. Acad. Sci. USA* **107**: 16184–16189. doi:[10.1073/pnas.1009513107](https://doi.org/10.1073/pnas.1009513107)
- Sarmiento, J. L., and J. R. Toggweiler. 1984. A new model for the role of oceans in determining the atmospheric pCO₂. *Nature* **308**: 621–624. doi:[10.1038/308621a0](https://doi.org/10.1038/308621a0)
- Schaum, C. E., and others. 2017. Adaptation of phytoplankton to a decade of experimental warming linked to increased photosynthesis. *Nat. Ecol. Evol.* **1**: 1–7. doi:[10.1038/s41559-017-0094](https://doi.org/10.1038/s41559-017-0094)
- Sherman, E., J. K. Moore, F. Primeau, and D. Tanouye. 2016. Temperature influence on phytoplankton community growth rates. *Global Biogeochem. Cycles* **30**: 550–559. doi:[10.1002/2015GB005272](https://doi.org/10.1002/2015GB005272)
- Sosik, H. M., and R. J. Olson. 2007. Automated taxonomic classification of phytoplankton sampled with imaging-in-flow cytometry. *Limnol. Oceanogr.: Methods* **5**: 204–216. doi:[10.4319/lom.2007.5.204](https://doi.org/10.4319/lom.2007.5.204)
- Tagliabue, A., L. Kwiatkowski, L. Bopp, M. Butenschön, W. Cheung, M. Lengaigne, and J. Vialard. 2021. Persistent uncertainties in ocean net primary production climate change projections at regional scales raise challenges for assessing impacts on ecosystem services. *Front. Clim.* **3**: 149. doi:[10.3389/fclim.2021.738224](https://doi.org/10.3389/fclim.2021.738224)
- Tanioka, T., and K. Matsumoto. 2017. Buffering of ocean export production by flexible elemental stoichiometry of particulate organic matter. *Global Biogeochem. Cycles* **31**: 1528–1542. doi:[10.1002/2017GB005670](https://doi.org/10.1002/2017GB005670)
- Taucher, J., and A. Oschlies. 2011. Can we predict the direction of marine primary production change under global warming? *Geophys. Res. Lett.* **38**: L02603. doi:[10.1029/2010GL045934](https://doi.org/10.1029/2010GL045934)
- Teng, Y.-C., F. W. Primeau, J. K. Moore, M. W. Lomas, and A. C. Martiny. 2014. Global-scale variations of the ratios of carbon to phosphorus in exported marine organic matter. *Nat. Geosci.* **7**: 895–898. doi:[10.1038/ngeo2303](https://doi.org/10.1038/ngeo2303)
- Toseland, A., and others. 2013. The impact of temperature on marine phytoplankton resource allocation and metabolism. *Nat. Clim. Change* **3**: 979–984. doi:[10.1038/nclimate1989](https://doi.org/10.1038/nclimate1989)
- Ustick, L. J., and others. 2021. Metagenomic analysis reveals global-scale patterns of ocean nutrient limitation. *Science* **372**: 287–291. doi:[10.1126/science.abe6301](https://doi.org/10.1126/science.abe6301)
- Van Mooy, B. A. S., and others. 2009. Phytoplankton in the ocean use non-phosphorus lipids in response to phosphorus scarcity. *Nature* **458**: 69–72. doi:[10.1038/nature07659](https://doi.org/10.1038/nature07659)
- Wang, W.-L., J. K. Moore, A. C. Martiny, and F. W. Primeau. 2019. Convergent estimates of marine nitrogen fixation. *Nature* **566**: 205–211. doi:[10.1038/s41586-019-0911-2](https://doi.org/10.1038/s41586-019-0911-2)
- Ward, B. A., S. Dutkiewicz, O. Jahn, and M. J. Follows. 2012. A size-structured food-web model for the global ocean. *Limnol. Oceanogr.* **57**: 1877–1891. doi:[10.4319/LO.2012.57.6.1877](https://doi.org/10.4319/LO.2012.57.6.1877)
- Weber, T. S., and C. Deutsch. 2010. Ocean nutrient ratios governed by plankton biogeography. *Nature* **467**: 550–554. doi:[10.1038/nature09403](https://doi.org/10.1038/nature09403)
- Zinser, E. R., Z. I. Johnson, A. Coe, E. Karaca, D. Veneziano, and S. W. Chisholm. 2007. Influence of light and temperature on *Prochlorococcus* ecotype distributions in the Atlantic Ocean. *Limnol. Oceanogr.* **52**: 2205–2220.

Acknowledgments

We thank all the scientists we have discussed these issues with over the last decade. We acknowledge the follow funding support for this work US National Science Foundation (OCE-1736891, 1848576, and 1948842 to A.C.M., OCE-1829916 to R.T.L., OCE-1756054 to M.W.L., GRFP to A.R.M., OCE-1827948 to KM), US Dept. of Energy Office of Science (ER65358 and DE-SC0016329 to R.T.L.), Simons Foundation (395890 to G.I.H. and S.A.L., 549931 to G.L.B., 329108 to D.M.K.), and US Dept. of Commerce NOAA (NA18OAR4320123 to G.I.H. and S.A.L.).

Conflict of Interest

None declared.

Submitted 16 February 2021

Revised 22 September 2021

Accepted 07 January 2022

Associate editor: James B. Heffernan