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Connections between bacteria and organic matter in aquatic ecosystems: Linking microscale ecology to global carbon cycling.

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Abstract

The primary aim of this chapter is to synthesize research relevant to the microscale interactions between bacteria and organic matter in freshwater and marine pelagic environments. Heterotrophic bacterioplankton provide an important ecosystem service by remineralizing dissolved and particulate organic material in aquatic ecosystems. However, both heterotrophs and organic matter are generally treated as "black boxes" in models of pelagic ecosystem metabolism owing to our poor understanding of their diversity and spatial/ temporal dynamics. Such models necessarily mask a complex set of interactions because of the difficulty in observing and quantifying this "microscale" ecology. Bacteria exhibit tremendous phylogenetic and metabolic diversity, and we now understand that organic matter comprises a heterogeneous matrix of particles, gels, polymeric matrices, colloids, and dissolved macromolecules. The physicochemical organic matter continuum is dynamic and patchy; which translates to a complex array of ecological microenvironments for bacterioplankton. The phylogenetic and functional diversity of bacteria is thus intertwined with the chemical and physical complexity of their organic matter resources. Characterizing bacterial–organic matter interactions at the appropriate temporal and spatial scales will fundamentally enhance our knowledge of pelagic ecosystems.

Introduction

In pelagic, aquatic ecosystems heterotrophic prokaryotes process roughly 50% of primary production (Cole et al. 1988) and can account for more than half of the microbial community respiration (Biddanda et al. 2001). Despite their relevance to global biogeochemical cycling, we know very little about the specific interaction between diverse bacterial populations and the organic matter they metabolize. Limnologists and oceanographers have historically treated pelagic environments as homogeneous at scales smaller than meters, yet small resource-rich patches could allow more efficient foraging and explain the high productivity of nutrient-depleted waters (McCarthy and Goldman 1979; Azam and Hodson 1981; Alldredge and Cohen 1987; Blackburn et al. 1998). According to our current understanding of the complex interactions between bacteria and organic matter, the functional and phylogenetic diversity of the bacterioplankton plays a central role in regulating metabolism in pelagic ecosystems. Here, we discuss how the physical and chemical heterogeneity of aquatic organic matter generates bacterial microhabitats, and we provide an overview of how bacteria in turn remineralize organic material. We then discuss the microscale ecology of bacterioplankton, focusing on how microenvironments shape bacterial productivity and diversity (Fig. 1). Finally, we connect these microscale interactions with ecosystem-scale impacts on bacterial metabolism of pelagic organic matter.

Characterization and dynamics of organic matter

Organic matter is the primary substrate supporting bacterial metabolism in pelagic habitats and recycles nutrients through the microbial loop. Furthermore, this material pro-

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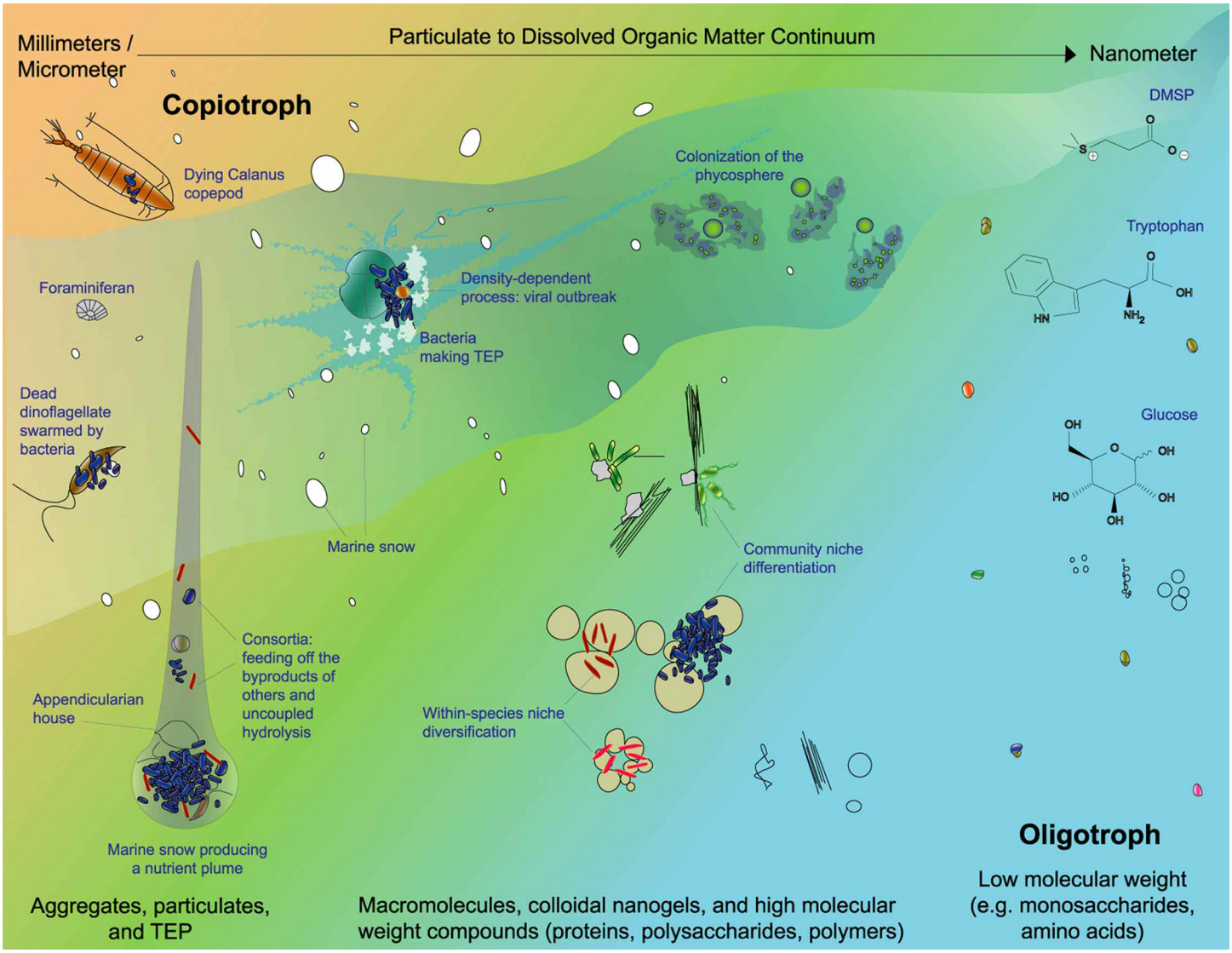

