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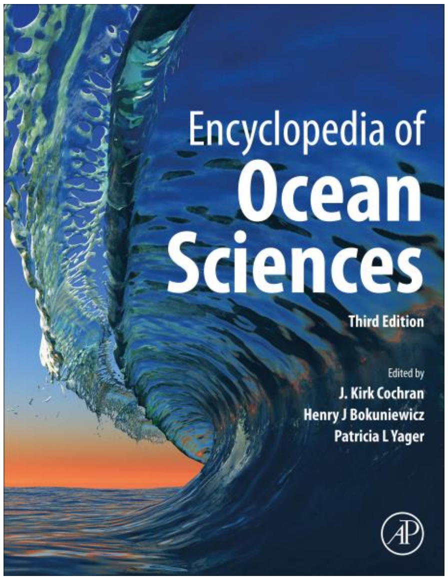

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Larkin Alyse A., Mackey Katherine R.M. and Martiny Adam C. 2019 Marine Cyanobacteria: Prochlorococcus and Synechococcus. In Cochran, J. Kirk; Bokuniewicz, J. Henry; Yager, L. Patricia (Eds.) Encyclopedia of Ocean Sciences, 3rd Edition. vol. 1, pp. 569-573, Elsevier. ISBN: 978-0-12-813081-0

dx.doi.org/10.1016/B978-0-12-409548-9.10984-4
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Marine Cyanobacteria: Prochlorococcus and Synechococcus

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Introduction: General Description and History

The marine cyanobacteria *Prochlorococcus* and *Synechococcus* represent two of the most abundant photosynthetic genera on the planet. While *Prochlorococcus* and *Synechococcus* have small cell sizes of ~0.5–1 μm and ~0.8–2 μm, respectively, they have been estimated to contribute ~25% of ocean primary production. Moreover, despite having small genomes for photosynthetic organisms (*Prochlorococcus* has the smallest known photoautotrophic genome at ~1.65–2.7 Mbp), both genera are highly diverse. Extensive in situ analyses have revealed the presence of phylogenetic clades that partition the ocean based on light, temperature, and growth limiting resources (i.e., nitrogen, phosphorus, and iron). Thus, studies of *Synechococcus* and *Prochlorococcus* have demonstrated their importance both in terms of marine biogeochemistry and microbial ecology.

The discoveries of both *Prochlorococcus* and *Synechococcus* were based on their unique pigmentation and size. In 1979, Waterbury and colleagues demonstrated the presence of *Synechococcus* cells across a range of marine environments based on their phycoerythrin pigments, which exhibit orange fluorescence. Later analyses of ocean samples revealed a high concentration of divinyl chlorophyll—a pigment not usually found in marine phytoplankton. Chisholm, Olsen and colleagues then identified *Prochlorococcus* populations based on their small cell size and red fluorescence and found that *Prochlorococcus* indeed harbored these unusual pigments. Combined, these early studies established that *Prochlorococcus* and *Synechococcus* were abundant and widespread in the ocean.

Distribution

Prochlorococcus and *Synechococcus* can reach abundances of up to ~10^5–10^6 cells per mL and are widely distributed (Fig. 1). *Prochlorococcus* is most abundant in hot, nutrient deplete tropical waters, declines sharply between 10°C and 15°C, and is mostly absent in high latitude waters. Vertically, *Prochlorococcus* is commonly found at highest abundance near the sunlit surface. However, in regions with clear water and high light intensities, cells may experience photoinhibition. In such regions, *Prochlorococcus* reaches peak abundance at the deep chlorophyll maximum lower in the water column. *Synechococcus* displays a more complex distribution pattern. The lineage is absent in some near-zero degree waters as seen in the Southern Ocean; although, certain cold-tolerant strains have been identified in polar waters. *Synechococcus* becomes highly abundant in temperate waters, with maximal abundance observed near 10°C. It is less abundant at intermediate temperature and has a local minimum at 20°C, leading to a band of depressed cell numbers at ~40°N/S. This decrease coincides with the temperature range where *Prochlorococcus* becomes abundant, suggesting that competition may be involved in depressing *Synechococcus* abundance. *Synechococcus* is found at intermediate cell abundance in tropical waters. The distribution of *Synechococcus* also peaks near the sunlit surface. As such, the geographic distribution of both *Prochlorococcus* and *Synechococcus* is closely tied to temperature, whereas light controls the water column profile.

