

Microorganisms and ocean global change

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The prokaryotic and eukaryotic microorganisms that drive the pelagic ocean's biogeochemical cycles are currently facing an unprecedented set of comprehensive anthropogenic changes. Nearly every important control on marine microbial physiology is currently in flux, including seawater pH, p_{CO_2} , temperature, redox chemistry, irradiance and nutrient availability. Here, we examine how microorganisms with key roles in the ocean carbon and nitrogen cycles may respond to these changes in the Earth's largest ecosystem. Some functional groups such as nitrogen-fixing cyanobacteria and denitrifiers may be net beneficiaries of these changes, while others such as calcifiers and nitrifiers may be negatively impacted. Other groups, such as heterotrophic bacteria, may be relatively resilient to changing conditions. The challenge for marine microbiologists will be to predict how these divergent future responses of marine microorganisms to complex multiple variable interactions will be expressed through changing biogeography, community structure and adaptive evolution, and ultimately through large-scale alterations of the ocean's carbon and nutrient cycles.

Marine microbial communities possess tremendous functional resilience, forged by their long evolutionary history in a constantly changing ocean environment. Nevertheless, in today's ocean, planktonic microorganisms are faced with a novel combination of challenges. Global-scale 'anthropogenic perturbations' (see Box 1 for full definition of this term and others used in this Review Article) of the Earth's carbon and nutrient cycles are rapidly altering nearly every chemical, physical and biological property that affects the growth of marine microorganisms. Currently, it is uncertain how the microbial networks that are the foundation of the ocean's life support systems will be reshaped by these many simultaneous anthropogenic changes.

The most directly quantifiable ecosystem-level impact from human intervention in the global carbon cycle is ocean acidification (Fig. 1). As much as a third of the carbon dioxide (CO_2) released to the atmosphere by fossil fuel combustion enters the surface ocean¹. There, it upsets the chemical equilibrium of the 'seawater carbonate buffer system', driving down pH. By the end of this century, proton concentrations in the surface ocean will be about double those of the preindustrial ocean, with potentially large implications for marine chemistry and biology².

Human CO_2 emissions also foster a host of emergent consequences that may be equally or more important than those of ocean acidification. The best-known indirect impact is 'greenhouse heating', which will increase the temperature of the sea surface by 1–10 °C over the next 100 years³, depending on location (Fig. 1). In general, the magnitude of this warming trend will be (and indeed already is) greatest at high latitudes including the Arctic and Southern Oceans, but tropical and temperate regions will be affected as well². Warming elevates chemical and biological reaction rates, and excessive levels can result in deleterious biochemical changes such as enzyme denaturation. Physical consequences of warming include reduced gas solubility and higher evaporation rates, as well as climatic changes such as increased precipitation and ice melting³. Every organism has a characteristic optimal thermal range, and temperature is consequently one of the primary determinants of organismal distributions in the ocean⁴.

A less widely recognized secondary impact of high CO_2 is that future warming and freshening (in many regions where ice melting, riverine and precipitation inputs will exceed evaporation) of the

shallow 'surface ocean mixed layer' will exacerbate existing density gradients relative to underlying colder, saltier seawater. This process of intensified 'stratification' will inhibit the vertical transport of critical deep-water nutrient supplies to plankton growing in the surface ocean (Fig. 1). In a related density-driven process, the surface mixed layer will also become shallower throughout large parts of the ocean, trapping microbial communities nearer to the surface where solar radiation is more intense (Fig. 1)³. Finally, the combination of reduced oxygen solubility (in warmer surface waters) and stratification-driven isolation from atmospheric ventilation (in deeper waters) is projected to cause a major loss of oxygen from the future ocean. Worldwide expansion of hypoxic waters will have large ramifications for microbial metabolism and diversity, and so also for the biogeochemistry of key nutrients such as nitrogen⁵ (Fig. 1).

Here, we review our current knowledge about the implications of the inter-related global change processes of acidification, warming, stratification, and deoxygenation for marine microbial biology and ecology. Although global change will ultimately affect all of the ocean's diverse ecosystems, our emphasis here is on the communities of planktonic microorganisms in the near-surface ocean that overwhelmingly support marine food webs and drive major elemental cycles. We take a biogeochemical approach, examining both consensus views and controversies regarding the likely future responses of the key microbial functional groups that control the ocean's carbon and nitrogen cycles. We explore open questions and new research trends, and attempt to offer a glimpse of the changing outlines of microbial biogeochemical cycles in the strange and unfamiliar ocean that will be part of our environmental legacy to future generations.

The marine carbon cycle and ocean global change

The ocean carbon cycle can be considered to begin with the diffusion and mixing of atmospheric CO_2 (μatm) across the sea surface into the immense reservoir of seawater dissolved inorganic carbon⁶. In the process, protons are released, thus driving ocean acidification (Fig. 2a). Photosynthetic microorganisms then fix some of this dissolved inorganic carbon, providing the particulate and dissolved organic carbon that supports most of the marine food web. The fate of most of this organic carbon is to be eventually respired back to CO_2 , largely by bacteria (Fig. 2a). A smaller portion of the

Box 1 | Glossary of terms.

Anthropogenic perturbations. Environmental changes due to human influences, such as ocean warming and acidification as a result of fossil fuel combustion.

Bacterial growth efficiency. The amount of bacterial carbon biomass produced relative to a given amount of organic carbon metabolized, generally expressed as a decimal fraction.

Bacterial photoheterotrophy. A process in which some bacteria can utilize solar energy that is captured by proteorhodopsins or bacteriochlorophylls but cannot fix CO₂, and so also require an exogenous source of organic carbon.

Biological pump. The process whereby CO₂ fixed by phytoplankton photosynthesis in the surface ocean is converted to particulate organic carbon, which then sinks into the underlying water column or sediments, potentially sequestering carbon away from the atmosphere for long periods of time.

Carbonate pump. A process that is analogous to the biological pump, except that it involves sinking of particulate inorganic carbon (calcium carbonate) produced by coccolithophores and other calcifying microorganisms.

Carbon-concentrating mechanism. Various biochemical mechanisms in photoautotrophs that increase the supply of CO₂ to the photosynthetic carbon-fixing enzyme RuBisCo, thus helping to avoid CO₂ limitation of photosynthesis.

Copiotroph. An organism that is specialized for living in nutrient-rich environments.

Ecotype. A distinct subpopulation of a species that is uniquely adapted to a particular environmental niche.

Eutrophication. Over-enrichment of water with nutrients, for instance through fertilizer or sewage runoff into coastal seawater.

