

The trophic tapestry of the sea

Matthew J. Church¹

Department of Oceanography, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822

Oceanic ecosystems are the largest habitats on Earth, and living biomass in these systems is dominated by planktonic microorganisms. Microbial ecologists have long sought to understand the role of environmental selection in shaping the diversity of planktonic microorganisms. The oceans have proven a dauntingly complex arena to conduct such studies. Marine ecosystems are immense and remote and hence chronically undersampled. Moreover, the enormous diversity of planktonic microorganisms challenges our most sophisticated computational capabilities. Only recently, through creative applications of new technologies have oceanographers begun to overcome some of these hurdles. In this issue of PNAS, Lauro et al. (1) use a comparative genome approach to provide insight into how environmental pressures have shaped microorganism lifestyles. The study highlights key differences in the genomes of two oceanic bacteria: *Sphingopyxis alaskensis*, an abundant α -proteobacterium adapted to low-nutrient oceanic environments, and *Photobacterium angustum*, a γ -proteobacterium that grows optimally in nutrient-enriched seawater. By examining the genetic underpinnings that differentiate these microorganisms the study uses the lens of molecular biology to view lifestyle features of ocean microbes.

Background

Tiny ($<2 \mu\text{m}$ in diameter), single-celled plankton are abundant in seawater and comprise some of the largest inventories of biomass on the planet (2). Planktonic communities contain representatives of all three domains of life (Bacteria, Archaea, and Eukarya), and these microorganism assemblages catalyze a dizzying array of ecosystem services vital to the habitability of Earth. The biodiversity of ocean microbes is staggering; a typical liter of seawater contains billions of cells and thousands of genetically distinct individuals. For decades aquatic ecologists have sought to understand how these planktonic communities sustain such diversity (3–5). Ecological theory predicts that at equilibrium multiple species competing for the same resource pools cannot stably coexist (6). However, nucleic acid sequence information derived from ocean plankton indicates these ecosystems are inhabited by some of the most diverse microorganism assemblages on the planet. Our under-

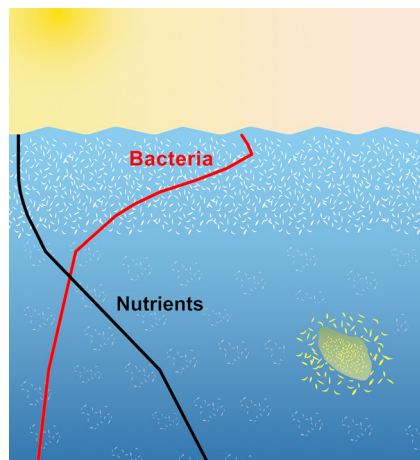


Fig. 1. Representation of the ocean as a microbial habitat; vertical gradients in sunlight are superimposed on depth-dependent changes in inorganic nutrient concentrations (black line). The majority of bacteria (vertical changes in abundance depicted by red line) exist as members of the free-living plankton (shown in white). These abundant oligotrophs are found throughout low-nutrient ocean ecosystems. Other groups of microorganisms (shown in yellow) appear specially adapted to use nutrient-enriched microhabitats enriched in organic nutrients such as those depicted by the colonized organic matter aggregate.

standing of how these communities evolve, what the forces are that collectively work to shape their biodiversity, and how this biodiversity is maintained remain issues at the forefront of microbial ecology.

The article by Lauro et al. (1) serves as an excellent example of how environmental genomics can inform our understanding of the types of selective pressures driving bacterial evolution in nature. Through painstaking comparison of genome features that differentiate *S. alaskensis* from *P. angustum*, Lauro et al. identify 43 lifestyle-distinguishing genetic markers that they use to formulate a model to characterize the trophic lifestyles of microorganisms. The resulting clustering of genome sequence space renders a remarkable tapestry of microbial lifestyles. Time will tell whether this model is sufficiently robust to predict the tapestry's topology at the increasingly finer scales likely required for the wave of metagenomic data emerging from the sea. Nonetheless, the model's reproduction of phenotypic characteristics based on genetic clustering reaffirms that DNA sequence information serves

as a powerful proxy for defining microbial lifestyles.

Location, Location, Location

To the casual observer ocean ecosystems may appear relatively homogenous; in reality, these environments are ripe with habitat heterogeneity. Climate forcing of ocean currents, wind-driven mixing, stratification, and upwelling all can contribute to seascape variability (7). Moreover, numerous biotic processes result in patchy resource distributions. Dead or decaying plankton cells, excrement, and spillage of cellular contents into seawater by grazing or viral lysis all can form transient "hot spots" of nutrients and energy substrates against an otherwise dilute resource pool (8, 9). Singularly or together these processes introduce habitat heterogeneity to the ocean. The rich extant biodiversity of oceanic plankton suggest marine microorganisms exploit this heterogeneity, effectively partitioning oceanic resources into countless ecological niches.

