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REVIEW

Microbial Ecology of Ocean Biogeochemistry: A Community Perspective

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The oceans harbor a tremendous diversity of marine microbes. Different functional groups of bacteria, archaea, and protists arise from this diversity to dominate various habitats and drive globally important biogeochemical cycles. Explanations for the distribution of microbial taxa and their associated activity often focus on resource availability and abiotic conditions. However, the continual reshaping of communities by mortality, allelopathy, symbiosis, and other processes shows that community interactions exert strong selective pressure on marine microbes. Deeper exploration of microbial interactions is now possible via molecular prospecting and taxon-specific experimental approaches. A holistic outlook that encompasses the full array of selective pressures on individuals will help elucidate the maintenance of microbial diversity and the regulation of biogeochemical reactions by planktonic communities.

When we try to pick out anything by itself, we find it hitched to everything else in the universe.

John Muir (1911)

Marine microbes are fundamental regulators of biogeochemical cycles [see the accompanying review by Falkowski *et al.* (1)]. While acquiring resources for metabolism and growth, archaea, bacteria, and protists transform C-, N-, P- and S-containing compounds in ways that affect their availability for biological production and their influence on Earth's climate. Questions about the relationships between plankton ecology and these transformations are at the heart of much ocean research and have existed since the investigations of Brandt, Lohmann, and others a century ago [as described in (2)]. Yet, despite a burgeoning toolbox of methods, most research into ocean biogeochemistry and associated microbial ecology is still framed in terms of "bottom-up" considerations (i.e., how do resources and abiotic conditions drive the distribution and function of microbes?). Ecological considerations and recent genomic findings demonstrate that a broader view is necessary. Agents of mortality, including grazers and lytic viruses, must exert strong selective pressure on populations of marine microbes. Additional interactions such as allelopathy and symbiosis also influence community structure and function. Fur-

ther, these processes interact with resource availability in numerous ways so that separate bottom-up versus "top-down" approaches to studying these ecosystems are of limited conceptual or experimental use. Marine microbes are truly hitched to everything else in the ocean universe. Thus, a community perspective is essential for understanding the distribution and function of microorganisms in Earth's oceans. By applying the cornucopia of new ocean research methods to questions of whole-community structure and function, we will gain insights into the regulation of biogeochemical cycling. A community perspective will also aid our understanding of the sources and functions of the vast genomic diversity housed in the oceans' microbes.

The Broader View: Ecological Considerations

Owing to physical and chemical constraints, nearly all primary and most secondary production in the oceans is performed by microbes. Little energy storage or accumulation of structural material is possible in a unicell; hence, in striking contrast to terrestrial ecosystems, almost no marine production accumulates as biomass. Except during bloom events, nearly all marine microbial production "turns over" in days to weeks through various mortality processes (3). In ocean regions remote from land, microbial mortality is mainly due to grazing by protists (4, 5); in other areas, disease, viral lysis, grazing by larger zooplankton, and perhaps microbial senescence can be substantial (6, 7). Cumulative mortality in approximate equivalence with growth leads to a

continual reshaping of the community at a fundamental level and a situation in which avoidance of mortality is tantamount to resource-based growth as a selective pressure on individual microbes (Fig. 1). From these considerations, one would predict that adaptations reducing mortality (e.g., escape behavior, defenses, resistance to infection, camouflage) must constitute a substantial part of the genotypic and phenotypic repertoire of marine microbes.

The Broader View: Genomic Considerations

Sequencing of cultured marine microbes and metagenomic surveys of natural environments are revealing genes related to community interactions. Using shotgun sequencing of fosmid clone termini, DeLong and co-workers (8) assessed the depth distribution of microbial genes in the North Pacific subtropical gyre. Deep-water sequences were enriched in genes for antibiotic synthesis, which are hypothesized to play a role in structuring particle-associated communities. The cyanobacterium *Synechococcus* is a major prokaryotic contributor to ocean primary production, and genomes of several isolates have been sequenced. Both Sargasso Sea and California Current isolates contain several different polysaccharide biosynthesis genes; the authors speculate that these allow changes in cell-surface characteristics, providing camouflage from or resistance to phage or predator attack (9). *Prochlorococcus* is another important genus of photosynthetic prokaryotes, one in which the links between genetics and ecophysiology are particularly well characterized. A survey of *Prochlorococcus* "ecotypes" in the Atlantic Ocean found that environmental gradients in light, temperature, and nutrient availability explained considerably less than half of the variability in spatial distribution for all but one ecotype (10). Unexplained aspects of distribution hinted at important but poorly characterized differences in competitive ability and susceptibility to grazing and viral lysis.