Adaptations to Environmental Conditions

Prochlorococcus and *Synechococcus* are commonly used as models for understanding how microorganisms adapt to different environmental conditions including light, temperature, nutrients, iron, and pH/$p\mathrm{CO}_2$.

Prochlorococcus and *Synechococcus* acclimate to light intensity and spectral quality differently as a result of their distinctive light harvesting systems. In *Synechococcus*, the main light harvesting system are phycobillisomes (PBS), which are large, pigment protein complexes located on the surface of the photosynthetic membrane and funnel light to the photosystems (PS). PBS comprise phycobiliproteins that bind different chromophores, each with a unique excitation maximum. Strains containing phycocyanin only are green in color and absorb orange to red wavelengths of light, whereas strains that also contain phycoerythrin are pink to orange in color and absorb in a broad range of blue to green wavelengths. Certain strains are capable of chromatic acclimation, in which the ratio of cyan-absorbing phycouribilin (PUB) and green-absorbing phycoerythrobilin (PEB) can shift in response to spectral quality. Together these light harvesting properties expand the niche for *Synechococcus*, enabling them to access regions of the spectrum other cells with strictly chlorophyll-based antennae cannot. The light spectrum available for phytoplankton growth is dependent on the presence of other compounds in the water and several studies have demonstrated how the availability of different wavelengths select for specific lineages of *Synechococcus*. This enables the lineage to thrive in both coastal and open ocean waters. In addition to spectral

https://doi.org/10.1016/B978-0-12-409548-9.10984-4

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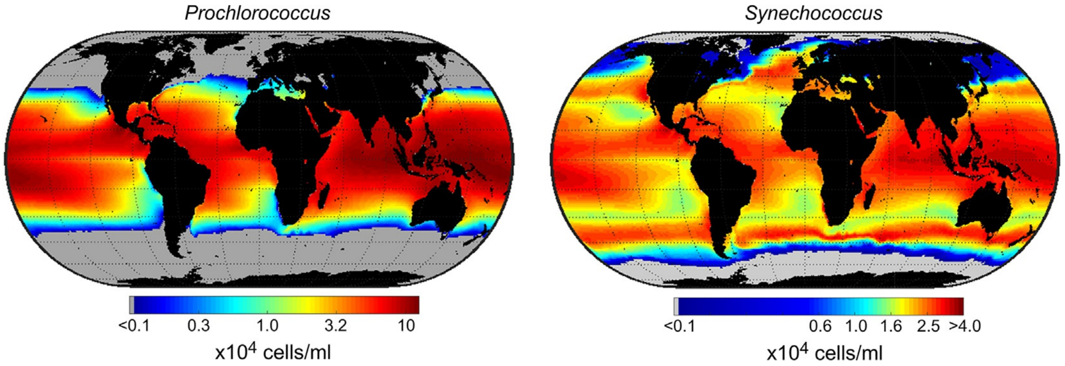

Fig. 1 The global surface distribution of *Prochlorococcus* and *Synechococcus*.

quality, *Synechococcus* strains possess a number of acclimation pathways for avoiding photoinhibition under high light intensity. These include reduction of antenna size via degradation of the PBS distal rods, energy re-distribution between PSI and PSII via state transitions, non-photochemical quenching via the orange carotenoid protein (OCP), accessory antenna formation around PSI by the iron stress induced protein (IsiA), regulation of chlorophyll synthesis, photosystem assembly and energy dissipation by high light inducible proteins (Hlips), and alternative photosynthetic pathways. The outcome is that *Synechococcus* is rarely inhibited by high light availability.

