Review

How do divergent ecological strategies emerge among marine bacterioplankton lineages?

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Heterotrophic bacteria in pelagic marine environments are frequently categorized into two canonical ecological groups: patch-associated and free-living. This framework provides a conceptual basis for understanding bacterial utilization of oceanic organic matter. Some patch-associated bacteria are ecologically linked with eukaryotic phytoplankton, and this observation fits with predicted coincidence of their genome expansion with marine phytoplankton diversification. By contrast, free-living bacteria in today's oceans typically live singly with streamlined metabolic and regulatory functions that allow them to grow in nutrient-poor seawater. Recent analyses of marine Alphaproteobacteria suggest that some free-living bacterioplankton lineages evolved from patch-associated ancestors up to several hundred million years ago. While evolutionary analyses agree with the hypothesis that natural selection has maintained these distinct ecological strategies and genomic traits in present-day populations, they do not rule out a major role for genetic drift in driving ancient ecological switches. These two evolutionary forces may have acted on ocean bacteria at different geological time scales and under different geochemical constraints, with possible implications for future adaptations to a changing ocean. New evolutionary models and genomic data are leading to a more comprehensive understanding of marine bacterioplankton evolutionary history.

Microscale heterogeneity and ecological strategies of marine bacteria

The dissolved organic matter (DOM) reservoir in the ocean (operationally defined as material passing through a 0.2 or 0.45 μm pore-size filter) contains as much carbon as the Earth's atmosphere [1]. The particulate organic matter (POM) reservoir of living plankton cells and detrital material (operationally defined as material unable to pass through these filters) is equivalent to ~3% of the DOM and is typically richer in both nitrogen and phosphorus [2,3]. This dichotomous view of marine organic matter is convenient for sampling and analysis but is not fully nuanced at the scale relevant to bacterial activities. For example, the discovery of materials in seawater ranging from biopolymer gels that assemble spontaneously from DOM, to viral particles, to nutrient plumes consisting of phytoplankton exudate [4–6], reveals the complex and transient microscale structure of organic matter encountered by bacteria [7,8]. These nanometer-to-millimeter

Glossary

Ancestral genome reconstruction: inferring content and size of ancestral genomes and the rate of lateral gene transfer, gene loss, and gene duplication along a rooted phylogeny.
Bacterioplankton: bacterial members of planktonic organisms that drift in the water.
Compositional artifact: sequences that cluster as a result of compositional similarity rather than biological relatedness.
Defense mechanism: biological process that protects organisms from external attacks.
Effective population size: size of an idealized population needed to generate as much neutral diversity as actually observed.
Free-living bacteria: pelagic bacteria able to grow under the low organic matter and nutrient concentrations typical of bulk seawater.
Genetic drift: evolutionary force causing allelic frequency change as a result of random sampling.
Genome streamlining: evolutionary process in which DNA loss dominates over DNA gain.
Lateral gene transfer: movement of genes between organisms by mechanisms other than descent.
Natural selection: evolutionary force causing allelic frequency change as a result of differential reproductive success; positive selection favors advantageous mutations, while purifying selection acts to eliminate deleterious mutations.
Noncoding RNA: RNA that is not translated into proteins.
Nonsynonymous mutation: mutation occurring in protein-coding genes that results in an amino acid change.
Obligate intracellular bacteria: bacteria living inside other cells and unable to survive outside.
Orthologs: homologous genes in different organisms that are related by descent.
Patch-associated bacteria: pelagic bacteria taking advantage of transient, often microscale organic matter and nutrient hotspots occurring in seawater.
Pelagic bacteria: bacteria living in open oceans or seas.
Pelagic ocean: open oceans or seas.
Post-transcriptional regulation: control of gene expression at the RNA level.
Pseudogene: gene-like DNA that has lost protein-encoding ability.
Quorum sensing: microbial regulatory mechanism in response to population density.
Spontaneous mutation: mutation arising from DNA replication error, lesions, transposable genetic elements, or other natural process.
Synonymous mutation: mutation occurring in protein-coding genes that does not produce an amino acid change.

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hotspots harbor nutrient concentrations up to three orders of magnitude higher than bulk seawater [9,10] and increase local bacterial productivity by up to an order of magnitude [4,10,11].