Experimental meta-space. The imaginary space occupied by an experimental design, as defined by a three-dimensional plot of the chosen values of the experimental variables.

Greenhouse heating. Warming of the Earth's surface caused by carbon dioxide and other greenhouse gases, such as nitrous

oxide and methane, which allow solar radiation to penetrate the atmosphere but then restrict losses of the resulting radiant heat.

Heterotrophic. A mode of nutrition in which an organism utilizes organic carbon as a carbon source.

Nitrogen isotopic disequilibrium. Deviation from the expected natural abundance ratio of the stable isotopes of nitrogen (¹⁴N and ¹⁵N), for instance due to preferential uptake of the lighter ¹⁴N isotope during many biological reactions.

Oligotroph. An organism that is specialized for living in nutrient-poor environments.

Oxygen minimum zone. Several large areas of the ocean, including the eastern tropical Pacific and the Arabian Sea, where subsurface waters are depleted of oxygen due to elevated bacterial respiration of sinking organic carbon originating from very high primary productivity in overlying surface waters.

Photoautotroph. An organism that uses solar energy to reduce carbon dioxide to organic carbon as a sole carbon source.

Protistan mixotrophy. An ecologically important process whereby many marine planktonic protists or algae can use organic carbon obtained through phagotrophy or osmotrophy, and also carry out oxygenic photosynthesis using chlorophyll.

Sigma factor. Multigenic transcriptional initiators that selectively control the specificity of RNA polymerase binding to promoter regions in the bacterial genome.

Stratification. Density-driven structuring of a water column in which lighter, warmer and/or less saline water overlies denser, colder and/or more saline water, thereby forming a physical barrier to mixing of the two water masses.

Surface ocean mixed layer. The upper layer of the ocean that is thoroughly mixed by the wind, and distinctly demarcated from underlying water layers by stratification.

Seawater carbonate buffer system. The dissolved inorganic carbon buffer system of the ocean that controls the pH of seawater, consisting of bicarbonate ions, carbonate ions and carbon dioxide.

particulate organic carbon produced sinks, and is thereby transferred by the 'biological pump' from surface waters into deeper waters or marine sediments, sequestering it away from the atmosphere for several thousand years or longer⁶. An alternate fate for surface ocean dissolved inorganic carbon is to enter the 'carbonate pump', as biomineralizing microorganisms such as coccolithophores use it to build their calcium carbonate shells. The stoichiometry of this process converts 1 mol of HCO₃⁻ to CO₂ for every mol converted into calcium carbonate, and thus biocalcification acts a source of CO₂ and consequent acidification. These dense CaCO₃ shells sink relatively rapidly, and the carbon they contain either dissolves to contribute to the vast deep-water inorganic carbon reservoir, or is stored in geological formations (Fig. 2a). Next, we will examine the current state of the marine global change microbiology field relative to three of the key processes in the ocean carbon cycle: microbial photosynthesis, calcification, and bacterial respiration (Fig. 2a).

Photosynthetic carbon fixation. Based on physiological first principles, phytoplankton photosynthesis might be expected to respond positively to higher seawater CO₂ concentrations. Currently, most marine 'photoautotrophs' must obtain scarce CO₂ using energetically expensive 'carbon-concentrating mechanisms'. This requirement should be partially relieved by increased rates of energetically less costly diffusive CO₂ uptake in a CO₂-enriched future ocean⁷. In practice however, phytoplankton responses to enhanced CO₂ availability are often hard to predict, ranging from positive to neutral or even negative. Changing CO₂ sometimes has only minor effects

on diatom communities⁸, especially relative to other drivers such as temperature⁹. Phytoplankton from environments with large seasonal CO₂ variations, such as Antarctic coastal waters, are generally well adapted to such fluctuations, and so may be relatively insensitive to carbonate chemistry changes¹⁰.

The influence of CO₂ on marine microbial communities often depends on interactions with temperature, nutrients and biology. For instance, a positive influence of high CO₂ on phytoplankton biomass in a Baltic Sea acidification experiment was neutralized by increased zooplankton grazing when warming was added to the elevated CO₂ treatment¹¹. Negative effects of acidification on growth rates of the Arctic diatom *Fragilariopsis cylindrus* (20–37% inhibition) were balanced out by roughly equivalent growth stimulation under rising temperatures¹². High CO₂ (1000 µatm) stimulates carbon fixation in cultures of the temperate marine diatoms *Thalassiosira weissflogii* and *Dactyliosolen fragilissimus* by 8% and 39%, respectively. However, these two species responded in opposite ways to a temperature increase from 15 °C to 20 °C, as the magnitude of this thermal shift exceeded the optimum growth temperature of *D. fragilissimus*, but not *T. weissflogii*¹³. Two studies have reported inhibition of nitrate uptake but not carbon fixation under high CO₂ in the diatom *Thalassiosira pseudonana*, resulting in elevated cellular C:N ratios, but the mechanisms underlying this response are not known^{14,15}. In general, it is often difficult to distinguish the direct influence of elevated CO₂ on algal carbon acquisition physiology from indirect effects of increased proton concentrations on cellular biochemistry. In practice, most phytoplankton acidification studies

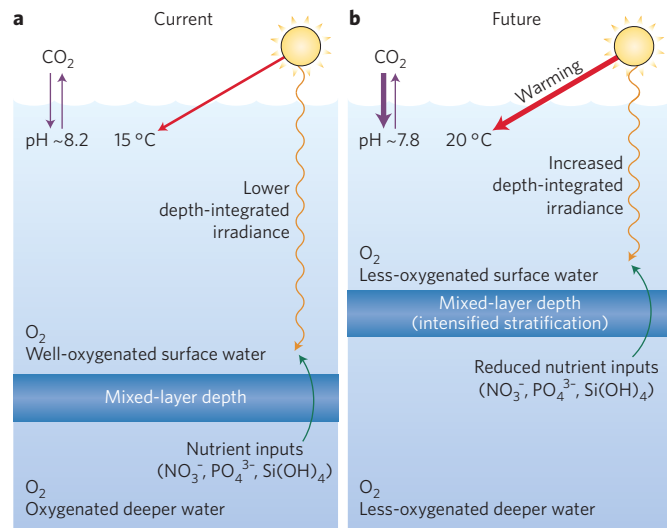


Figure 1 | Anthropogenic global change effects on key chemical and physical factors that influence the growth and community composition of marine planktonic microorganisms. a,b, The current ocean (a) versus the future ocean (b), circa the year 2100. Among the changes occurring across this time span that will have important impacts on marine microbiology are increases in atmospheric CO_2 uptake and concomitant decreases in ocean pH; warming of the surface ocean; shallowing of the surface mixed layer, resulting in increases in depth-integrated light exposure; intensified density-driven stratification, leading to lower vertical fluxes of nutrients such as nitrate, phosphate, and silicate; and reduction of seawater oxygen concentrations in both the surface mixed layer and the underlying deep ocean.

have not attempted to distinguish between these two tightly coupled components of a changing seawater carbonate buffer system.