In contrast to *Synechococcus*, *Prochlorococcus* lacks PBS and instead uses a divinyl chlorophyll a_2/b_2 complex for light harvesting in addition to the photosystem itself. *Prochlorococcus* is divided into two phylogenetic groups (discussed below) that are adapted to high light (HL) and low light (LL) conditions, corresponding to their depth distribution in the water column. The presence of HL and LL *Prochlorococcus* was first suggested by a bimodal distribution in the red (chlorophyll) fluorescence of cells from subsurface samples. Isolates from these populations later revealed differences in their chlorophyll composition, growth irradiance maxima, and cell size. In addition to divinyl chlorophyll *a* and *b*, *Prochlorococcus* cells also contain zeaxanthin and α-carotene, making their pigmentation unique among all photosynthetic organisms. The light harvesting antenna of *Prochlorococcus* are best adapted to capture blue wavelengths, which predominate in oligotrophic regions of the global ocean. While *Synechococcus* does not absorb blue light as well as *Prochlorococcus*, it is capable of absorbing green wavelengths through its PEB pigments. As a result, *Synechococcus* is equipped to grow in green light, which is prevalent at the surface (~0–30 m) as well as in coastal waters. This difference in pigment composition likely influences the biogeography of *Prochlorococcus* and *Synechococcus*. In clear, oligotrophic regions, *Prochlorococcus* can grow at much higher abundances than *Synechococcus* deeper in the water column. Hence, whereas the light acclimation strategies of *Synechococcus* contribute to its broad geographical distribution, light affects *Prochlorococcus* populations by selecting for faster growing phylogenetic groups that are adapted to different depth and light intensities.

Both lineages show evidence for adaptation to different temperature regimes whereby some subclades are more abundant at low versus high temperature. Several *Prochlorococcus* genes with unknown functions are only found in lower temperature environments. In *Synechococcus*, it appears that interactions between temperature and photosystem functioning are central to temperature adaptation. Specifically, under near-optimal temperatures when growth rate is high and the demand for photosynthesis is greatest, *Synechococcus* uses state transitions to funnel more energy into the photosynthetic electron transport chain and simultaneously up-regulates synthesis of several key photosynthetic proteins. Whereas, the opposite is true under sub-optimal growth temperatures. This process of balancing energy demand with supply appears to affect the photosynthetic response of *Synechococcus* to temperature; however, the exact molecular mechanisms underlying temperature adaptation are unknown.

Prochlorococcus and *Synechococcus* show clear adaptations to the availability of phosphorus (P) and nitrogen (N). Although both nutrients are mostly present in inorganic forms (phosphate for P, nitrate and ammonium for N), they can also be found in various other chemical entities. P availability can limit growth in certain ocean regions including the western North Atlantic Ocean and Mediterranean Sea. Under P limitation, *Prochlorococcus* and *Synechococcus* up-regulate genes associated with phosphate transport as well as genes facilitating the replacement of P in cell membrane lipids. Sub-lineages adapted to low P also contain genes that allow cells to access alternative forms of P (e.g., phosphoesters). N availability can limit growth in many parts of the ocean and the response to N limitation mirrors that of P. *Prochlorococcus* and *Synechococcus* up-regulate genes associated with ammonium transport and, thus, increase the transport and affinity of reduced N. Furthermore, sub-lineages adapted to low N also contain genes that allow cells to access alternative forms of N including nitrate, nitrite, urea, and certain forms of organically bound N. Cells may also reduce their cellular N requirements. This can be done by reducing photosynthetic pigments and, possibly, other not-yet-characterized cellular components. In sum, there is ample evidence of adaptation to low nutrient conditions that affects both the uptake and requirement of P and N.

Aside from macronutrient availability, the availability of trace metal micronutrients shapes the genomes and biogeographical distributions of *Prochlorococcus* and *Synechococcus*. *Prochlorococcus* living in iron limited regions of the ocean show a reduction in the number of iron-containing proteins that are present in the photosynthetic pathways. In *Synechococcus*, the loss and retention of iron

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acquisition and iron-containing genes appears to be linked strongly to macronutrient availability. Specifically, *Synechococcus* isolated from Fe limited environments survives over a broad range of Fe concentrations by partitioning Fe among different uptake and storage proteins. In contrast *Synechococcus* isolated from a low N environment lacks this adaptive response, suggesting the small yet significant N cost of retaining Fe response proteins can offset the benefit of Fe adaptability when N is chronically scarce and Fe:N ratios are stable and high.