Fig. 1. Artistic rendition of bacterial microscale interactions with organic matter.

vides a physical surface that structures aquatic prokaryotic and eukaryotic communities. Historically, the study of organic matter in aquatic systems was a largely technique-driven science, which has now evolved to emphasize the biochemical and optical characterization of compounds and identification of their origins. Frequently, organic matter is differentiated by size, origin, reactivity, or chemical composition. We present a brief summary of approaches to classifying and characterizing pelagic organic matter.

Size continuum of organic matter—Organic matter has been traditionally classified by size (Fig. 2): filters with a pore size ranging from 0.1 to 1 µm are used to separate particulate organic matter (POM), which is retained on the filter from the dissolved organic material (DOM) that passes through the pores. Tangential flow ultrafiltration is used to further separate submicron organic matter into two (or more) subclasses, low molecular weight (LMW-DOM) and high molecular weight (HMW-DOM), which are typically differentiated at the 1-kD size cutoff. Although this classification scheme has ecological implications (e.g., organics in the particulate phase tend to sink in the water column, whereas dissolved compounds remain suspended), organic matter subdivisions are largely operational. In fact, organic matter should be seen as a size continuum of truly dissolved, colloidal, and particulate phases that are dynamically interrelated and interconverting (Sharp 1973; Amon and Benner 1994; Verdugo et al. 2004). Keeping in mind the concept of the size continuum of organic matter, we briefly present the main characteristics and properties of each size class (Fig. 2).

The smallest size class of organic matter is the LMW-DOM, formed by truly dissolved compounds with a molecular weight of less than 1 kDa. LMW-DOM is the major fraction of

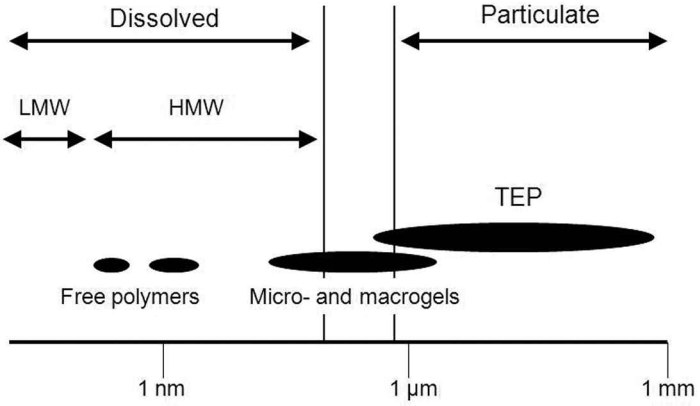

Fig. 2. Size continuum of pelagic organic matter (redrawn with permission from Verdugo et al. 2004)

the bulk DOM (approximately 65% to 80%) in the open ocean (Ogawa and Tanoue 2003) and is more variable in coastal waters and freshwater, ranging from 50% to 90% (Sanudo-Wilhelmy and Taylor 1999; Repeta et al. 2002; Gobler and Sanudo-Wilhelmy 2003). In the open ocean LMW-DOM is generally refractory, containing the remains of large molecules, whereas in freshwater, LMW-DOM is generally composed of labile sugars and amino acids (Coffin 1989; Covert and Moran 2001). LMW-DOM is the least characterized fraction of organic matter in the ocean because of the difficulty of the methods for concentrating and desalting this fraction. Colloids or HMW-DOM span the boundary between truly dissolved compounds and particles (Wells 1998), and range in size between about 0.1 and 1 µm in diameter, with a molecular weight greater than 1 kDa. The term "colloid" refers to the "sticky" surface properties of these compounds, which makes them prone to aggregate. These compounds are large enough to acquire an interface, with distinct internal physicochemical properties compared to the surrounding water. Colloids or HMW-DOM are considered biolabile compounds that support heterotrophic production (Amon and Benner 1994; Santschi et al. 1995). However, in terrestrially influenced systems HMW-DOM includes refractory compounds, such as humics (Covert and Moran 2001; Meyer et al. 1987).

