

Review

Marine Bacterioplankton Seasonal Succession Dynamics

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Bacterioplankton (bacteria and archaea) are indispensable regulators of global element cycles owing to their unique ability to decompose and remineralize dissolved organic matter. These microorganisms in surface waters worldwide exhibit pronounced seasonal succession patterns, governed by physicochemical factors (e.g., light, climate, and nutrient loading) that are determined by latitude and distance to shore. Moreover, we emphasize that the effects of large-scale factors are modulated regionally, and over shorter timespans (days to weeks), by biological interactions including molecule exchanges, viral lysis, and grazing. Thus the interplay and scaling between factors ultimately determine the success of particular bacterial populations. Spatiotemporal surveys of bacterioplankton community composition provide the necessary frame for interpreting how the distinct metabolisms encoded in the genomes of different bacteria regulate biogeochemical cycles.

Role of Bacteria in Marine Biogeochemical Cycling

Bacteria are a keystone of the marine microbial food web owing to their sheer abundance and level of activity, and they are able to rapidly respond to physicochemical gradients and environmental changes. Bacterial generation times in surface seawater may vary from a few hours to several days ([1,2] and references therein), leading to a multitude of potential population dynamics patterns and biological interplays with other microbes and higher organisms. Notably, **heterotrophic** bacteria (see [Glossary](#)) are the only organisms that efficiently assimilate and transform **dissolved organic matter** (DOM) in marine ecosystems. The importance of this process is evident when considering that photosynthetic cyanobacteria and single-celled eukaryote phytoplankton carry out roughly half of the **primary production** of the Earth [3], and ~50% of the organic carbon produced is channeled through heterotrophic bacteria [4]. Moreover, microorganisms significantly regulate the cycling of elements such as nitrogen (N) and phosphorus (P). Given the central role of marine bacteria in biogeochemical processes, and considering the divergence of genetically encoded metabolisms and physiologies among taxa, disentangling bacterial seasonal **succession** patterns and their consequences is important.

Advances in microbiological and molecular biology techniques have resulted in a rapid expansion of knowledge in microbial oceanography. For example, while marine bacteria were recognized to influence N turnover in aquatic systems as early as 1898 [5], only in recent decades have specific steps in nutrient cycling and the molecular mechanisms been identified. Notably, new metabolisms, or so far unrecognized variants of known metabolisms, have been discovered fairly recently. These include, for example, **proteorhodopsin** (PR), **photoheterotrophy**, and cryptic sulfur cycling [6–8]. The dependence of such processes on particular

Trends

Seasonal succession in bacterioplankton is observed in polar, temperate, and tropical regions, and the amplitude in population dynamics often increases with distance from the equator.

Intriguingly, novel sequencing methods for identifying bacterial populations allow teasing apart how key physical, chemical, and biological factors shape bacterial community composition at different spatiotemporal scales.

A challenge in microbial oceanography consists of providing direct evidence for cause–effect linkages between dissolved organic matter quantity/quality and the dynamics of specific bacterioplankton.

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Box 1. Microbial Species Concept

The interpretation of seasonal succession and population dynamics depends intimately on how species are defined. This is a challenge for asexually reproducing microorganisms because it is difficult to apply the traditional species concept that was developed for higher organisms with sexual reproduction. In effect, microbial ecologists often use a pragmatic approach for defining populations that is based on molecular advances in bacterial taxonomy. In bacterial taxonomy, a microbial species is traditionally defined according to a polyphasic approach as a set of individuals isolated in culture that experimentally show >70% DNA–DNA hybridization levels and that are distinguishable from other taxa by phenotypic traits [95]. Experimental comparisons showed that 70% DNA–DNA hybridization approximately corresponds to ~97.0–98.5% 16S rRNA gene sequence identities, and these identity levels are typically used for clustering analysis of operational taxonomic units (OTUs). In both taxonomic descriptions of new species and for defining populations in microbial ecology, such sequence identity levels are commonly used, albeit they likely represent conservative estimates of the genetic and functional diversity among microbes. Interestingly, studies on the applicability of average nucleotide identity (ANI) values over entire genomes are currently advancing the understanding of the microbial species concept [95]. Overall, a major contemporary challenge for microbial ecologists is how to apply the information from molecular techniques for differentiating between microbial populations or species in the natural environment.