Increasing pCO_2 is expected to decrease the pH of ocean waters by the end of the century. However, only limited experimental and in situ data exists regarding the response of *Prochlorococcus* and *Synechococcus* to elevated atmospheric CO_2 levels. A small amount of research suggests that *Synechococcus* may increase in abundance, or in its relative ratio to *Prochlorococcus*, at higher pCO_2. However, laboratory results only saw increased photosynthetic efficiency at higher pCO_2 and elevated temperature, suggesting temperature dependent enzyme kinetics may play a role in increased growth. Additionally, an alternative study showed decreased growth rates for *Synechococcus* at lower pH. Thus, the mechanistic relationship between pCO_2 and *Synechococcus* growth is unclear. *Prochlorococcus*, on the other hand, has only exhibited no effect or decreased growth rates at elevated pCO_2. A recent study has shown that this may be caused by decreased catalase production by "helper" bacteria such as *Alteromonas*, which results in less hydrogen peroxide removal from seawater and higher oxidative stress for *Prochlorococcus*. In sum, predicting the response of *Prochlorococcus* and *Synechococcus* to elevated CO_2 levels remains a challenge because of the interactive effects between CO_2, temperature, and nutrients, as well as interactions between these cyanobacteria and heterotrophic microbes.

Phylogenetic Diversity of *Prochlorococcus* and *Synechococcus*

Molecular analyses of *Prochlorococcus* and *Synechococcus* have revealed extensive phylogenetic diversity. At a broad level, specific phylogenetic clades have been associated with ocean conditions including light, iron, temperature, and macronutrients (Fig. 2). As a result, these clades have been referred to as "ecotypes." According to Cohan's ecotype hypotheses, an ecotype is a phylogenetically-delineated bacterial population that is ecologically distinct and occupies a unique environmental niche. In *Prochlorococcus*, a hierarchy of ecotypes has been described (Fig. 2). *Prochlorococcus* can be divided into high-light and low-light adapted ecotypes. The low-light adapted ecotypes are characterized by high chlorophyll content and high divinyl chl b_2:a_2 ratios. The cells also tend to be larger. There are multiple clades among with the low-light ecotype. These subclades have a layered water column distribution. The LLI clade is found right below the deep chlorophyll maximum followed vertically by the LLII/III clade and then LLIV at the bottom of the euphotic zone. A number of other low-light adapted clades exist, but their exact vertical distribution is not yet fully determined. The high-light adapted ecotype is characterized by lower amounts of chlorophyll and smaller cells. The high-light ecotype can first be divided into low- and high-iron ecotypes. The low-iron ecotype (clades HLIII and HLIV) is primarily found in warm, iron limited but macronutrient replete regions like the eastern equatorial Pacific Ocean. The high-iron ecotypes include a low- (HLI) and a high-temperature ecotype (HLII). A temperature of 20°C separates these two ecotypes. Thus, HLI is found at the upper latitudinal edge of the overall *Prochlorococcus* distribution as well as near or above the deep chlorophyll maximum (where the temperature is lower than the surface). The high-temperature adapted HLII is the most abundant *Prochlorococcus* ecotype and is found in most tropical and subtropical ocean environments. Thus, there is a clear link between adaptations to specific ocean environments and the biogeography of *Prochlorococcus* ecotype diversity.