Heterotrophic marine bacteria are responsible for the metabolism of this organic carbon matrix. Similar to the marine chemists' convenient classification of the organic matter pool into DOM and POM, marine microbial ecologists often categorize pelagic bacteria (see Glossary) into free-living and patch-associated cells. Even at this gross distinction, studies have shown that it coincides with identifiable phylogenetic and metabolic differences [12–15]. Patch-associated bacteria generally have large and variable genomes that harbor genes enabling a variety of metabolic and regulatory capabilities [16–20]. These genes are thought to equip cells to take advantage of patches of organic matter through motility and chemosensory behavior, and to grow rapidly under favorable conditions such as during phytoplankton blooms [21–24]. Free-living cells typically have smaller genomes and show fewer metabolic and regulatory capabilities, are characterized by high-affinity nutrient transporters that allow growth in extremely nutrient-poor seawater [25–28], and have lower mRNA inventories per cell [12]. This simplified division of patch-associated and free-living ecological strategies, while also not fully nuanced at the scale of bacterial adaptation and evolution, nonetheless has value in conceptualizing bacterial roles in oceanic flux of carbon [29,30].

Recent genomic and metagenomic analyses suggest that the dichotomy of patch-associated and free-living strategies has evolved multiple times in phylogenetically related lineages in the ocean [31]. These include, for example, the patch-associated *Roseobacter* clade (frequently particle-associated, having large cells and large genomes) versus the free-living SAR11 clade (frequently living singly, having small cells and small genomes) in the Alphaproteobacteria, and the patch-associated Alteromonadales and Vibrionaceae lineages versus the free-living SAR86 clade in the Gammaproteobacteria. An average cultured *Roseobacter* has a genome size of 4.5 million base-pairs (Mbp) and a genomic G+C content of 60% [32], while SAR11 cells have genome sizes between 1.2 and 1.5 Mbp and a genomic G+C content of 29–30% [33]. These considerable differences in genomic traits are similarly found in marine gammaproteobacterial lineages [16,18,28]. At an even finer phylogenetic scale, recent studies highlight the occurrence of several lineages in the *Roseobacter* clade that fit the free-living pattern interspersed in the phylogenetic tree with lineages typical of a patch-associated life history, varying in genome size and G+C content by a factor of two between groups [19,32,34,35]. These divergent ecological strategies are ancient; they have been in some marine Alphaproteobacteria lineages for up to 800 million years [19].

As these life history strategies represent taxa that dominate marine microbial communities and are often responsible for the majority of carbon flux and transformation, elucidating their evolutionary origins is important for understanding how genetic diversity is assembled within and between lineages. A number of studies have proposed that natural selection is the primary evolutionary force driving these ecological diversifications [25,36–38]. Here, we consider that while selection appears to be efficient during their recent evolutionary history, the ecological strategies of marine bacteria originated in the far more ancient oceans in which biological and geochemical contexts were quite different than recent conditions. As described below, increasing evidence from phylogenomic and population genetic analyses suggests that a broader view of the evolutionary mechanisms giving rise to the present-day ecological strategies in marine bacterial lineages is in order, and that the role of nonselective mechanisms may have been significant.

Deciphering ancient ecological diversification of bacterioplankton lineages through phylogenomics

Because ecological strategies of marine bacterioplankton correlate with genome content and size [37], one approach to understanding the evolutionary origin of divergent ecological strategies is to reconstruct the ancestral genomes giving rise to the evolutionarily related but ecologically divergent marine bacterial lineages. This requires a robust phylogeny, and different evolutionary placements may lead to contrasting outcomes. The highly streamlined marine SAR11 clade, for instance, has been placed in multiple locations in the Alphaproteobacteria phylogeny [39–42]. Placement closer to groups with a high G+C content, including roseobacters and other alphaproteobacterial lineages, provides stronger support of genome streamlining, while placement closer to the G+C-poor endosymbiont Rickettsiales lends less support [19]. Therefore, the key step to understanding the ancient diversification of the marine SAR11 and roseobacters is to resolve their evolutionary relationship, which is challenging because they are deeply branching lineages and have distinct base composition (Box 1). One recent study has provided evidence that the clustering of SAR11 and Rickettsiales is a compositional artifact [43].

Based on the composition-corrected Alphaproteobacteria tree, the first SAR11 cell was predicted to be streamlined from its ancestor by a factor of two [43] around 1000–800 million years ago [19], potentially coinciding with an ecological transition from a patch-associated ancestor to a free-living descendent (Figure 1). Further gene loss occurred gradually through the extant SAR11 lineages, although at a reduced rate [43] (Figure 1). By contrast, the early *Roseobacter* population diversified into two ecologically distinct lineages taking contrasting evolutionary trajectories. While the genomes of one were reduced toward a highly streamlined lineage (represented by strain HTCC2255), the genomes of the other underwent a significant expansion with an acceleration of lateral gene transfer predicted as the underlying mechanism [19]. The timing of this genome expansion coincided with the diversification of modern eukaryotic phytoplankton around 250 million years ago [19] (Figure 1).

Being simple is one way to succeed

A possible role of natural selection in reductive genome evolution of marine planktonic lineages [36–38] (Box 2) is supported by evidence from comparative analyses with obligate intracellular bacteria. Although these two