microbial species (Box 1) and successional dynamics among bacterioplankton (here broadly used to refer to planktonic and particle-attached bacteria and archaea, excluding photosynthetic cyanobacteria) have yet to be explored. The tremendous development of bacterial diversity analysis, from some handfuls of cloned **16S rRNA gene** sequences from single samples in the early 1990s to thousands of 16S rRNA gene tag sequences now in hundreds of samples across the globe, has resulted in comprehensive databases for the dominant populations and recognition of the enormous biodiversity dwelling in the so-called ‘rare biosphere’ [9–13].

Improvements in uncovering the biodiversity of bacterioplankton are paralleled by the discovery of pronounced differences in spatiotemporal distribution patterns among populations. High-resolution time-series analysis of bacterial community composition now allows the identification of patterns in seasonal bacterial succession, thereby providing insights also into potential drivers of these dynamics. It is imperative to reveal these succession patterns because different bacterial populations have distinctive metabolisms and divergent resource preferences, thereby having the potential to regulate the temporal variability in biogeochemical processes. Even if different populations were able to use the same suite of (in)organic compounds, they would likely diverge in their affinity for uptake or metabolic efficiency. Moreover, differences in interspecies interactions – between bacteria or between bacteria and photosynthetic phytoplankton, protist grazers, and phages – will influence seasonality patterns and bacterial ecosystem functioning. Seasonal succession in bacterioplankton was early inferred from analyses of changes in bacterial community composition over 1 year periods [14,15]. Importantly, verification that such dynamics are indeed seasonal was provided by Fuhrman *et al.* who employed a suite of statistical methods to confirm patterning in community composition, demonstrating that patterns are repeatable over several years, and that environmental factors can predict temporal patterns [16].

We review here articles on advances in understanding marine bacterioplankton seasonal succession dynamics. Given the biogeographic patterns in marine bacterial diversity [17–19], and that seasonal variability in several key environmental factors increases with increasing latitudes from the equator (for example temperature, irradiance, and nutrient dynamics), the review is structured into three sections. These sections summarize the dynamics in polar, temperate, and tropical areas (Figure 1), with dynamics in temperate waters being presented first because general plankton dynamics are most intensely studied here (note the as yet low number of studies in the southern hemisphere). We then discuss some particular factors with an important influence on succession.

Glossary

16S rRNA gene: gene encoding the RNA of the small subunit of the prokaryotic ribosome; a key gene for investigating phylogenetic diversity and taxonomy of microorganisms.

Chemolithoautotroph: organism that obtains its energy from reduced inorganic compounds and produces organic carbon from carbon dioxide.

Dissolved organic matter (DOM): is often characterized as labile, semilabile, or recalcitrant with respect to how the carbon constituent is available for consumption by heterotrophic microorganisms.

Heterotroph: organism that relies on organic carbon for obtaining both energy and cellular building blocks (does not fix carbon dioxide).

Metagenomics: DNA-based community analysis of functional genes using high-throughput sequencing techniques.

Metatranscriptomics: RNA-based community analysis of functional genes using high-throughput sequencing techniques.

Photoheterotroph: organism that relies on organic carbon for obtaining cellular building blocks (does not fix carbon dioxide) and reducing power but that can use sunlight for energy.

Primary production: conducted by photosynthetic organisms.

Proteorhodopsin (PR): a light-driven proton pump situated in the cell membrane.

Succession: the ecological process of sequential replacement of organisms over time (organism taxa levels could be e.g., species, genera, or families).

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