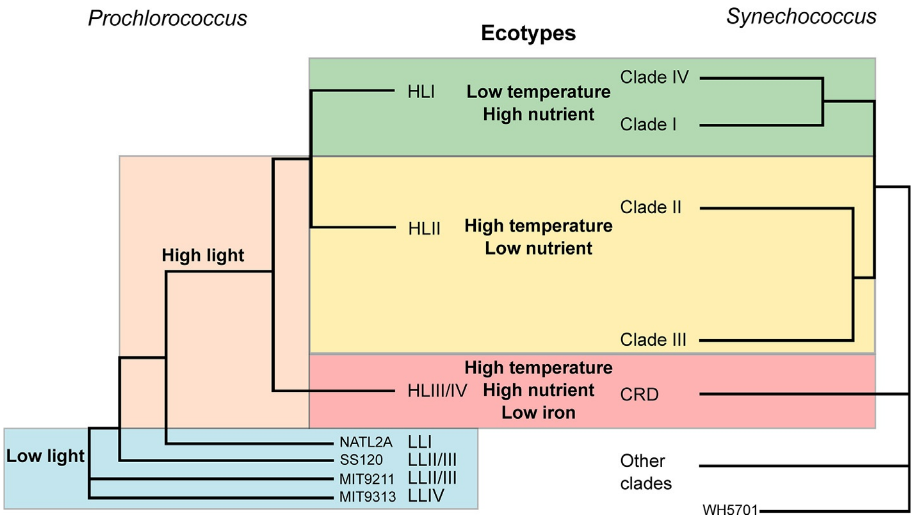

Fig. 2 Conceptual phylogenetic trees of *Prochlorococcus* and *Synechococcus*, which depict the taxonomic relationships between the dominant clades of the two genera. The ecotypes of *Prochlorococcus* and *Synechococcus* are highlighted by the colored blocks. Here, ecotype is defined as a monophyletic clade that is associated with a unique set of environmental conditions. In the *Synechococcus* tree, "other clades" primarily refers to clades V/VI, VIII, IX, and XVI, whose phylogenetic relationships vary depending on the genomic region examined.

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In *Synechococcus*, similar ecotypes have also been described, albeit with some notable distinctions. *Synechococcus* can broadly be divided into three major ecotypes, but their exact phylogenetic relationship is still a matter of debate (Fig. 2). The first ecotype (CRD) occupies low-iron environments and parallels the HLIII and HLIV clades in *Prochlorococcus*. The CRD clade was first discovered in the iron limited upwelling region by the Costa Rica Dome but has subsequently been found in other low iron environments. The second ecotype (Clades II and III) dominates warm, low macronutrient environments and parallels the HLII clade in *Prochlorococcus*. As such, this ecotype is abundant in tropical and subtropical waters. The third ecotype (Clade I and IV) is found in temperate and sub-polar waters. This ecotype partly parallels HLI in *Prochlorococcus* but has a much broader latitudinal distribution (as *Synechococcus* as a whole has a wider latitudinal distribution than *Prochlorococcus*). In addition, multiple phylogenetic clades have been described in *Synechococcus* but their exact distribution and physiology is not yet known. *Synechococcus* is also unique in that the group does not contain well defined light-adapted ecotypes or a clear vertical separation in genetic diversity. As such, light adaptations including pigment ratios do not correspond with deeply conserved ecotypes identified via multi-locus sequence analysis. Instead, horizontal transfer of genes involved in photosynthesis appears to control light adaptation. Thus, the organization and biogeography of *Prochlorococcus* and *Synechococcus* phylogenetic diversity share many similarities but also some clear differences.

Beyond the ecotype phylogenetic level, recent studies have demonstrated the presence of microdiverse *Prochlorococcus* and *Synechococcus* sub-taxa that show systematic variability in their relative abundance across both spatial and seasonal environmental gradients. These sub-ecotype microdiverse populations generally have high sequence similarity and thus represent the highest microbial taxonomic resolution examined in situ to date. Studies of *Prochlorococcus* and *Synechococcus* at the microdiverse phylogenetic level have a number of advantages. First, the distribution of microdiverse taxa can help identify subtle differences in biogeochemical regimes in situ. Second, biotic interactions with heterotrophic microbes as well as susceptibility to viral lysis and grazing have been hypothesized to act on bacterial populations at fine phylogenetic scales. Therefore, patterns of microdiversity may reveal critical top-down ecological processes that influence *Prochlorococcus* and *Synechococcus*. Third, identifying microdiverse taxa located at the extreme edges of the *Prochlorococcus* and *Synechococcus* geographic distribution, and subjecting those taxa to growth experiments, may aid in predicting responses to climate change. In addition to systematic biogeography, microdiverse *Prochlorococcus* and *Synechococcus* sub-ecotype taxonomic groups are associated with unique suites of environmental parameters.