Modelling studies predict that future global changes, particularly warming and lowered nutrient availability, may drive phytoplankton community shifts from large cells such as diatoms towards smaller taxa such as picocyanobacteria^{16–18}. This trend towards reduced phytoplankton cell sizes will reduce storage of sinking particulate organic carbon by the ocean's biological pump (Fig. 2b). However, the picocyanobacteria that dominate in many open ocean ecosystems possess carbon-concentrating mechanisms that can be more effective than those of many eukaryotic algae⁷, and so these cyanobacteria may not benefit energetically from elevated CO_2 to the same extent as eukaryotes. Indeed, some studies have reported minor or absent effects of acidification on the productivity and abundance of picocyanobacteria^{19,20}.

Some coastal and estuarine cyanobacteria, such as *Lyngbya* spp., produce potent toxins and are considered harmful algal bloom (HAB) species²¹. Warming is thought to stimulate these harmful cyanobacterial blooms²². Higher temperatures can also increase toxin production, growth rates and ecological dominance of eukaryotic HABs such as the neurotoxin-producing diatom *Pseudo-nitzschia* spp.²³. During an anomalous 2014/2015 US West Coast warming event, *Pseudo-nitzschia* formed a record-breaking regional toxic bloom extending from British Columbia to central California, and leading to extreme levels of toxins in marine food webs²⁴. Cellular toxicity of *Pseudo-nitzschia* spp. increases by 40–300% at projected year 2100 CO_2 levels, relative to present day CO_2 conditions, especially during nutrient-limited growth^{25,26}. Similar enhanced toxicity or growth with rising CO_2 and/or temperature has also been observed in a number of HAB dinoflagellates^{27,28}, although decreased or unchanged cellular toxicity has been reported for some groups^{29,30}. Even if toxicity is unaffected, the elevated growth rates and biomass often observed under high CO_2 and warming suggest increasingly damaging HAB events under future climate conditions.

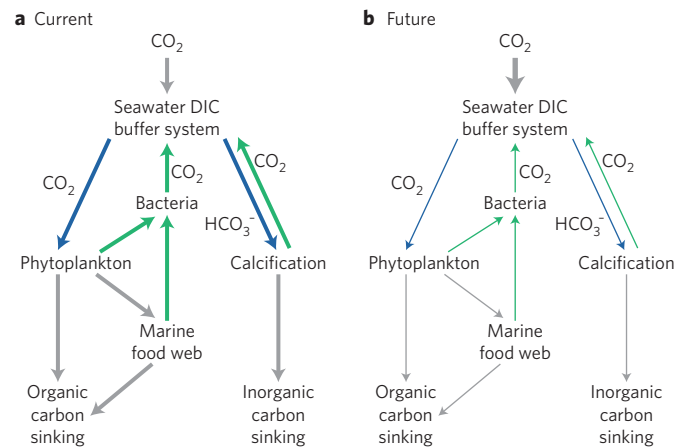


Figure 2 | Impacts of anthropogenic global change on physical, chemical and biological components of the ocean carbon cycle. a,b, The current carbon cycle (a) versus the future carbon cycle (b). Microbially driven processes that are considered in the main text and result in uptake of dissolved inorganic carbon (DIC) are shown with blue arrows, and those that release CO_2 are depicted in green; processes not explicitly addressed in detail in the text are shown with grey arrows. Projected changes in the future ocean carbon cycle relative to the present include increased uptake of CO_2 from the atmosphere into the seawater DIC buffer system, and decreases in microbial photosynthetic CO_2 fixation and incorporation of HCO_3^- into calcium carbonate shells. The net result of these changes may be future decreases in vertical export fluxes of organic and inorganic carbon, reduced organic carbon flow into the marine food web, lower levels of bacterial production and biomass, and smaller releases of CO_2 by microorganisms via respiration or as a byproduct of calcification.

To fully evaluate the effects of the matrix of ocean global change variables on primary producers, it is necessary to obtain full reaction norm curves for each factor under multiple conditions of each interacting co-variable³¹. Reaction norms (also known as functional response or performance curves) measure a physiological property, such as growth rate, across a broad range of an environmental variable such as temperature or CO_2 . This allows determination of a species' maximum and minimum tolerance limits for that factor, as well as defining the range over which growth is optimal³². However, studies examining (for instance) growth rates at multiple CO_2 concentrations across a full range of relevant temperatures or nutrient levels are logistically challenging, and have only rarely been attempted³³.

In general, elevated CO_2 effects on phytoplankton community structure and productivity are temperature- and nutrient-dependent, making reliable predictions problematic. In addition, important ecological interactions such as protozoan grazing and 'protistan mixotrophy' have not yet been fully incorporated into our picture of environmental change in the ocean³⁴. Studies are needed that employ interactive multiple variable experimental designs and consider higher levels of biological complexity, such as whole communities encompassing multiple trophic levels^{35,36}.

Calcification. Microbial calcification in the ocean is dominated by the unicellular haptophyte algal group known as coccolithophores, which are ubiquitously distributed except in the polar seas and form massive spring blooms in areas like the North Atlantic³⁷. Biogenic calcification links surface seawater carbonate chemistry with geological-timescale storage of carbon in oceanic sediments (Fig. 2a), and calcium carbonate provides ballast that speeds up the transport of sinking organic particles to the deep ocean³⁸. Whether the CO_2 produced by coccolithophore calcification serves as a supplemental source of inorganic carbon for their

photosynthesis has been debated, but recent evidence suggests that it does not³⁹.

Coccolithophore calcification has been examined in more depth and detail relative to ocean acidification than any other marine microbial process^{40,41}. A pioneering study in this field demonstrated that calcification rates of two coccolithophore species were reduced by 16–45% at lowered pH⁴², which could ultimately reduce ballasting of marine particles and hence carbon export to the deep ocean (Fig. 2b)³⁸. In general, many of the numerous studies subsequently published on this subject support this original finding^{37,40}. However, this conclusion is equivocal, as there is considerable strain- and species-level diversity in coccolithophore acidification responses. Some are relatively unaffected^{42–44}, and a few are even more heavily calcified at low pH^{45,46}.

