

# *Prochlorococcus*: Approved for export

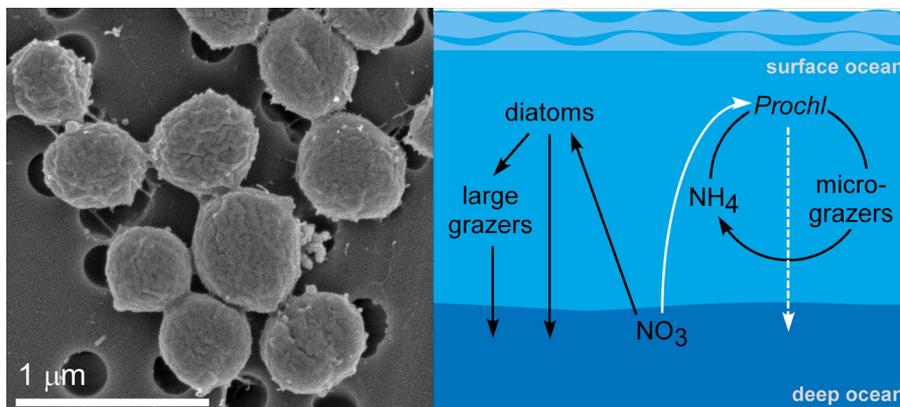
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The oceans account for approximately half of global carbon fixation (1), but unlike plant-dominated terrestrial environments, marine photosynthesis is dominated by single-celled microbes, or phytoplankton. These phytoplankton are the engines that drive marine food webs and biogeochemistry. Among the vast variety of phytoplankton found in the open ocean, the non-nitrogen-fixing cyanobacterium *Prochlorococcus* is the most numerically abundant (2). Thus, understanding the diversity, physiology, and ecology of *Prochlorococcus* is critical to describing and predicting the biological processes and patterns that originate at the base of the marine food web and their implications for carbon dioxide uptake and climate variability. In this issue of PNAS, Martiny et al. (3) provide compelling evidence that some strains of *Prochlorococcus* can use nitrate ( $\text{NO}_3^-$ ), which is the most abundant form of fixed nitrogen in the oceans and often limits production, further expanding the importance of this tiny organism.

As the smallest known marine phytoplankton, *Prochlorococcus* has a streamlined genome of roughly 2,000 genes (4), unlike eukaryotic algae, which can have well over 10,000 genes (5). But the tradeoff for this simple complement of genes is a reduced metabolic potential, limiting the ability to use some nitrogen compounds. Nevertheless, *Prochlorococcus* dominates in most tropical and subtropical open ocean environments because its small diameter and large surface area to volume ratio affords a competitive advantage for the limited light and nutrient resources (Fig. 1 Left). The nitrogen requirement for this growth is largely supplied by urea  $[(\text{NH}_2)_2\text{CO}]$  and ammonium ( $\text{NH}_4^+$ ), which in turn are largely generated either directly or indirectly (mediated by bacterioplankton) by the small protozoa grazers that feed on *Prochlorococcus*. Thus the growth of *Prochlorococcus* is part of a tightly coupled loop dependent on recycled nitrogen (Fig. 1 Right).

In certain areas, ocean currents bring new nitrogen in the form of  $\text{NO}_3^-$  to the upper sunlit waters, stimulating photosynthesis and primary production. However, this new nitrogen was thought to be unavailable to *Prochlorococcus* because none of the genome sequences from laboratory strains contain the single gene (assimilatory nitrate reductase)



**Fig. 1.** *Prochlorococcus* is the smallest marine phytoplankton and important to the marine nitrogen cycle. (Left) Scanning electron micrograph of *Prochlorococcus* (strain MIT9312). (Right) Conceptual diagram of the uptake of some major nitrogen compounds by various phytoplankton groups and their contribution to export production. Diatoms and *Synechococcus*, among other types of phytoplankton, can use new  $\text{NO}_3^-$  and therefore contribute substantially to the draw-down of carbon dioxide from the surface ocean (and atmosphere). *Prochlorococcus* was thought to be in a tightly coupled cycle living only on  $\text{NH}_4^+$  and urea, which is supplied directly or indirectly (by bacterioplankton) by micrograzers. However, Martiny et al. (3) provide strong evidence that *Prochlorococcus* can also use  $\text{NO}_3^-$  and therefore may contribute more substantially to carbon export from surface waters.

necessary for nitrate utilization. But other, larger types of prokaryotic and eukaryotic phytoplankton, including *Synechococcus* and diatoms, do have this gene and therefore are able to bloom. Although *Prochlorococcus* establishes the baseline of primary production driven by recycled  $\text{NH}_4^+$  and urea, only the phytoplankton that can use  $\text{NO}_3^-$  such as diatoms can respond to the pulses of high-nitrogen waters, ensuring that they can take advantage of these nitrogen oases.