Organic particles and aggregates range in size from <1 µm to >10 cm. Aggregates are formed through the collision and subsequent adhesion of smaller particles and dissipate due to consumption or turbulence; large aggregates can also include enhanced levels of inorganics and are frequently colonized by bacteria and higher trophic level organisms. We distinguish two size classes of organic aggregates: macroscopic aggregates (>500 µm) and microscopic aggregates (1 to 500 µm). Macroaggregates, also known as marine, lake, or river snow due to their resemblance to snowflakes (Silver et al. 1978), are the best-studied size class of organic matter for bacterial colonization (Simon et al. 2002). They have an average abundance ranging from 1 to 100 L^{-1} and dominate the sinking flux of particulate organic matter, falling between 5 and 200 m d^{-1} (Alldredge and Gotschalk 1988; Alldredge and Gotschalk 1989; Turner 2002). The composition of these large aggregates is highly variable, with discernable remnants of larvacean houses, phytoplankton, fecal pellets, and miscellaneous detritus (Turner 2002). Microaggregates or small aggregates can be similar to macroaggregates in composition. However, certain classes of microaggregates have distinct properties and are identified by staining with dyes.

The best-studied class of aggregates, spanning the size range of micro- to macroaggregates, is the transparent exopolymer particles (TEP) that can be visualised by staining with Alcian Blue. TEP are sticky particles formed by the spontaneous polymerization of acidic polysaccharides produced by phytoplankton (Passow and Alldredge 1994; Alldredge et al. 1993; Passow 2000). This stickiness allows TEP to act as the interstitial matrix that binds larger macroaggregates, which sediment through the water column. However, TEP can form low-density particles that ascend in the water column and accumulate at the surface (Azetsu-Scott and Passow 2004; Mari 2008). Lesser known classes of microaggregates are Coomassie-stained particles (Long and Azam 1996; Berman and Viner-Mozzini 2001), which are enriched in proteins and DAPI yellow particles (Mostajir et al. 1995) which are produced from plankton detritus in fecal micropellets. A recently described class of polysaccharide-rich, transparent particles are the filter-fluorescing particles, which are revealed by simultaneous staining with Alcian blue and SYBER Gold (Samo et al. 2008).

Marine gels are spatially organized and stabilized by chemical (covalent) and physical cross-links (e.g., electrostatic interactions, hydrogen bonding, hydrophobic/hydrophilic interactions, van der Waals forces). The aggregation of organic and inorganic particles is dependent on their density (related to the probability of collision), and physical processes such as turbulence or laminar shear. On the other hand, various processes transform large particles into smaller sizes, including mechanical disruption, consumption by detritivores, and microbial decomposition or gel dispersion (Mari and Kiorboe 1996; Orellana and Verdugo 2003).

Other methods of organic matter classification—The size continuum of organic matter is linked to a continuum of reactivity, from refractory material with turnover times from centuries to millennia (Williams and Druffel 1987), to very labile material that is turned over within minutes (Cherrier et al. 1996). According to this criterion, DOM is classified into at least three fractions: refractory material comprising >90% of total DOM (Ogawa and Tanoue 2003); the biologically labile fraction of DOM with rapid turnover rates (from minutes to days), which results in nanomolar concentrations in the open ocean (Keil and Kirchman 1999; Skoog et al. 1999); and the semilabile fraction of DOM, which is reactive over months to years and accumulates in surface waters (Carlson and Ducklow 1995; Cherrier et al. 1996). The chemical composition of organic matter is likely a primary determinant of its reactivity.

Although in several studies investigators have sought to characterize organic matter by its elemental compositions, e.g., C-to-N ratios, (Ogawa and Tanoue 2003), most DOM remains chemically uncharacterized (Williams and Druffel 1987; Hedges et al. 2000; Kam et al. 2006). Indeed, the contribution of the major identifiable chemical constituents, i.e., amino acids, carbohydrates, and lipids, may not exceed 30% of bulk DOM. In contrast, 80% of particulate organic matter is formed of these three constituents.

The properties of organic matter are linked to its source material. In pelagic systems, organics are derived from two distinct sources: local primary production (autochthonous sources) and allochthonous sources, including external inputs from surrounding terrestrial ecosystems, the deep ocean by upwelling and convective processes, and dust deposition. A significant correlation between chlorophyll and prokaryotic cell abundance among diverse ecosystems suggests that bacterial metabolism may be coupled to photosynthetically fixed carbon (Cole et al. 1988; Gasol and Duarte 2000). Yet, lakes and certain regions of the oceans are often net heterotrophic (Duarte and Agusti 1998; Williams et al. 2004), suggesting either that primary production and allochthonous sources simultaneously supply bacterial carbon demand or that primary and secondary production are spatially or temporally uncoupled. Terrestrial material supplied to lakes is generally thought to be recalcitrant; however, there is evidence of significant consumption of terrestrial-derived carbon (Pace et al. 2004). In contrast, in the ocean terrigenous DOM appears to comprise only a small fraction (0.7%-2.4%) of the total DOM, but its residence time (21-132 years) is much shorter than that of marine DOM (Opsahl and Benner 1997). Riverine discharge of organic matter is an important source of nutrients to the coastal ocean, where 25% of marine primary production occurs. This material is oxidized by photochemical and bacterial processes in a timescale from months to years

Dissolved organic matter has also been characterized and classified on the basis of its optical properties. The portion of the DOM that absorbs solar radiation is known as "gelbstoff," "gilvin," "yellow matter," or, more widely accepted, "chromophoric dissolved organic matter" (CDOM) (Nelson and Siegel 2002). The ratio of CDOM to DOC away from the coast is low (1%, [Hayase and Shinozuka 1995]), but in certain areas CDOM can represent a significant fraction of DOM (e.g., up to 70% in the Wadden Sea [Laane and Koole 1982]). This CDOM is formed from terrestrial humic and fulvic acids, although in areas far from terrestrial influence, formation can occur through polymerization of phytoplankton-derived fatty acids, sugars, amino acids, and other small molecules (Harvey et al. 1983) and may be catalyzed by ultraviolet (UV) radiation (Harvey et al. 1983) or mediated by microbial transformations (Nelson et al. 1998; Rochelle-Newall and Fisher 2002). Although there have been attempts to chemically characterize CDOM (Repeta et al. 2002), this material is primarily classified and quantified based on optical properties.