Interactions with temperature^{47–49}, light^{47,50}, nutrients^{51,52} and UV radiation⁵³ can also modulate the effects of ocean acidification on calcification. Although numerous experiments have addressed these complex multivariate interactions, interpretation of their results is complicated by the fact that they have used many different coccolithophore strains from different regions. Differing combinations of global change variables such as CO₂, temperature, and light also result in ‘experimental meta-spaces’ that are not readily comparable, as is demonstrated by data from six published coccolithophore growth experiments (Fig. 3)^{42,43,47,49,50,52}.

Carbon fixation is undersaturated with respect to present day CO₂ levels in many, but not all, coccolithophores³⁷. Thus, ocean acidification could inhibit calcification, while simultaneously stimulating photosynthesis and growth. This outcome was seen in a North Atlantic acidification experiment, which produced a dense bloom of rapidly growing but very lightly calcified coccolithophores⁴⁸, and such strains may be superior competitors in the future ocean⁴⁴. The positive effects of increasing CO₂ on photosynthesis may also underlie a reported increase in North Atlantic coccolithophore abundance over the last ~50 years⁵⁴.

Coccolithophores are generally well adapted to high light levels, suggesting future shallower mixed layer conditions may favour their growth and dominance^{47,50,55}. Moderate levels of warming (~3–5 °C) can decrease calcification rates by 50% (ref. 49), or by up to 75% when combined with elevated CO₂ (ref. 47). In contrast, coccolithophore growth and carbon fixation rates often respond positively⁴⁸ or not at all^{47,49} to the same temperature increases. Thus, as with acidification, the net result of warming may be production of less calcified cells and consequent reductions in ballasting of sinking organic carbon.

Bacterial heterotrophy. Planktonic marine ‘heterotrophic’ bacteria range from ‘oligotrophs’, such as the ubiquitous alphaproteobacterial clade SAR 11, specializing in low-nutrient, open ocean environments⁵⁶, to ‘copiotrophs’, such as some Flavobacteria that occupy nutrient-rich niches including living phytoplankton cells and sinking organic particles⁵⁷. This tremendous functional diversity makes it difficult to generalize about responses of heterotrophic bacteria to ocean global change, but some trends have nevertheless emerged from recent experimental work.

Bacterial communities have been suggested to be relatively resilient to ocean acidification⁵⁸; for instance, Arctic SAR11 ‘ecotypes’ are relatively unaffected by lowering pH⁵⁹. Heterotrophs are also less likely to be directly sensitive to changes in CO₂, compared to autotrophs. Indeed, some experiments have shown little or no effect of projected future acidification on heterotrophic bacterial abundance^{60,61} or community structure^{62–64}.

In contrast, other plankton assemblage acidification studies have found increases in bacterial numbers^{65,66} and taxonomic dominance shifts^{61,67}. In these natural community experiments, it is difficult to rigorously distinguish between direct and indirect effects of acidification. Reported increases in bacterial protease and glucosidase

activities could be due to the relatively low pH optima of some of these exoenzymes, or to changes in the quality or quantity of dissolved organic carbon produced by the phytoplankton^{60,66,68}. Metatranscriptomes from one ocean acidification experiment demonstrated increased expression of proton pump genes by various bacterial taxa, including proteorhodopsins, respiratory electron transport systems and membrane proton transporters, suggesting their involvement in cellular pH homeostasis⁶⁹.

In contrast to acidification, experimental warming studies in diverse marine regimes have consistently demonstrated increased bacterial production, respiration and biomass, and sometimes lower ‘bacterial growth efficiency’^{70–73}. This may reflect direct thermal effects on metabolism⁷¹, or indirect effects of elevated dissolved organic carbon releases by phytoplankton at higher temperatures^{74,75}. Two warming experiments in the Baltic Sea reported bacterial community structure changes favouring the Bacteroidetes, a group that is particularly adapted to enzymatically break down large molecular weight organic compounds produced by phytoplankton^{62,73}. Warming sometimes correlates with reduced cell size in currently abundant bacterial taxa⁷⁶, or with dominance shifts towards small-celled groups like SAR 11^{59,77}. Such cell size changes could be related to changes in cellular carbon allocation due to elevated growth and respiration rates at higher temperatures⁷⁶. Protozoan grazing rates also increase rapidly in step with temperature^{71,72}, setting up a potential thermally driven arms race between marine bacteria and their chief predators.

Shallower mixed layers and consequent higher mean irradiances could benefit energetics of ‘bacterial photoheterotrophs’, although concomitant increases in ultraviolet radiation may also inhibit some bacterial groups⁷⁸. Future expansion of suboxic zones also has major implications for marine microbial ecology and nitrogen cycling. A glimpse into bacterial communities in future larger suboxic zones may be afforded by present-day low-O₂ environments, which are often dominated by the *Cytophaga*–*Flavobacterium*–*Bacteroides* group⁷⁹.

The marine nitrogen cycle in a changing ocean

Nitrogen is the limiting nutrient for photoautotrophs throughout most of the world’s oceans. The full nitrogen biogeochemical cycle occurs in seawater, although there are major exchanges as well with marine sediments, the atmosphere and the continents. Atmospheric nitrogen (N₂) is reduced to the level of ammonium and organic nitrogen by planktonic diazotrophs (Fig. 4a). This process is carried out largely by planktonic cyanobacteria, although heterotrophic bacteria make a substantial but poorly quantified contribution⁸⁰. This fixed nitrogen is then either assimilated by other microorganisms or oxidized by aerobic, chemoautotrophic nitrifying bacteria and archaea, first to nitrite (NO₂[−]), and then to nitrate (NO₃[−]) (Fig. 4a). The multiple reductive steps of dissimilatory denitrification occur in several large water column ‘oxygen minimum zones’ (OMZs) and in hypoxic marine sediments (Fig. 4a). In anaerobic ammonium oxidation, also known as anammox, chemoautotrophic Planctomycetes bacteria couple nitrite reduction to ammonium oxidation, with N₂ as the end product (Fig. 4a). Here, we consider the information currently available on the effects of global change processes on all of these major facets of the marine nitrogen cycle.