However, Martiny et al. (3) use an array of metagenomic sequence data from the Global Ocean Survey (6) representing many different oceanographic regions, to provide the first evidence that some types of *Prochlorococcus* may contain the nitrate reductase gene (*narB*). Using field RNA samples, they further demonstrate that this putative *Prochlorococcus* gene is expressed, strongly suggesting that *Prochlorococcus* has the ability to use  $\text{NO}_3^-$ . Although preliminary, this finding has two substantial implications for our understanding of the functioning of the oceans.

The ability to use  $\text{NO}_3^-$  alters our conception of how *Prochlorococcus* fits into the marine food web and in particular what limits and regulates its growth. Although it may use  $\text{NO}_3^-$ , *Prochlorococcus* does not dominate in oceanic regions with high  $\text{NO}_3^-$  concentrations such as coastal upwelling, open ocean up-

welling (e.g., eddies or equatorial regions), or high latitudes. These observations suggest that other factors control *Prochlorococcus* growth and biomass in these areas. These factors may include both “bottom-up” processes such as other nutrient limitation (non-nitrogen), allelopathic interactions from other microbes, or competition from faster growing  $\text{NO}_3^-$ -using phytoplankton (e.g., *Synechococcus*, diatoms) and “top-down” processes such as tightly controlled grazing by their protistan predators. Evidence from nutrient addition experiments suggests that *Prochlorococcus* populations are tightly regulated by grazers, but there is support for bottom-up regulation of these populations as well (7). Interestingly, *Synechococcus*, which is a close cyanobacterial cousin of *Prochlorococcus*, utilizes  $\text{NO}_3^-$  and does bloom in some of these regions. Although *Synechococcus* and *Prochlorococcus* have many similarities in their genomes, cell properties (e.g., size), and physiologies and therefore have overlap-

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ping habitats (8), something unique about *Prochlorococcus* prevents it from flourishing in these high- $\text{NO}_3^-$  waters.

The second implication of this finding is that *Prochlorococcus* may be more important in exporting carbon from the upper ocean than originally thought. In the tightly coupled growth and grazing cycle driven by  $\text{NH}_4^+$  and urea, nutrients and carbon are recycled continuously in the upper ocean (Fig. 1 *Right*). Although carbon dioxide is quickly consumed by the phytoplankton, this uptake is balanced by losses to grazing and release to the upper ocean (and atmosphere).  $\text{NO}_3^-$  can also be involved in this fast spinning cycle when microbes convert  $\text{NH}_4^+$  to  $\text{NO}_3^-$  through a process called nitrification. In nutrient-poor regions of the oceans, approximately half of the  $\text{NO}_3^-$  consumed by phytoplankton is recycled through this process (9), thus the ability to use  $\text{NO}_3^-$  gives *Prochlorococcus* access to another part of this rapidly cycling nitrogen pool. But in systems where new nitrogen (such as  $\text{NO}_3^-$ ) is added, a net export of carbon from the surface ocean can occur, if biomass is removed from the surface layers via direct sinking or packaging of cells in dense zooplankton fecal pellets. This so-called export production (or biological pump that draws down carbon diox-

ide from the atmosphere into the ocean) was thought to be largely driven by large, fast-sinking algae, but more recent evidence suggests that small cells, such as *Prochlorococcus*, may be equally important in this process that is significant for the global climate (10). Additive tracer experiments have shown that natural populations of *Prochlorococcus* can take up  $\text{NO}_3^-$  and that it significantly contributes to new production (10). Because the potential of *Prochlorococcus*

### Some types of *Prochlorococcus* may contain the nitrate reductase gene (*narB*).

to use  $\text{NO}_3^-$  has only recently been demonstrated, its contribution to new and export production has not historically been included in models of open ocean marine ecosystems (Fig. 1 *Right*). Incorporating this finding into these models has the potential to revise and possibly increase our estimate of the contribution of marine photosynthesis to carbon uptake by the oceans.

With the metagenomic data presented in Martiny et al. (3) there are now two compelling and complementary lines of evidence that *Prochlorococcus* can use  $\text{NO}_3^-$  (3, 11), yet none of the  $\approx 50$  strains isolated to date has been shown to contain the *narB* gene. Nevertheless, we already know that the genus *Prochlorococcus* comprises several different genotypes that can differ in their gene complement and physiology (12) and ecologies (13), each exhibiting its own niche differentiation. Inventories of the known ecological types (or ecotypes) show that the culture collections do not account for all of the *Prochlorococcus* found in the oceans (14), and this discrepancy is most acute deeper in the water column. This depth is exactly where new  $\text{NO}_3^-$  fluxes are highest and *narB*-containing *Prochlorococcus* would be expected to be found. In addition to targeting isolates of  $\text{NO}_3^-$ -assimilating *Prochlorococcus* from these areas, direct quantification of the contribution of *Prochlorococcus* to new (and export) production should be pursued. More challenging, but equally important, areas of future study will be to determine what limits *Prochlorococcus* growth in areas of high  $\text{NO}_3^-$  and why it does not participate in the bloom dynamics characteristic of many other  $\text{NO}_3^-$ -using phytoplankton.

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