As well as absorbing light, CDOM also fluoresces when excited by UV and blue light (fluorescent dissolved organic matter, FDOM). The two major FDOM components are the humic and protein fractions (Mopper and Schultz 1993; Coble 1996). Fluorescence excitation–emission matrices (EEMs) (Coble et al. 1990; Coble 1996) provide information on the number and type of fluorophores present in DOM and their relative intensity, allowing some decomposition of the heterogeneity of the CDOM pool. EEM spectroscopy has been successfully applied to differentiate between CDOM of terrestrial and pelagic origin (Coble 1996; Mcknight et al. 2001). EEMs have also been shown to provide information on changes in CDOM resulting from physical forces, biological transformations, or photobleaching that occur in the environment (Murphy et al. 2008; Mladenov et al. 2009; Nelson et al. 2009).

Bacteria interactions within the size continuum of organic matter—Organic matter pools interconvert through biological and physical processes. An increase in size is mediated by annealing, aggregation, or biological uptake, while matter decreases in size through physical fragmentation or biological dissolution. Because the metabolism of organic matter by marine microbes has been previously reviewed, e.g., (Azam et al. 1983), we focus on other organic matter transformations.

Although heterotrophic bacterioplankton are thought of as organic matter sinks (Azam et al. 1983), they can also produce specific pools of organic carbon and nitrogen (Kaiser and Benner 2008; Tremblay and Benner 2009). For example, microbial metabolism will consume the labile fraction of organic matter, enhancing the relative abundance of refractory materials (Brophy and Carlson 1989; Ogawa et al. 2001; Kawasaki and Benner 2006; Kaiser and Benner 2008). This bacterial generation of refractory DOM has recently been dubbed the "microbial carbon pump" (Jiao 2006). Moreover bacteria can have a strong influence on DOM optical quality (Nelson et al. 2004; Yamashita and Tanoue 2008) through production of refractory fluorescent organic matter by DOM oxidation (Yamashita and Tanoue 2008). Bacteria also produce chromophoric organic matter in lakes; Mladenov et al. (2008) have suggested that bacteria drive CDOM distributions in high alpine lakes. The quality and persistence of CDOM generated by bacteria are dependent on factors such as the availability of inorganic nutrients (Biers et al. 2007) or previous photoalterations of DOM (Ortega-Retuerta et al. 2009).

In addition to modifying the optical properties and lability of dissolved organic material, bacterioplankton are now understood to play a key role in the generation and modification of TEP and marine gels. Bacteria have the potential to generate TEP, releasing polysaccharides and TEP as free exopolymers or as capsular material (up to 25% of the respired carbon [Stoderegger and Herndl 1998]). TEP production is modulated by environmental variables such as turbulence (Stoderegger and Herndl 1999; Passow 2002), the presence of phytoplankton (Grossart et al. 2006), and nutrient availability. Finally, bacteria can influence the assembly and aggregation

mechanisms of marine gels by releasing amphiphilic compounds that could undergo the self-assembly of DOM networks by hydrophobic interactions (Ding et al. 2008).

Resource heterogeneity and microscale bacterial ecology

Microscale features containing organic and inorganic nutrients may be hotspots of bacterial activity, allowing bursts of uptake and reproduction that drive much of the total bacterial productivity in a low-bulk nutrient background (Azam 1998). We focus on the implications of organic matter patchiness at microscopic scales (micrometers to millimeters), which is the same scale at which bacteria sense and respond to their environment (Azam 1998; Azam and Malfatti 2007; Seymour et al. 2009). These nutrient patches are likely preferentially exploited by copiotrophs rather than oligotrophs, which efficiently use low levels of background nutrients (Poindexter 1981; Polz et al. 2006). Aquatic microenvironments may exert fundamental controls on the diversity, dynamics, abundance, and gene flow in patch-adapted bacterial populations as well as influencing the rate of organic matter remineralization in aquatic environments. Understanding micro- and macroscale coupling of bacteria with organic matter is important in linking the ecology of heterotrophic microbes with their role in aquatic biogeochemistry.

Here, we explore two strategies bacteria use to exploit aquatic microenvironments: physical colonization/attachment to a substrate, and transient clustering mediated by chemotaxis and motility. However, these adaptive strategies are interdependent processes. For example, bacteria attach to and colonize marine snow particles (Jackson 1989), and degradation of the marine snow by these attached bacteria produces a wake of nutrients that is preferentially used by motile bacteria (Moeseneder and Herndl 1995). Although colonization and clustering are distinct strategies, they are intertwined in the use of transient resources.