Nitrogen fixation. Nitrogen-fixing cyanobacteria such as colony-forming *Trichodesmium* and unicellular *Crocospaera* supply much of the new bioavailable nitrogen entering low-nutrient open ocean ecosystems⁸⁰, which encompass perhaps 75% of the ocean’s surface (Fig. 4a). The recently discovered photoheterotrophic, symbiotic cyanobacterial group UCYNA also contributes prominently to global N₂ fixation⁸⁰, but will not be addressed here as nothing is currently known about their responses to global change. Culture studies have suggested that *Trichodesmium* and *Crocospaera* may thrive under future high-CO₂ ocean conditions, although CO₂ responses

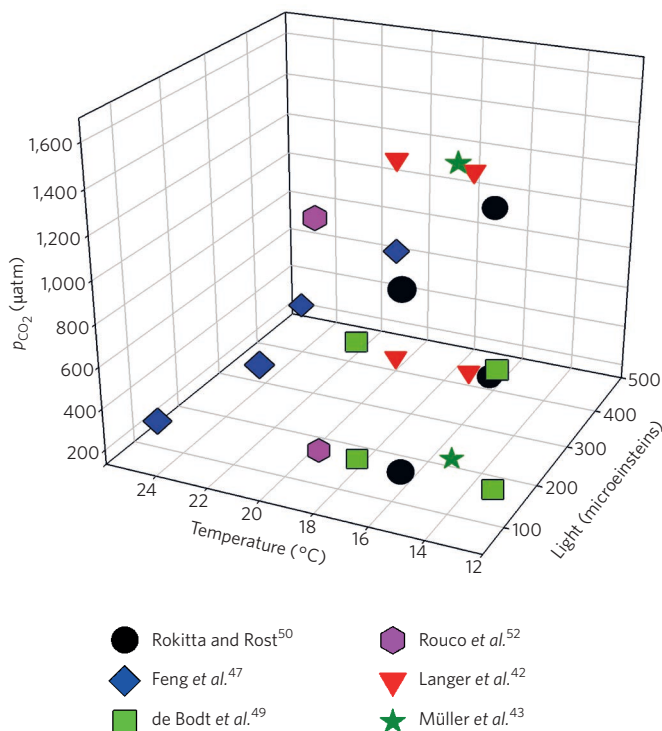


Figure 3 | The diversity of CO₂, temperature and light conditions used in six published coccolithophore global change experiments. Differences in the experimental treatments used leads to each study occupying a distinct experimental meta-space relative to these three key variables, making direct comparisons of results potentially problematic. p_{CO_2} , partial pressure of carbon dioxide.

can differ even between closely related taxa^{81–84}. Constitutive upregulation of *Trichodesmium* N₂ fixation and growth following long-term selection at high CO₂ is a surprising but evolutionarily and biogeochemically significant observation⁸⁵ (see section ‘Marine microbial evolution’). Some field studies have documented positive effects of elevated CO₂ on N₂-fixation rates and abundances^{20,86,87}, but others did not see a CO₂ response^{88–90}, possibly due to regional or taxonomic differences. A meta-analysis of published experiments concluded that, regardless of other factors, oceanic acidification will have a substantial positive impact on diazotroph growth¹⁸.

Fewer studies have addressed global change factors other than CO₂. Warming may favour *Crocospaera* over *Trichodesmium*, as the former is better adapted to higher temperatures⁹¹; range shifts for both groups are also likely (see section ‘Community structure and biogeographic changes’). Decreasing O₂ levels in the future ocean⁵ might favour N₂ fixers in general, as all known nitrogenase enzymes are strongly inhibited by oxygen⁸⁰. This is especially an issue for *Trichodesmium*, as it fixes N₂ during the day while simultaneously carrying out oxygenic photosynthesis. Unicellular N₂-fixing cyanobacteria may benefit less from future reduced O₂, since their nitrogenase activity occurs at night when O₂ concentrations are at a diel minimum⁷⁶.

Enhanced ocean stratification will expose N₂ fixers to more ultra-violet radiation (UVR)³. Studies have confirmed UVR inhibition of N₂ fixation in freshwater cyanobacteria^{92,93}, but whether this also applies to marine N₂ fixers is unknown. *Trichodesmium* is probably more vulnerable to UVR inhibition than unicellular N₂ fixers, simply because of its daytime nitrogenase activity and its habit of forming floating surface blooms in full tropical sunlight⁸⁰.

Saturating light levels may partially antagonize the stimulatory effects of ocean acidification on N₂-fixing cyanobacteria^{94–96}, with

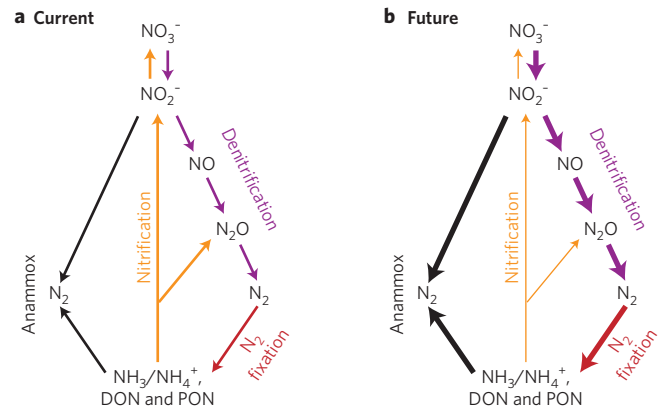


Figure 4 | Anthropogenic global change effects on the microbially mediated ocean nitrogen cycle. a, The current nitrogen cycle. **b**, The future nitrogen cycle. Potential changes will include increases in N₂ fixation (red arrow), denitrification (purple arrows) and anammox (black arrows), as well as decreases in nitrification (orange arrows). The oxidation state of the major forms of nitrogen ranges from +5 (NO₃⁻) to +3 (NO₂⁻), 0 (N₂) and -3 (NH₃/NH₄⁺, particulate organic nitrogen (PON), and dissolved organic nitrogen (DON)). The future net trend of these changes in microbial nitrification, denitrification, anammox and nitrogen fixation is likely to lead to a shift away from nitrate and nitrite and towards the reduced nitrogen species, relative to the present-day ocean.

potential implications for a more stratified ocean. The nutrients iron and phosphorus typically limit or co-limit diazotrophs in the current ocean⁹⁷; it is thought that future iron inputs may increase, while phosphate supplies will be decreased¹⁰. Iron limitation often negates the positive effects of CO₂ (refs 81 and 98), but enhanced N₂ fixation under high CO₂ persists during phosphorus limitation^{99,100}. While laboratory experiments examining high CO₂ or warming alone often suggest that N₂-fixing cyanobacteria could be among the most successful microorganisms in the future ocean, multivariable culture experiments sometimes suggest a more nuanced perspective on marine N₂ fixation and global change.