In the following sections, I present examples of how community processes can drive biogeochemical cycling of Si, C, and N, as well as the climatically important gas dimethyl sulfide (DMS). I then outline two research areas in which further investigation promises to elucidate mechanistic links between community ecology and biogeochemistry.

Paradigms Lost

Current paradigms, largely revolving around resource acquisition and abiotic conditions, are often insufficient to explain major patterns of functional group dominance in the sea [see the accompanying

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review by Green *et al.* (11)]. For example, in the absence of chronic iron limitation, the spring primary production increase in temperate and high-latitude seas is largely manifested as blooms of diatoms. There is little evidence from experimental laboratory-based work that diatoms have consistently higher growth rates than photosynthetic flagellates under the cold, high-nutrient conditions of early spring (12), nor are they consistently more tolerant of turbulence (13). Superior nutrient uptake and storage capacity have also been invoked as determinants of diatom success in the spring bloom niche (14). However, during the inception and increase of the spring bloom, nutrient concentrations far surpass those limiting to uptake or growth. Thus, diatom blooms cannot be explained solely as the outcome of superior environmental tolerance or “simple” resource competition among photosynthetic protists (although blooms are often modeled this way). We do know that the diatom species that dominate blooms experience less grazing mortality than do co-occurring species (15, 16). The reasons are poorly understood, and the existing hypotheses are not yet strongly substantiated. One possibility is that blooming diatoms have grazing-resistant morphologies; another is that they produce defensive chemicals (17, 18). There may also be a mismatch between temperature optima for growth of diatoms relative to growth of their potential predators (12). Allelopathic inhibition of competitors by diatoms has been hypothesized as a contributing factor (19). The need for a mechanistic and hence a predictive understanding of diatom blooms is a priority because of their substantial biogeochemical and ecological consequences, including their role in ocean C and Si cycling, as well as their importance in food webs supporting large benthic and pelagic animals.

For other major biogeochemical processes, including global rates of N₂ fixation and denitrification, we have very little knowledge of how communities might regulate the abundance and biogeochemical transformation rates of the relevant microbes. Denitrifiers inhabit low-oxygen zones in the ocean’s interior. Observations from the Black Sea and European fjords show that protistan grazers of bacteria, such as ciliates and heterotrophic flagellates, also inhabit low-oxygen waters. We also know that microaerobic and anaerobic protists can form consortia with bacteria (20, 21). However, the role of these predatory and symbiotic relationships in regulating the abundance and activity of denitrifiers is largely unknown.

Volatile Communities

Biogeochemical processes involving ocean-atmosphere S exchange are strongly dependent on community composition and function. The volatile compound DMS is produced by both prokaryotic and eukaryotic marine microbes through enzymatic cleavage of dimethyl sulfoniopropionate (DMSP). Fluxes of DMS from the ocean to the atmosphere directly influence Earth’s climate,

because DMS molecules can act as cloud condensation nuclei, increasing cloud cover over the ocean. DMS fluxes have been remarkably difficult to predict from environmental variables alone, because community interactions play a role in nearly all aspects of DMS production. In addition to an abundance of DMSP-containing microbes, large DMS fluxes can only be generated if there are high rates of processes promoting DMSP cleavage combined with low rates of bacterial DMSP demethylation; the latter converts the molecule to products other than DMS.

Communities determine DMS fluxes by several processes (Fig. 2), including preferential grazing on prey that contain low levels of DMSP or lyase. Extensive interstrain variability in these properties has been found (22, 23), which may be related to differential allocation of cellular resources to resource acquisition, defense, signaling, and other survival needs. Although poorly understood, preferential grazing could also select for either demethylating or DMS-producing bacteria. Released DMSP is a chemical signal that can reduce grazing, potentially promoting blooms, and viral lysis can cause release of DMS from

host cells (24, 25). Although still incompletely understood, this is one of the most thoroughly investigated microbial systems of those involved in a major biogeochemical transformation. Data collected to date demonstrate that a knowledge of community processes will be essential for a mechanistic and predictive understanding of DMS fluxes. There is little doubt that community ecology will prove equally important for understanding other biogeochemical cycles.