Bacteria interact with all of the types of organic matter portrayed in Figs. 1 and 2, from attachment to large aggregates to chemotaxis toward and uptake of dissolved material. Because attached bacteria can be physically separated from free living cells by filtration, particles are one of the best-studied aquatic microenvironments. Research has focused on marine snow due to its potential for deep-sea carbon export (Alldredge and Silver 1988; Turner 2002). However, microaggregates are orders of magnitude more abundant than marine snow, and particles vary in composition and lability. Multiple lines of evidence indicate that particles are an important habitat for bacteria: a significant fraction of particles are colonized (Long and Azam 1996), bacterial density in particles is higher than in seawater (Caron et al. 1982), and up to half of the total prokaryotic cells in the water column can be particle attached (Crump et al. 1998). Moreover, particle-associated bacteria appear to be more metabolically active, with higher per cell levels of hydrolytic enzymes (Karner and Herndl 1992; Smith et al. 1992), and higher per cell biomass production compared to free-living bacteria (Crump et al. 1998). With high cell densities, chemical signaling between cells becomes more efficient, and bacterial isolates from particles are more likely to produce antagonistic substances that inhibit other bacteria from colonizing particles (Long and Azam 2001a; Long et al. 2003; Long et al. 2005). These observations suggest that particles provide a significant nutrient resource for bacteria and that attached bacteria may be more metabolically active than their planktonic counterparts (Alldredge 1979; Hebel et al. 1986; Long and Azam 1996).

Although bacterial particle attachment is easier to observe, transient clustering in resource-rich patches may be responsible for a large fraction of microbial activity. Aquatic bacteria are observed to cluster in response to features such as lysed cells and algae (Barbara and Mitchell 2003; Blackburn et al. 1998). Additionally, their motility and chemotaxis parameters are well matched to the spatial and temporal scales of environmental nutrient patches (Stocker et al. 2008), allowing bacteria to position themselves in response to chemical gradients. Transient sources of patches include excretion events and sloppy feeding by metazoans, as well as DOM released from particles. Bacterial use of patchy conditions by rapid uptake of nutrients is supported by evidence of multiphasic uptake kinetics of D-glucose and amino acids (Azam and Hodson 1981; Fuhrman and Ferguson 1986; Ayo et al. 2001), suggesting that either individual bacteria have multiple transport systems or taxa are optimized for different substrate concentrations. In either case, bacterial communities can use variable nutrient levels and increase uptake under pulsed resource conditions.

Bacteria that are able to assimilate high concentrations of substrates can enhance their exposure to organic matter pulses by clustering in nutrient rich microenvironments. In a mesocosm experiment, artificial mixing of seawater decreased bacterial metabolism, which suggests that patchiness enhances productivity over an even distribution of the same total nutrients (Moeseneder and Herndl 1995). The idea of bacterial clustering is supported by patchy counts of prokaryotic cell numbers in small-scale samples (Daubin et al. 2003), and clustering can be artificially generated by adding a nutrient source (Blackburn et al. 1998; Krembs et al. 1998a; Krembs et al. 1998b).

Additionally, there is little known about the compounds that drive aggregation in aquatic systems, because bacterial clustering has been observed only in relation to complex materials (e.g., cell lysates, algal exudates). At the same time genomic and metagenomic studies have revealed large numbers of chemoreceptors in environmental bacteria (DeLong et al. 2006; Lauro et al. 2009), suggesting that bacterioplankton sense and respond to their chemical environment through taxis. The study of bacterial aggregation is further complicated by the fact that clustering and motility may be temporally variable and not energetically advantageous below a threshold of organic matter patchiness. However, a single daily encounter of patch-adapted bacteria with a marine-snow particle is predicted to supply sufficient nutrients to maintain

bacterial activity (Kiørboe et al. 2002). Our conception of aquatic bacterial chemotaxis is based on studies of the enteric *Escherichia coli*, with its characteristic "run and tumble" random walk. Yet the efficiency of chemotaxis in a turbulent environment is predicted to be enhanced for marine bacteria by fast swimming speeds and a rapid "run-reverse" rather than "run and tumble" motility (Mitchell et al. 1996; Stocker et al. 2008). Although the extent and importance of chemotaxis-driven clustering is not yet known, the investment of bacteria in motility and chemotaxis suggests they derive a substantial benefit from pelagic microenvironments.

Bacterial phylogenetic and functional diversity at the microscale—Organic matter hotspots may not only enhance bacterial productivity but also select for bacterial types that are adapted to specific types of organic matter, eukaryotes, or surfaces. Because the vast majority of bacteria are not culturable using standard methods, bacterial diversity is typically measured by using 16S rRNA gene sequences as a proxy for distinct bacterial types. Increasingly these 16S rRNA surveys are being supplemented or replaced by metagenomic, transcriptomic, or microarray approaches that examine the abundance or expression of numerous genes (Dupont et al. 2010, this volume). A new strategy to identify ecologically distinct bacterial clades relies on relating sequence types to their distribution along physicochemical parameters and in microenvironments (Johnson et al. 2006; Hunt et al. 2008; Fraser et al. 2009). In fact, a number of published studies have revealed bacterial partitioning in aquatic microenvironments (Table 1), primarily between particulate and free-living bacterial populations. Although the idea of microenvironment-adapted bacterial populations is supported by these studies, we cannot overlook methodological limitations and the publication bias that may discriminate against research that has revealed no difference between aquatic microhabitats. Particle-attached bacteria are likely a subset of the free-living population, because attached bacteria shed offspring into the plankton, which then can colonize new particles (Tolker-Nielsen et al. 2000). Thus the frequency of a bacterial type in a given microenvironment is more important than the observation of type in that environment. Although in some studies investigators have observed specific groups only in particle-attached fractions (Huber et al. 2003), this finding may have been an artifact of limited sample size rather than a reflection of a true absence in the free-living fraction. Particles within a given size class are likely to be chemically heterogeneous, and a succession of bacterial types is likely to occur as organic matter is remineralized. Specific bacterial types are also likely to aggregate around nutrient point sources, but comparisons of microscale bacterial diversity can be confounded by attachment to particles, polymerase chain reaction (PCR) bias, experimental error, or mixing of water masses with distinct origins (Kirchman et al. 2001; Long and Azam 2001b). Yet in the absence of the ability to cultivate many of these strains or identify their ecological niche, observing partitioning of bacterial types or functional genes along environmental gradients and in distinct habitats may help to identify ecological populations (Fraser et al. 2009).