Nitrification. In marine plankton assemblages, the first step of nitrification is largely carried out by ammonia-oxidizing archaea (AOA), particularly the Thaumarchaea, with minor contributions by ammonia-oxidizing bacteria (AOB). The bacteria *Nitrospina* and *Nitrospira* are important in the subsequent oxidation of nitrite to nitrate¹⁰¹. Peak rates of water column ammonia oxidation often occur in the twilight zone, just below the sunlit surface ocean, as nitrifiers appear to be light sensitive¹⁰². Incomplete nitrification is also the dominant oceanic source of the potent greenhouse gas nitrous oxide (N₂O) (Fig. 4a)¹⁰³.

Oceanic nitrification appears to be especially vulnerable to pH reductions. Open ocean acidification experiments under realistic end-of-century carbonate system conditions have demonstrated decreases in ammonia oxidation and N₂O production rates of 8% to ~60% and 2% to 24%, respectively^{104–106}. These inhibitory effects have been attributed to the incremental protonation of NH₃ (the substrate for microbial ammonia oxidizers) to NH₄⁺ as seawater pH decreases¹⁰⁴. As much as half of the nitrate supply to surface phytoplankton communities is believed to originate from recent ammonia oxidation just below the euphotic zone¹⁰², and ongoing rapid acidification may decrease nitrification rates here by 3–44% over the coming decades¹⁰⁴. In contrast, some experiments in coastal waters and marine sediments show neutral or slightly positive effects of reduced pH on nitrification^{105–108}, and coastal AOA isolates are quite resistant to acidification¹⁰⁹. Much of global marine nitrification occurs in the deep ocean¹⁰², where anthropogenic acidification impacts are not

currently evident, as fossil fuel-derived atmospheric CO₂ has not yet fully penetrated into the ocean's lowest layers. However, this is virtually certain to happen progressively over the next several thousand years^{2,110}, with potentially negative effects on nitrification here.

Acidification experiments examining nitrifier community composition responses reported increases in the relative abundance of the AOB group *Nitrosomonas*¹¹¹. Whether increased availability of CO₂ in seawater could promote carbon fixation by nitrifying chemoautotrophs has not been investigated, but the presence of carboxysomes in many AOBs¹¹² suggests that they may employ carbon-concentrating mechanisms to obtain additional CO₂ for carbon fixation, as do many phytoplankton⁷. Most global change-related research has focused on ammonia oxidizers, with little attention paid to nitrite oxidation, even though this nitrate production pathway provides the main nitrogen source to many plankton communities.

Likewise, relatively little is known about how warming may affect nitrification, but three existing studies suggest that ammonia oxidizers may be relatively insensitive to changing temperature^{113–115}. Although nitrification is an aerobic process, it occurs at high rates in transitional regions around OMZs, where O₂ is low but not fully depleted (1–90 µmol O₂ per litre)¹⁰¹. Global proliferation of suboxic waters could greatly expand this important nitrifier niche. Possible implications of future shallower, more intensely illuminated mixed layers for light inhibition of underlying marine nitrifier communities have not been studied. To confidently predict the overall future trends in nitrification in a changing ocean, a new generation of multiple variable interactive studies incorporating concurrent acidification, increased irradiance, deoxygenation and warming may be needed.

Denitrification and anammox. Denitrification is limited to environments where oxygen is nearly fully depleted (<~5 µmol O₂ per litre), at which point a variety of mostly heterotrophic microorganisms switch to nitrate as a terminal electron acceptor. Although N₂ gas is the ultimate end product of denitrification, N₂O can also be released when the reductive process is incomplete (Fig. 4a). Perhaps two-thirds of marine denitrification and anammox occurs in marine sediments, with the rest happening largely in several large water column OMZs^{116,117}.

Geochemical proxies, such as 'nitrogen isotopic disequilibrium' in marine sediment cores, suggest that denitrification is positively correlated with ocean deoxygenation over thousands of years¹¹⁸. Shipboard studies show substantial expansion in suboxic water volume in recent decades, accompanied by intensified denitrification^{119–121}. With progressive climate warming and stratification, this oxygen loss is projected to continue into the foreseeable future. Although in some mid-water OMZs O₂ depletion may not progress far enough to allow denitrification¹²¹, other areas with already low O₂ concentrations will probably cross this threshold.

Anammox should also respond positively to the growth of OMZs, as nitrogen isotopic labelling experiments suggest it is strongly negatively correlated with O₂ concentration¹²². However, potential inhibition of ammonia oxidation by ocean acidification (see section 'Nitrification') may diminish the fluxes of nitrite required to support anammox⁸⁶; anammox bacteria will also have to compete with intensified future denitrification for available nitrite supplies¹²³. As for nitrifiers, the possible impacts of increased ocean CO₂ on carbon fixation by anammox bacteria have not been examined.

One biogeochemical model predicts a threefold increase in global suboxic water volume, and a fourfold increase in denitrification over the next ~2,000 years¹²⁴. Another predicts near-term future losses of ~17 Tg (7 × 10¹² g) of fixed nitrogen for each global increment of 1 mmol m⁻³ O₂ lost¹¹⁷. Two other models agree that oxygen losses will continue but instead predict that the volume of water with O₂ levels low enough to support denitrification will

actually decrease^{125,126}. Anthropogenic pollution-derived nutrient and iron fertilization also contributes to ocean deoxygenation, due to bacterial respiration of the excess organic carbon produced by phytoplankton^{10,127,128}. This 'eutrophication' process will substantially add to the effects of warming and drive additional ocean O₂ depletion, further accelerating microbial nitrogen loss processes, particularly in the coastal zones that receive most human nutrient inputs. Although these coastal regimes comprise only a small fraction of the ocean, they are disproportionately important to fisheries harvests, and so the appearance and expansion of nearshore O₂-depleted dead zones is a serious environmental problem¹²⁷.

Biological responses to ocean global change

The net consequences of climate change and ocean acidification for the marine cycles of carbon and nitrogen will ultimately be determined by the biological responses of the microbial assemblages of the ocean. These dynamic living components of global elemental cycles are capable of actively modulating their responses to global change in a variety of ways. Any discussion of microbiology in a changing marine environment would be incomplete without taking these biotic processes into consideration. Here, we address how current communities of marine microorganisms (Fig. 5a) may accommodate to a changing ocean through one or more of three types of biological responses: community structure changes (Fig. 5b), biogeographic range shifts (Fig. 5c) and adaptive evolution (Fig. 5d).

