

samples. In addition to measuring elemental abundances, some studies have also measured isotopic compositions of H, C, and N; taken together, the combined data set is more in agreement with a relatively wet lunar interior as well as a common origin for water and other associated volatiles in the Earth-Moon system (2, 10–12). Such links are further strengthened by results of dynamical modeling of the Moon formation event, which suggest that the material forming the magma disc around the proto-Earth after the putative giant impact could have retained volatiles sufficiently well relative to what was believed to be the case previously (13). Thus, a giant-impact origin of the Moon does not necessarily require the formation of an anhydrous Moon, and the presence or absence of water cannot be used as evidence for or against various mod-

els involving some variations of the giant-impact origin of the Moon.

Over the past decade, considerable improvements in analytical instrumentation and advances in numerical modeling have led to a dramatic change in our understanding of lunar volatiles. An approach that combines multi-element and multi-isotopic measurements on the same samples provides better constraints on the volatile history of lunar samples and of their source regions. A series of new measurements and experiments need to be performed to confirm some of the predictions based on numerical modeling and in turn would provide data for refining such models. A better understanding of the volatile inventory of the lunar interior will not only improve our understanding of the origin and evolution of the Earth-Moon system but will also provide

key insights into the origin and sources of volatiles necessary for life.

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10.1126/science.1253266

GENETICS

Being Selective in the *Prochlorococcus* Collective

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Marine phytoplankton are a key component in global biogeochemical cycles and marine food webs. The structure and function of phytoplankton communities varies throughout the oceans, organized by ocean circulation and resource delivery, and is intertwined with the acclimation (physiological plasticity) and adaptation of the organisms to the prevailing conditions. Cyanobacteria of the genus *Prochlorococcus* are a dominant component of such communities in oligotrophic (nutrient-poor) regions of the oceans between 45°N and 40°S (1). On page 416 of this issue, Kashtan *et al.* (2) use single-cell genomics to describe the genotypes of individual *Prochlorococcus* cells co-occurring at the Bermuda-Atlantic Time-series Study site in the Sargasso Sea. The work provides a detailed view of the population genetics of this organism, revealing an array of diverse genotypes that hint at the evolutionary and environmental forces that generate and maintain *Prochlorococcus* diversity. More generally, the study brings a new dimension to what can be done today in environmental

microbiology by combining single-cell isolation from the field with DNA sequencing technologies.

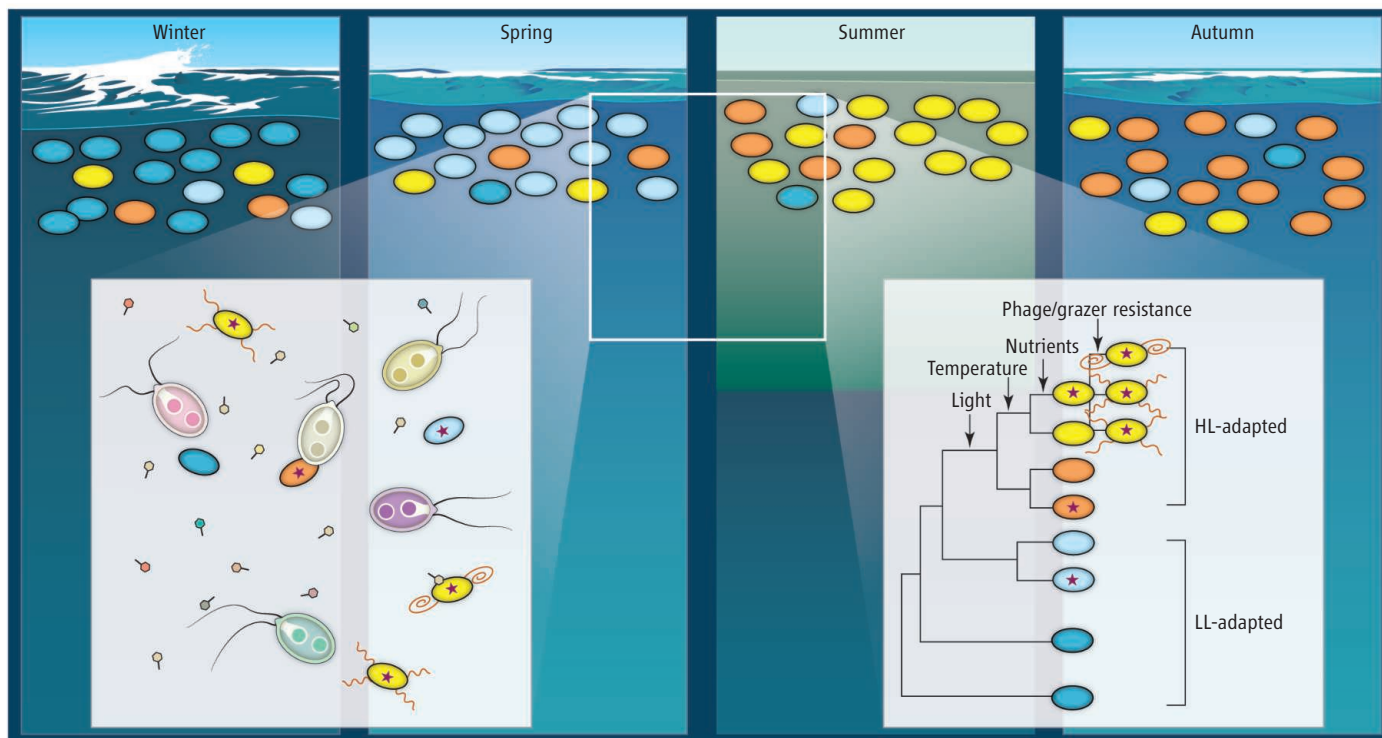
The *Prochlorococcus* genus contains distinct ecotypes or clades that are adapted to the different seasonal and geographical light and nutrient gradients in the sunlit upper layers of the ocean (3, 4) (see the figure). These population adjustments occur within *Prochlorococcus* communities even though overall population density is relatively constant, at 100,000 cells/ml in surface waters (5). Kashtan *et al.* analyzed single-cell genome sequences from cells collected at three different times of the year. They found subpopulations at the whole-genome level that correlate with the relationships defined previously by ribosomal RNA sequences—an important confirmation of the value of the more traditional methods used to identify clades and assess community diversity and dynamics. Moreover, they found that although the overall genetic diversity was maintained in each sample collected during different seasons, there were changes in the abundance of specific genotypes that led to their dominance in certain conditions. The environment thus appears to select winning genotypes from the *Prochlorococcus* collective, likely according to differential fitness in changing environmental conditions, refuge