Bacterial interactions with the pelagic food web—Phytoplanktons are the main source of autochthonous organic matter in pelagic ecosystems (Cole et al. 1982), and serve as the primary carbon source for many heterotrophic bacteria in areas such as the open ocean that have few external carbon inputs. This tight linkage between primary production and bacterial consumers implies that the composition and physiology of the phytoplankton community likely exerts strong pressures on the diversity and dynamics of co-occurring bacteria. Moreover, algae provide diverse microhabitats for bacteria, which can cluster in the nutrient-enriched phycosphere surrounding algal cells (Bell and Mitchell 1972), live as intracellular symbionts, and colonize extracellular polysaccharides and phytoplankton cells (Cole 1982; Malfatti and Azam 2009). Algae produce an array of compounds on the DOM-POM organic matter continuum from LMW compounds such as monosaccharides to particles (Fig. 2). Carbon exudation by algae has been reported to vary between <1% to 50% of total photosynthetically fixed carbon (Hellebrust 1974), and the quality of algal extracellular products can vary considerably (Bruckner et al. 2008). Although bulk coupling of algae and heterotrophic bacteria is well established, the extent to which bacteria cluster around photosynthesizing or dying algae remains controversial (Jackson 1987; Bowen et al. 1993). Bacteria can also affect bloom aggregation dynamics, generating aggregates by colonizing algal cells or dissipating particles by consuming algal-released compounds (Grossart et al. 2006). However, not all bacterial-algal interactions are beneficial, some bacteria also display algicidal properties and may play a role in bloom termination (Grossart 1999; Mayali et al. 2008). Because bacteria are generally better competitors for nutrients than larger eukaryotic cells, they may starve algae of nutrients (e.g., nitrogen), potentially stimulating the release of carbon compounds as a sink for excess carbon, further feeding bacteria (Kirchman 1994; Guerrini et al. 1998; Cotner and Biddanda 2002). These complex interactions between phytoplankton and bacteria include elements of mutualism, commensalism, and parasitism.

Phytoplankton exert a control on the phylogenetic composition of co-occurring bacterial populations, presumably primarily through the quality and quantity of organic matter produced (Fandino et al. 2001; Schäfer et al. 2002; Pinhassi et al. 2004; Grossart et al. 2005; Grossart et al. 2006; Kent et al. 2007). Shifting bacterial populations have been observed during the course of phytoplankton blooms (Riemann et al. 2000). Certain bacterial groups such as the *Roseobacter* appear to be adapted to a phytoplankton-associated lifestyle, because they are enhanced in the presence of algae (Grossart et al. 2005; Sapp et al. 2007), exhibit chemotaxis toward algal products (Miller et al. 2004), display algicidal properties (Mayali et al. 2008), and degrade the algal products dimethylsulfoniopropionate (DMSP) and glycolate (Moran et al. 2003; Moran et

Table 1. A review of the literature on the partitioning of bacterial types between aquatic microenvironments

Organism	Location	Habitat	How measured*	Related to habitat Yes/No	Reference
Bacteria	Deep-sea vent	Particles	Clone libraries	Yes	(Huber et al. 2003)
Bacteria	Mediterranean	Particles	Clone libraries	Yes	(Acinas et al. 1999)
Bacteria	Columbia river estuary	Particles	Clone libraries	Yes	(Crump et al. 1999)
Bacteria	San Francisco Bay	Particles	DGGE	No	(Hollibaugh et al. 2000)
Bacteria	Freshwater mesocosm	Particles	Functional screens	No	(Worm et al. 2001)
Bacteria	Mediterranean	Particles	T-RFLP	Yes	(Moeseneder et al. 2001)
Bacteria	Freshwater mesocosm	Particles	DGGE	Yes	(Riemann and Winding 2001)
Bacteria	Coastal ocean	Marine snow	Clone libraries	Yes	(DeLong et al. 1993)
Bacteria	Freshwater mesocosm	Diatom aggregates	FISH	Yes	(Knoll et al. 2001)
Bacteria	Salt marsh	Particles	FISH	Yes: γ Proteo No: others	(Dang and Lovell 2002)
Bacteria	Estuary	Particles	DGGE	Yes	(Selje and Simon 2003)
Flavobacteria	Southern Ocean	Particles	DGGE	No	(Abell and Bowman 2005)
Photobacterium spp.	Ocean	Fish light organs	MLSA	Yes	(Ast and Dunlap 2005)
Vibrio spp.	Coastal ocean	Sediment/oysters	ERIC-PCR Phage	No Yes	(Comeau and Suttle 2007)
Vibrio spp.	Coastal ocean	Particles	Gene sequences	Yes	(Hunt et al. 2008)
Vibrio spp.	Chesapeake Bay	Zooplankton	FODC	Yes	(Heidelberg et al. 2002)