Microdiverse populations of *Prochlorococcus* and *Synechococcus* appear to occupy unique niches defined by multidimensional trait axes. Both *Prochlorococcus* and *Synechococcus* sub-ecotype taxonomic groups have been shown to be strongly and differentially influenced by temperature, light, macronutrient concentrations, and iron availability. The unique niche space occupied by each microdiverse taxon composes a part of the overall fundamental niche of *Prochlorococcus* or *Synechococcus*. The fundamental niche of a genus is defined by Hutchinson as the n-dimensional set of environmental conditions or resources wherein a taxon could potentially survive. This differs from the realized niche, or the set of conditions where a taxon is found in the environment, which is limited by biotic interactions, dispersal limitation, and the absence of specific environments. The aggregated fundamental niche of each microdiverse taxa drives the total realized niche of *Prochlorococcus* and *Synechococcus* as a whole, or the actual abundance distribution of these genera in the environment (Fig. 3). In comparison to other microbial genera, preliminary research suggests that *Prochlorococcus* and *Synechococcus* may have relatively high microdiversity. Thus, the microdiversity of *Prochlorococcus* and *Synechococcus* is a fundamental characteristic of these Cyanobacteria that allows them to dominate across a broad range of

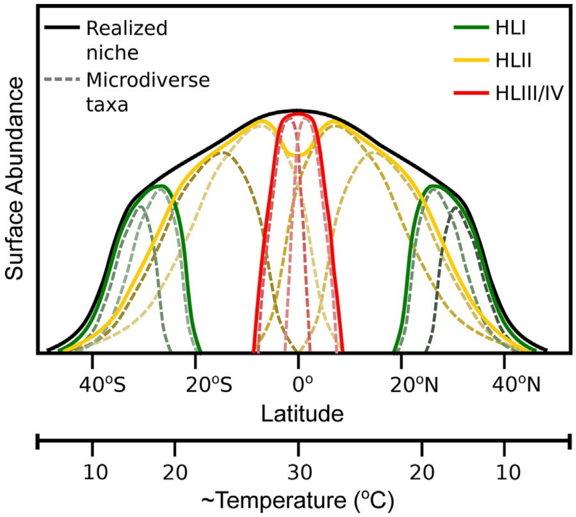

Fig. 3 An idealized diagram of the abundance distribution, or realized niche, of *Prochlorococcus* in the surface ocean. Each ecotype contributes to the overall abundance of *Prochlorococcus*. In turn, each microdiverse taxon partially delineates the shape of the distribution of each ecotype. Therefore, the aggregated niches of the microdiverse groups directly drive the overall distribution of *Prochlorococcus* across the global ocean. In contrast to the ecotype distributions, which have been empirically demonstrated in the Atlantic, Pacific, and Indian Oceans, the microdiverse taxa depicted here are theoretical.

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environmental conditions in the global ocean. As sequencing technology continues to improve in the future, researchers will have increasing access to the tools necessary to examine *Prochlorococcus* and *Synechococcus* at microdiverse phylogenetic scales.

Conclusions

Prochlorococcus and *Synechococcus* are abundant and widely distributed marine Cyanobacteria that are critically important for ocean biogeochemistry and ecosystem functioning. By contributing up to 25% of the ocean's primary production, these two genera funnel a significant proportion of the energy driving marine food webs. Niche models have projected that *Prochlorococcus* and *Synechococcus* cell numbers will increase 29% and 14%, respectively, with elevated ocean temperatures by the end of the 21st century. This increased abundance may also expand their contribution to marine carbon fixation. However, significant uncertainties exist regarding the ability of these two genera to expand in both cellular abundance and geographic distribution. For example, interactions between *Prochlorococcus*, *Synechococcus*, and other microbes, including viruses, may have unknown effects on the ability of these Cyanobacteria to migrate into new regions. Despite these uncertainties, extensive research on the phylogenetic structure of *Prochlorococcus* and *Synechococcus* populations has made these two genera model systems for understanding microbial adaptation. As a result, future research may be able to elucidate the link between genetic and functional diversity in these Cyanobacteria and provide a unique opportunity to understand microbial responses to climate change.

Further Reading

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