from phages and grazers, and other extrinsic and intrinsic factors (6, 7).

Kashtan *et al.* conclude that the previously defined ecotypes are in fact a collection of many coexisting subpopulations. Each has a distinct “genomic backbone” consisting of highly conserved alleles of a majority of “core” genes and a smaller distinct set of flexible genes that is associated with a particular set of core gene alleles. Although conserved within clades, these combinations are different between clades. Furthermore, variation within clades appears to be targeted to specific regions of the genome, implying a mechanism for generating genetic diversity that links the core and flexible genomes. This fine-scale co-variation between the core alleles and flexible gene content represents previously unknown microdiversity within wild *Prochlorococcus* populations of co-occurring cells. In reality, the extent of diversity is remarkably high, with as much as 3% of the genome being affected at the sub-clade level; the authors propose that this is because these backbone subpopulations diverged at least a few million years ago. If this is the case, it would suggest an ancient niche partitioning that is stable over long time scales. Genes that appear to be particularly prone to nucleotide variations in both the core and flexible gene

Single-cell sequencing reveals the microdiversity of the most abundant photosynthetic organism on Earth.

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***Prochlorococcus* diversity in the ocean.** Seasonal selection of genotypes (different-colored cells) from similar-sized populations of the *Prochlorococcus* collective throughout a schematic annual cycle. (Inset) Bottom left: An idealized population of plankton in which different genotypes of *Prochlorococcus* coexist with different protist grazers (flagellated cells) and different phages (not to scale). (Inset) Bottom right [adapted from (9)]: Diversification based on physical parameters (temperature, light, and nutrients) may be operative at higher taxonomic levels, whereas the fine-scale “leaves” of the tree are likely maintained by biological phenomena such as nutrient acquisition and phage/grazer resistance. Stars and squiggles indicate the importance of the cell surface in fine-scale genotype selection (HL, high light-adapted ecotypes; LL, low light-adapted ecotypes).

sets encode proteins that are involved in the interface that the cell presents to the external environment (e.g., by modifying the cell surface). In future studies, it will be of interest to ascertain the rates of diversification of these proteins and how they have varied over time. It will also be important to go beyond genome sequencing and examine the expression of these alleles in the different populations throughout the year.

What must also be addressed is how the diversity is maintained and on which scale it is acting (8). With the cell surface implicated as a major driver of microdiversity, the biotic environment seems likely to be playing a large role (9). This might be a result of the arms race between predator and prey and/or between virus and host. Depending

on physical transport of cells (e.g., by ocean currents and wind-driven mixing), this might further mean that an individual genotype is never eaten by the same grazer twice (or infected by the same phage twice)—which would slow the pace of biotic selection—or that locally there is some sort of biological network where more rapid coevolution occurs (10, 11).

The work by Kashtan *et al.* is necessarily descriptive; the oceanographic context is simplified, the study is based on only three sampling dates, and the mechanisms that drive genome structure changes over the proposed time scales are not addressed. The authors also focused only on high light-adapted (HL) ecotypes; it is likely that low light-adapted (LL) ecotypes will display even greater diversity. Although the results essentially support an “everything is everywhere but the environment selects” regime (12), further work is required to show whether the same genotypes come back year after year, and if not why not. Furthermore, it will be interesting to extend the observations beyond the Sargasso Sea to assess whether ocean circulation can ensure a global distribution of the same seed populations. Given the huge effective population size of *Prochlorococcus* and the modeling of physical mixing that the authors present, this appears likely to be the case, but it will be important to show that the different genotypes are indeed everywhere, at least at population levels that can be detected by ultradeep sequencing.

By providing a new window into natural microbial communities, DNA sequencing-based technologies seem likely to continue to provide dramatic increases in our understanding of the evolution and ecology of phytoplankton populations. Key questions in microbial oceanography that can now be addressed include how adaptation to the environment organizes populations into biomes (networks of interacting organisms) having specific biogeochemical functions, the relative role of acclimation and genetic adaptation in shaping these networks, and the importance of physical transport and intermingling of populations by ocean circulation with respect to local adaptation. No doubt *Prochlorococcus* will continue to lead the way in revealing the ocean’s secrets.

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10.1126/science.1253817