*DGGE, denaturing gradient gel electrophoresis; T- RFLP, terminal restriction fragment length polymorphism; FISH, fluorescence in situ hybridization; MLSA, multilocus sequence analysis; ERIC-PCR, enterobacterial repetitive-element intergenic consensus sequence polymerase chain reaction; Phage, phage-sensitivity assays; FODC, fluorescent oligonucleotide direct count.

al. 2004; Lau and Armbrust 2006). Current models of aquatic carbon cycling group "phytoplankton" and assess their collective impact on bacterial populations; yet work with cultures has shown strain-specific interactions of bacteria with phytoplankton (Long et al. 2003; Grossart et al. 2005; Sapp et al. 2007; Bruckner et al. 2008). The difficulty of growing phytoplankton without heterotrophic bacteria (axenically) has long been noted (Grossart 1999); recent studies have revealed that heterotrophic bacteria in phytoplankton cultures serve to reduce oxidative stress (Morris et al. 2008) and provide vitamin B_{12} (Croft et al. 2005). Given the importance of bacterial-algal coupling, there is a promising area of research into the complexity of these interactions.

Although the link between phytoplankton and bacteria is quite strong, pelagic metazoans offer distinct, stable habitats for aquatic bacteria. Zooplankton offer multiple niches for bacteria, including pathogenesis, gut colonization, and surfaces; and specific bacterial populations have been shown to associate with zooplankton and large particles (Tang et al. 2006a; Hunt et al. 2008). Moreover, dead zooplankton are concentrated sources of organic matter that can be rapidly colonized by bacteria (Tang et al. 2006b). Closely related bacterial sequence types also appear to have distinct pathogenic associations with fish species, suggesting that fish also provide distinct habitats for bacterial specialization (Nicolas et al. 2008).

Microenvironments rich in organic matter could serve as hotspots of biological activity across multiple levels of the food chain (Seymour et al. 2009), resulting in strong top-down control from grazers and viruses on patch-specialized bacteria and enhanced transfer of carbon between size fractions. Motile protistan grazers are adept at feeding at aggregates (Fenchel and Blackburn 1999), and enhanced grazing under patchy conditions transfers organic matter to higher trophic levels (Del Giorgio et al. 1996; Seymour et al. 2009). In contrast, free-living bacterioplankton are thought to consume smaller size fractions of organic matter and are grazed at lower rates (Giovannoni and Stingl 2005; Sowell et al. 2008; Seymour et al. 2009); therefore they are likely to serve as a DOM "sink" (Ducklow et al. 1986).

Predation by viruses is also enhanced in patchy microenvironments because both cell concentrations and patch-specific bacterial types are in higher abundance (Riemann and Grossart 2008; Lauro et al. 2009). In contrast to grazing, viral-mediated cell lysis will transfer bacterial biomass to smaller size fractions of POM and DOM, which is likely to be taken up by bacteria as part of the viral loop (Riemann and Middelboe 2002). Although copiotrophs have enhanced reproduction due to the availability of nutrients in patches, this advantage may be counterbalanced by enhanced top-down control through grazing and viral predation. In spite of small population sizes, rapid growth coupled with strong top-down control implies that copiotrophs may contribute disproportionately to rapid nutrient cycling in pelagic food chains.

How microscale ecology shapes bacterial diversity—Aquatic microbial ecologists have long been puzzled by the "paradox of the plankton" (Hutchinson 1961): how the vast diversity of

microbes can coexist with the same basic resource requirements in seemingly unstructured aquatic environments. This paradox has grown increasingly relevant as we observe tremendous bacterial diversity in broad gene surveys, including variability below the level at which species are generally identified (Acinas et al. 2004; Venter et al. 2004; Sogin et al. 2006). It is clear that the rich physical and chemical mosaic of organic matter substrates in aquatic environments (Fig. 1) acts to structure bacterial populations, allowing bacteria with common metabolic capabilities to avoid competition through both habitat and metabolic niche differentiation. In several recent studies bacterial clades with >99% 16S rRNA gene-sequence identity have been found to exhibit specialization on different forms of organic matter (Hunt et al. 2008; Ivars-Martinez et al. 2008). Because marine bacteria lack geographic barriers that inhibit gene flow, habitat differentiation may play a role in speciation by enhancing spatial or temporal isolation of clades (Papke and Ward 2004; Ivars-Martinez et al. 2008; Fraser et al. 2009). Even with a million bacterial cells in a milliliter of water, if these cells were evenly distributed a bacterium would be ~100 μm or >100 body lengths from its closest neighbor. The high cell densities in pelagic microenvironments could increase DNA exchange through enhanced conjugation and transduction among populations with similar lifestyles, enhancing speciation through microenvironmental specialization. Moreover, patch-adapted bacteria, like pathogens, may have smaller effective population sizes than clades with a passive, oligotrophic lifestyle, allowing more rapid sweeps of genes through copiotroph populations (Fraser et al. 2009). The local organic matter microenvironment may play a crucial role in microbial ecology: just as the organic matter shapes the community structure of heterotrophic bacteria, so bacteria shape the composition and abundance of the aquatic DOM-POM continuum through metabolism and remineralization.

Scaling up: linking microscale ecology of bacterioplankton to ecosystem process

The interaction between bacterioplankton and organic matter drives many of Earth's biogeochemical cycles, but the complexity of these two key players limits our ability to model their connections. Investigations of microbial interactions with dissolved and particulate organic matter at ecologically relevant scales may clarify ecosystem processes, both through insights into fundamental interactions and by addressing fine-scale heterogeneity in biogeochemical dynamics. In this section we discuss how microscale interactions between organic matter and bacterioplankton have potential ramifications for large-scale biogeochemical cycling of pelagic environments.