Cell Surfaces: A Focus of Selective Pressures

The role of the cell surface in simultaneously mediating resource acquisition and defending or camouflaging the cell against agents of mortality is poorly understood for free-living microorganisms. Features of pathogen cell surfaces are better known and might offer some insights into universal mechanisms. Every resource acquired by a microbe involves some aspect of the cell surface, including receptors, transporters, and cell surface-associated enzymes. Given the high ion specificity of transmembrane pumps and channels (26), the amount of cell surface area for such structures is, in itself, a potentially limiting resource. How, then,

does the constellation of resource uptake requirements affect the landscape of the individual cell surface? It is this landscape that many grazers perceive and respond to during feeding. We know that alteration of prey cell surfaces by lectin binding or coating with various organics affects the feeding rates of flagellates (27, 28). Marine *Synechococcus* genomes contain multiple polysaccharide synthesis genes (9, 29); analogous to the antigenic variation of pathogens to avoid host-mediated phagocytosis (30), these genes may allow cell-surface changes in response to grazing pressure. Host specificity of viral infection may also depend on specific cell-surface oligosaccharides (31). These and other observations indicate that mortality operates in part through recognition (or lack thereof) of cell-surface properties, which in turn may be influenced by resource acquisition. A research focus on microbial cell surfaces is likely to elucidate how these organisms successfully adapt to the suite of selective pressures they face.

Allelopathy

Allelopathic interactions, in which microbes actively inhibit their competitors, are poorly understood for marine microbial communities. Allelopathy has long been invoked as a mechanism promoting blooms, although distinguishing inhibition from resource competition can be experi-

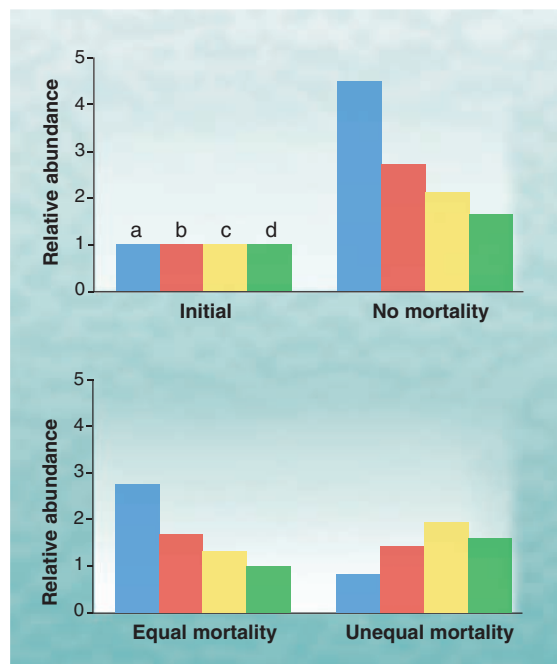


Fig. 1. Hypothetical microbial community with four major taxonomic groups (indicated by the lowercase letters and associated colors), present initially (**top left**) at equal abundances. With no mortality (**top right**), the fastest-growing taxon (“a”) dominates the community after 5 days of growth. (**Bottom left**) Equal rates of mortality on all taxa yield reduced abundances—hence, potentially reduced biogeochemical activity—due to generalized removal of microbes while they are growing. (**Bottom right**) Unequal rates of mortality lead to shifts in species dominance and fundamental restructuring of the community. In this case, the two slowest-growing taxa (“c” and “d”) dominate after 5 days. Growth rates [k (days⁻¹): a = 0.30, b = 0.20, c = 0.15, d = 0.10; mortality rates [g (days⁻¹): a = 0.35, b = 0.13, c = 0.02, d = 0.01; abundance (A) at 5 days = $A_{\text{initial}}e^{(k-g)5}$. Data taken from (38).

mentally challenging (19). Production of lytic agents has been demonstrated for both prokaryotic and eukaryotic marine microbes and interpreted as a mechanism for simultaneously reducing competition or predation and obtaining dissolved organic nutrients [i.e., “kill and eat your predator” (32)]. Allelopathy may be more widespread than anticipated and may encompass tactics including the release of reactive oxygen species and antibiotics (33, 34). Sublethal allelopathy could be particularly effective in shaping community structure and function by altering growth and loss rates. For example, microbes are known to release nontoxic signaling compounds that alter the behavior of conspecifics, competitors, and/or predators (35, 36). The release of siderophores that bind up iron and other trace nutrients in a form unavailable to competitors could also be seen as a form of allelopathic inhibition (37).