Community structure and biogeographic changes. The quickest and easiest way for marine plankton communities to respond to environmental shifts is through changes in community composition (Fig. 5a,b). Relative abundance changes will occur in current assemblages as those species that are best able to grow and compete under the altered conditions become ecologically dominant (Fig. 5b). In fact, such marine microorganism community structure shifts occur constantly in response to natural environmental variability. Thus, the resilience of plankton community structure and function to future anthropogenic perturbations will be partly a function of responses that are based on existing genotypic and phenotypic diversity.

Most planktonic marine microorganisms are associated with relatively well-defined biotic provinces in the ocean¹²⁹, and shifts in their current ranges constitute another important kind of biological response to changing ocean conditions (Fig. 5). In fact, considerable evidence indicates that as for plants and animals, the biogeographic boundaries of marine phytoplankton and bacteria are already rapidly shifting in response to climate change^{130,131} (Fig. 5a,c). Microbial expansions into new habitats are constrained by the ocean's physical circulation patterns, such as entrainment in currents or eddies^{132,133}. Anthropogenic transport vectors such as ship ballast water transfers can also introduce invasive microorganisms like toxic algae into new environments^{134,135}.

Changing ocean temperatures are a major factor driving climate-related range shifts of marine microorganisms^{4,131,136,137} (Fig. 5c). Documented range expansions attributed to warming include new appearances of temperate dinoflagellates and coccolithophores in high-latitude subpolar regions^{130,137}. Warming-induced range expansions have been predicted to increase total global biomass of tropical picocyanobacteria by 14–29% over the next century¹³⁸. Similar thermally driven shifts towards higher latitudes are also likely for N₂-fixing cyanobacteria^{139,140}, although *Trichodesmium* and *Crocospaera* could disappear from parts of their current tropical ranges where future warming may exceed their maximum thermal tolerance limits^{4,91} (see model species 1 and 3 responses, Fig. 5c). Selection by higher temperatures may lead to the emergence of more thermally tolerant ecotypes of these current dominant groups (see section 'Marine microbial evolution'), or alternately other existing taxa may replace them in the tropical N₂-fixation functional niche (Fig. 5b).

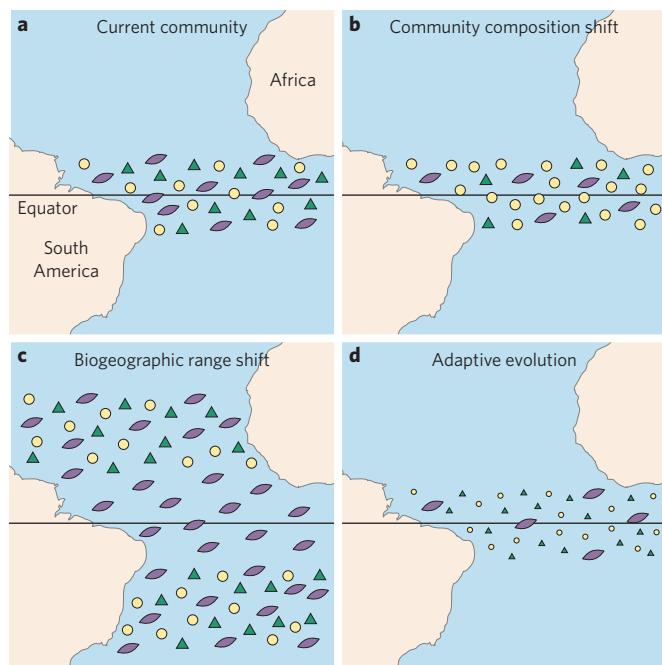


Figure 5 | Possible biological responses of a model phytoplankton community to climate change. Shown are three potential ways in which a hypothetical tropical Atlantic phytoplankton assemblage consisting of species 1 (yellow circles), species 2 (purple spindles) and species 3 (green triangles) could respond to future sea surface warming and reduced nutrient supplies due to enhanced stratification. **a**, Current distribution and abundance of the three species in the model community. **b**, Community composition shift, whereby species 1 has an intrinsic relative fitness advantage under the changed conditions, and so outcompetes species 2 and 3. **c**, Biogeographic range shift, in which all three species expand their ranges into higher latitudes with progressive warming. In the scenario illustrated here, species 1 and 3 are excluded from their former tropical range due to warming that exceeds their maximum tolerance limits, while species 2 with a higher thermal maximum continues to thrive in the low-latitude tropics. **d**, Adaptive evolution, as lower nutrient availability selects for the evolution of smaller cell sizes in species 1 and 3. In this scenario, species 2 is unable to adapt by reducing cell size, and so is outcompeted by the other two species that have evolved more favourable phenotypes under the altered conditions. These three types of biological responses are not mutually exclusive, so more than one may occur concurrently. In addition, in the real ocean the responses of much more complex networks of microorganisms will also be influenced by many other interacting biotic and abiotic factors.

Much emphasis has been placed on how warming will affect microbial biogeography and community structure, with perhaps too little attention paid to other global change processes. For instance, a modelling study argues that ocean acidification will be more important than warming in structuring future marine plankton communities¹⁸. A decade-long time series record of tropical plankton community structure suggests that most species accommodated to changes in temperature and light, but most failed to change their realized niches relative to nitrate availability¹⁴¹. A model based on a ~50-year North Atlantic phytoplankton assemblage record shows that thermally driven poleward migration occurred at a rapid rate of ~13 km per decade. However, this expected northward movement was accompanied by an unforeseen eastward shift across the basin that was even faster (~43 km per decade), due to interactive changes in circulation, mixed layer depth, nutrients and irradiance¹⁴². Responses of plankton community structure and biogeography to climate change have been evaluated using a trait-based approach, whereby characteristics

such as light responses, nutrient requirements and mixotrophy collectively influence responses to environmental variability^{143,144}. Cell size is a particularly important trait to consider in relation to global change, as expected shifts toward smaller cells in a more nutrient-limited future ocean will reduce their sinking rates, and so constrain the export of carbon by the biological pump^{16,144}. These approaches that move beyond emphasizing temperature alone promise to yield more robust insights into how microbial distributions, diversity and biogeochemistry may change in the future ocean.

Marine microbial evolution. Marine microorganisms are characterized by tremendous population sizes, short generation times and high genetic diversity. All of these attributes, along with others such as an unknown but presumably considerable potential for horizontal gene transfer, will facilitate their ability to respond evolutionarily to climatic shifts^{31,145}. Thus, strong directional selection imposed by anthropogenic change has the potential to drive rapid adaptation by many populations of marine microorganisms, thereby fundamentally reshaping plankton communities (Fig. 5a,d).