Such habitat complexity can be overlain against a highly structured resource field. For example, strong vertical gradients in sunlight and bioessential nutrients define upper ocean ecosystems, and microorganisms capitalize on the niche space afforded by such gradients (5, 10, 11). In the thin skin of the upper ocean where sunlight is bountiful, phototrophic microorganisms capture light energy for synthesis of organic material. This photosynthetically produced organic matter fuels innumerable cellular metabolisms within the ocean's food web. However, microbial life is notoriously leaky, and a major fraction of this organic matter solubilizes to dissolved constituents in seawater. This diffuse, but reactive, pool of dissolved organic matter (DOM) serves as the primary food source for diverse assemblages of heterotrophic prokaryotes. The vast majority of these heterotrophic microbes exist as free-living members of the plankton, and their utilization of DOM is a major component of the ocean's carbon cycle (12). An important consequence of photosynthetic cellular production is the depletion of bioessential inorganic nutri-

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¹E-mail: mjchurch@hawaii.edu.

ents throughout the well-lit regions of the sea (Fig. 1). Major life-requiring sources of inorganic nutrients (nitrogen, phosphorus, iron) are often found at vanishingly low concentrations in the upper ocean (7). The dilute pool of nutrient resources promotes fierce competition, resulting in tightly linked food web dynamics. However, rapid turnover in planktonic biomass also provides countless opportunities for fine-tuning of cellular processes through genetic diversification.

Finding the Right Lifestyle

The comparative genome approach of Lauro et al. (1) demonstrates that gene content can reflect diversification among microbial trophic strategies. On one end of the microbial lifestyle spectrum lie the oligotrophs, organisms specifically adapted to life in low-nutrient environments; the other end holds the copiotrophs, microbes specialized for life in nutrient-enriched habitats of the sea. Given the high demand for nutrient and energy resources in the ocean it is not altogether surprising that many of the numerically dominant microbes found in seawater are adapted to growth on dilute substrate pools. Isolates of *Pelagibacter ubique*, strains of cyanobacteria belonging to the genus *Prochlorococcus*, and metagenomic sequences obtained from low-nutrient marine systems sampled by the Global Ocean Survey (13) all cluster in genome space among oligotrophs (1). Oligobacteria share several common features: they are extremely small (some $<0.2 \mu\text{m}$ in diameter), grow very slowly (doubling times of >1 day), and possess broad specificity, but high-affinity substrate transport systems (14, 15). Such adaptations enable these organisms to extract a wide spectrum of compound classes from seawater (e.g., small peptides, lipids, simple sugars) even at very low

substrate concentrations (16). Overrepresentation of lipid metabolism pathways and low numbers of rRNA operons also appear characteristic of the oligotrophic lifestyle (1), suggesting oligotrophs value acquisition of energy at the expense of rapid growth (17). The small number and low diversity of substrate receptors reflects life as a generalist, capitalizing on the broad biochemical complexity of ocean DOM pools.

Intriguing patterns have begun to emerge from genome and metagenome

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sequences of marine microorganisms that provide clues to many of the selective pressures imposed on life in the sea. Notably, many of the oceanic oligotrophs appear to have reduced their gene content to conserve energy and nutrient demands associated with gene replication, regulation, and repair (14, 18, 19). However, it remains unclear how genome streamlining impacts the breadth of ecological space these organisms occupy. The loss of specific biochemical pathways could result in finer and finer partitioning of ocean niches, with associated loss of functional diversity. Alternatively, genome streamlining could reinforce those genetic pathways that enable broader functional capacity, for example through mixotrophy, while reducing redundant and nonessential genes. Evidence for fine-scale partitioning of resources can be observed in the

genome sequences of *Prochlorococcus* and SAR11 bacterial lineages (10). Ecotypic variation among these organisms appears to permit very closely related relatives to coexist in distinct, non-competitive ecological space (10, 11).

In contrast to the majority oligotrophs, copiotrophic microorganisms capitalize on the variable resource-enriched habitats in the sea. Copiotrophs are large ($>1 \mu\text{m}$ in diameter), grow rapidly (doubling times of hours), carry relatively large genomes, and have evolved complex systems for sensing and responding to their environment (1). Relaxed selective pressure to conserve gene content appears to have permitted these organisms to evolve numerous and diverse, highly specialized substrate transport systems. Intriguingly, metagenomic analyses of deep-sea microplankton suggest such characteristics may typify microbial lifestyles in the cold, energy-starved habitats that dominate the ocean's interior (20).

Aided by studies such as this one by Lauro et al. (1), ecologists are becoming empowered with tools to assimilate the torrent of genome and metagenome sequences emerging from the ocean. Several striking patterns have already begun to emerge: (i) the ocean harbors functionally diverse microorganisms; (ii) gene content reflects strong environmental selective pressures; (iii) numerically dominant ocean microorganisms minimize their genome size, with concomitant biogeochemical and ecological consequences; and (iv) the complex milieu of ocean resources favors flexible metabolic capabilities. Analyses such as those reported by Lauro et al. are indispensable for testing hypotheses about the strategies microorganisms use to acquire resources and how such strategies reflect selective pressures that collectively shape plankton biodiversity.

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