Research Prospects

Marine microbes drive globally important biogeochemical cycles, and we are in the midst of an explosion of data concerning the genomic diversity that underlies this microbial activity. At the same time, there is growing evidence that community interactions—including various sources of mortality, allelopathy, symbiosis, and others—exert strong selective pressure on marine microbes. Marine microbial distribution and diversity cannot be understood without considering the entire suite of selective pressures on individual microbes. By the same token, study of community processes is essential for an understanding of ecosystem function, including important biogeochemical transformations. Progress will require that genomic and other surveys be conducted and interpreted with an eye for molecules that underlie not only environmental tolerance and resource acquisition but also cell-cell and population interactions of various types. New molecular techniques are beginning to be coupled with community-level experimentation and hypothesis testing; there is ample scope for more research of this type, especially that which targets key functional groups of marine microbes. Implementing these suggestions will require collaborations between scientists with historically divergent views of marine microbes, including community ecologists, geneticists, and oceanographers. The resulting holistic approach to how we conceptualize, observe, and experiment with microbial communities will be required to achieve a synthesis of microbial ecology and biogeochemistry.

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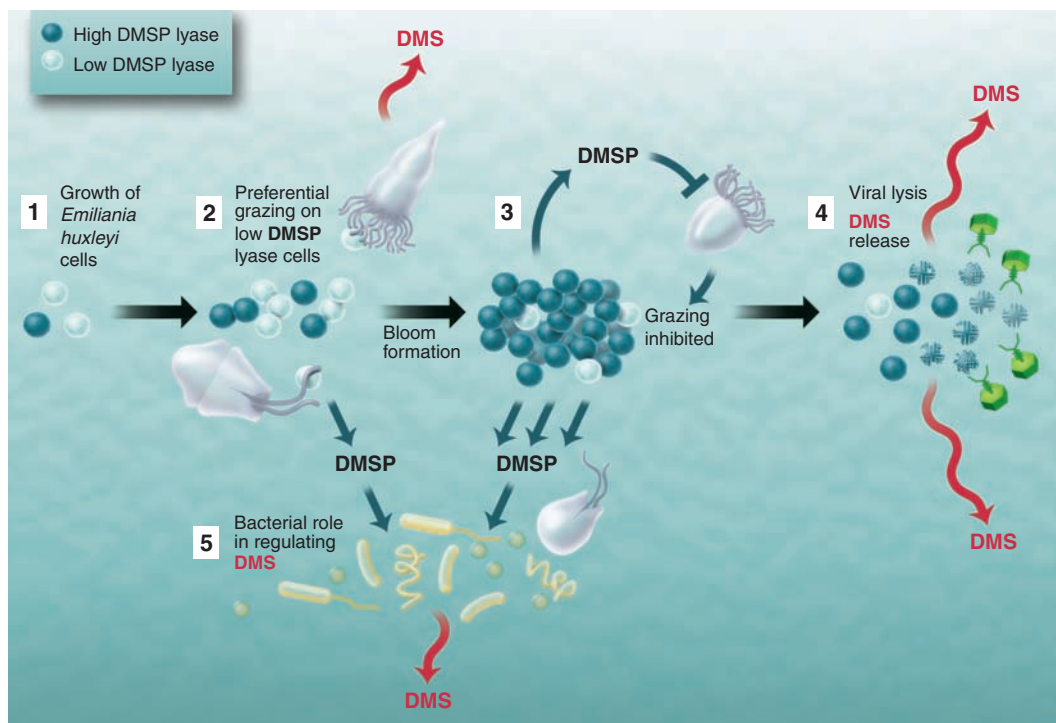


Fig. 2. Microbial community processes potentially regulating production of the climate-active gas DMS. (1) Environmental conditions promote growth of DMSP-containing *Emiliana huxleyi* cells. (2) Protist grazers respond by increasing abundance and grazing activity; grazing results in the release of DMS (39). Grazing deterrence by *E. huxleyi* cells with high DMSP lyase activity (shaded cells) allows an *E. huxleyi* bloom to form (22) and limits DMS output. (3) High concentrations of *E. huxleyi* cells are associated with high levels of DMSP release (40); dissolved DMSP inhibits protist grazing (25), promoting further bloom formation. (4) Viral lysis of cells in an aging bloom promotes DMS release (24). (5) DMSP is metabolized by bacteria including *Roseobacter*; propensity for the bacterial community to produce DMS versus demethylate DMSP is determined by community composition (41), shaped in part by differential mortality (e.g., due to nanoflagellate grazing selectivity) and competition for resources.

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