Long-term records of evolutionary responses to past climate change are available for a few biomineralizing microbial taxa. Paleo-oceanographers use the ocean sedimentary record to examine changes in the abundance, community composition, mineralization and isotopic fractionation of calcifying coccolithophores and foraminifera (protozoan zooplankton), or silicifying diatoms and silicoflagellates, in relation to proxies for past atmospheric CO₂ or sea surface temperature^{146,147}. These deep-time studies offer insights into the responses of mineralizing microorganisms to climatic shifts over geological timescales. Their conclusions sometimes do⁴⁵ and sometimes do not^{148,149} resemble results of brief manipulative experiments using modern plankton. As the timescale of anthropogenic global change lies between these two extremes, the two types of studies offer useful bounds on probable microbial evolutionary responses over the coming decades.

Laboratory experimental evolution studies of adaptive responses of marine phytoplankton to global change stressors provide the lower temporal limit to this picture. A 500-generation study of the coccolithophore *Emiliania huxleyi* under selection by elevated CO₂ demonstrated increased fitness (by 2–7%) and partially restored calcification (by up to 50%), relative to cells exposed briefly to acidification¹⁵⁰. However, no additional growth rate increases were observed over a further 250–500 generations of selection¹⁵¹. Another *Emiliania huxleyi* evolution experiment using a CO₂–temperature factorial matrix design found that selection by warming increased growth rates (16%) but not calcification, while adaptation to warming and acidification together enhanced calcification by 101%¹⁵². Cell lines of the globally distributed marine picoplankter *Ostreococcus* with the most initial physiological plasticity adapt most rapidly and easily to acidification¹⁵³, and this is further facilitated by selection under fluctuating environments¹⁵⁴.

In the marine N₂-fixing cyanobacterium *Trichodesmium*, large physiologically plastic increases in growth and N₂-fixation rates that are typically seen during short-term exposures to high CO₂ (35–100%)^{83,85,95,96,99} become constitutive following 850 generations of selection⁸⁵. This transition from plasticity to adaptation, or genetic assimilation, is accompanied by increased expression of particular multiple gene transcription-regulating ‘sigma factors’¹⁵⁵. Interactions between adaptation of *Trichodesmium* to high CO₂ and simultaneous co-limitation by iron and phosphorus (a common condition for N₂ fixers in the ocean¹⁰) result in a unique emergent phenotype. This adaptive response includes a transition to smaller-sized cells (by 18–59%)^{100,156} capable of maintaining relatively fast growth rates despite low nutrient concentrations (Fig. 5d), as well as a novel proteome configuration that allows co-limited cells to maintain the abundance of critical cellular proteins such as those of photosystem I at levels similar to those seen in nutrient-replete cells¹⁰⁰.

Only a few studies have addressed marine microbial evolution in global change experiments using complex communities composed of multiple species such as those found in nature (Fig. 5d). Individual phytoplankton species have been isolated out of short-term (weeks) natural assemblage CO₂ and/or warming experiments, and subsequently maintained under selection by the same factors for ~1 year. These selected cell lines were then used in competition experiments with artificial communities structured to resemble the original natural experimental communities. Results suggest that short-term global change experiments with unacclimated populations may be fairly good predictors of competitive success for long-term CO₂- or warming-adapted diatoms¹⁵⁷, but not dinoflagellates¹⁵⁸. In another large-volume natural community mesocosm experiment, the diatom *Skeletonema* evolved growth rates that were ~30% higher following 107 days of selection by high CO₂ (ref. 159). The future will certainly bring many more such experiments examining evolutionary processes in complex natural communities (Fig. 5d), and employing ever more realistic selection regimes incorporating interacting multiple global change drivers^{35,36}.

Future microbially mediated ocean biogeochemical cycles

It is possible to make best-guess estimates of future biogeochemical trends based on our ever-improving knowledge about ocean microorganisms and global change. For the ocean carbon cycle, it seems inevitable that anthropogenic CO₂ entering the surface ocean will continue to swell the dissolved inorganic carbon pool, progressively lowering ocean pH (Fig. 2b). The preponderance of current evidence suggests that this acidification process will directly inhibit calcification by most coccolithophores, thus reducing sinking calcium carbonate export fluxes and incidentally minimizing calcification as a CO₂ source term (Fig. 2b). Some studies suggest that higher seawater CO₂ concentrations and/or warming could be beneficial to photosynthesis by particular microbial photoautotrophs, but we suggest that overall, any such stimulatory effect will probably be over-ridden by the negative effects of intensified stratification and concomitant nutrient limitations. The result may be net reductions in biological carbon fixation, thereby constricting supplies of organic carbon to sinking export fluxes, heterotrophic bacteria and the marine food web (Fig. 2b). This downsizing of the ocean's biological carbon cycle may yield a less productive future ocean, with less capacity to take up and store further inputs of fossil fuel CO₂, and a dwindling supply of harvestable biological resources.

For the nitrogen cycle, the inhibitory effects of ocean acidification on ammonia oxidation, coupled with higher rates of denitrification and anammox in the expanding volume of deoxygenated seawater, may tend to shrink the global inventory of the oxidized nitrogen species nitrate and nitrite (Fig. 4b). Nitrate concentrations will also be substantially lower in surface waters due to the physical barrier to vertical resupply imposed by intensified stratification. The net trend will be a shift in the future ocean nitrogen cycle towards reduced species, such as ammonium and dissolved and particulate organic nitrogen. This is especially true if increased CO₂ and warming promotes larger inputs by N₂ fixers into the reduced nitrogen pool (Fig. 4b), a conclusion which must, however, be tempered by the possibility that iron and phosphorus limitation (or co-limitation) of N₂ fixers may ultimately limit the magnitude of these stimulatory effects¹⁰.

Despite these emerging predictions based on our present knowledge, it is clear that accurately forecasting the shape of changes in the microbially-mediated nitrogen and carbon cycles of the future ocean requires assembly of a coherent picture from a puzzle that still lacks many key pieces. In particular, interactive effects between all of the many global change drivers are seldom well understood for any single microorganism, much less for diverse microbial

networks and the entire ecosystems in which they are embedded³⁵. To make matters worse, published experiments are often difficult to rigorously cross compare, frustrating straightforward interpretations. Finally, the nature of biological responses such as biogeographic and community composition shifts, as well as the potential role of adaptive evolution, remain largely enigmatic and will require much further exploration before we can confidently project the outlook for marine microorganisms and their associated biogeochemical cycles in the rapidly changing future ocean.

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Author contributions

D.A.H. developed much of the material presented and wrote the paper, with major contributions from F.F.

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Competing interests

The authors declare no competing financial interests.