The taxonomic structure and resulting metabolic potential of bacterioplankton communities determines the fate of dissolved and particulate organic matter in pelagic ecosystems. Likewise, aquatic organic matter is one of the most heterogenous biological resource pools on earth (Hansell and Carlson 2002; Findlay and Sinsabaugh 2003). This trophic intersection between a metabolically diverse consumer community and a biochemically diverse resource is unparalleled in ecological theory. Below, we outline how biogeochemical cycling may be influenced by the microscale structuring of bacterioplankton communities associated with pelagic organic matter. We first discuss the relevance of microscale bacterioplankton interactions to pelagic biogeochemical pathways, including organic matter bioavailability, pelagic trophic structure, and ecosystem metabolic balance. We then address the implications of microscale diversification for theoretical ecosystem function, including resource use efficiency, functional stability, and adaptation to environmental change.

Scale considerations in organic matter lability—Although heterotrophic bacterioplankton form associations with pelagic organic matter of all size classes and origins, interactions at the submicron scale are the least well understood yet also the most likely to exhibit microscale patchiness relevant to biogeochemical processes. Unlike particulate material, which can be consumed by metazoans, bacteria are the dominant sink for this large pool of submicron "dissolved" organic matter. Because DOM is the major pool of carbon in pelagic lake and marine ecosystems, its bioavailability and recycling rates have major consequences for global carbon cycling (Hansell and Carlson 2002; Findlay and Sinsabaugh 2003). Excellent reviews address the biogeochemical implications of bacterioplankton remineralization of particulate organic particles (e.g., [Simon et al. 2002]) and therefore we focus here on the microscale biogeochemical relevance of interactions between bacterioplankton and nonparticulate DOM.

The bioavailability or lability of organic matter is determined by the interaction of bacterioplankton community metabolism and the composition of the DOM pool. DOM lability is a key parameter in aquatic biogeochemical models and is necessary to quantify rates of nutrient remineralization, rates of respiration, and support of microbial growth. The importance of the DOM source in defining composition and lability is well established, with a community exhibiting different growth and consumption patterns on DOM derived from distinct pools (Del Giorgio and Davis 2003; Carlson et al. 2004; Langenheder et al. 2006; Perez and Sommaruga 2006). Moreover, seasonal shifts in organic matter composition are reflected in predictable changes in bacterioplankton community structure in diverse habitats (Morris et al. 2005; Nelson 2008). Unfortunately, attaching broad classifications to the lability of organic matter pools is impossible and highly system specific. For example, while DOM derived from phytoplankton senescence is frequently considered labile, this may not always be the case, depending on the ambient nutrient field and the nutrient status of the phytoplankton (Carlson 2002).

As in the bacterioplankton, our classification system for organic matter lacks criteria for identifying ecologically meaningful units, further confounding efforts to link bacterial com-

munity composition to organic matter turnover. Research into the relative importance of community structure and DOM composition on lability has yielded mixed results, with studies emphasizing either the importance of the organic matter source or community source to eventual metabolism (Carlson et al. 2002; Carlson et al. 2004; Judd et al. 2006; Kritzberg et al. 2006; Langenheder et al. 2006; Lennon and Pfaff 2005; Perez and Sommaruga 2006). Additionally, environmental factors that modulate lability, including temperature, nutrient field, and other factors, also affect bacterial community structure (Carlson 2002; Del Giorgio and Cole 1998). Linking microscale heterogeneity in community structure to microscale variations in rates of organic degradation may serve to determine the links between bacterial community composition and function.

Ultimately, the fate of a large fraction of pelagic carbon is dependent on how efficiently bacteria convert organic carbon to biomass (bacterial growth efficiency) rather than respire it as CO_2 (Del Giorgio and Williams 2005). Much of the apparent variation in bacterial growth efficiency is determined by community adaptation to specific organic matter sources (Del Giorgio and Davis 2003). The growth efficiency of bacterioplankton is dependent on DOM concentration as well as spatial distribution in conjunction with community structure. Bacterial growth efficiency may be more tightly linked to cell environmental and physiological conditions than either growth rate or carbon demand, and, as noted by Azam and Malfatti (2007), determining fine-scale regulators of growth efficiency is critical to modeling the interaction of community structure and ecosystem metabolic balance. One recent example is the discovery that local viral outbreaks can have a significant influence on nutrient enhancement of bacterial growth efficiencies by throttling the shunt of microbial organics back into the organic matter pool (Motegi et al. 2009). In nutrient-rich patches such as particles, bacterial growth efficiency estimates differ greatly between measured values (approaching 0.5) and those modeled from macroscale correlations (approaching 0.1) (Simon et al. 2002). This discrepancy suggests that the efficiency of organic matter remineralization by bacterioplankton is poorly represented when we ignore microscale heterogeneity. Although scale-dependent heterogeneity in rates (for example enhanced microscale bacterial production or respiration) is well recognized and thought to average out at coarser scales, evidence of heterogeneity in parameters such as growth efficiency (ratios of rates) at smaller scales can have striking implications because it implies differing scale dependencies of rate measurements, highlighting the importance of integrating fine-scale bacterioplankton–organic matter interactions into ecosystem models.

At the microscale, DOM lability is spatially heterogeneous, and this heterogeneity may translate into marked differences in overall ecosystem DOM removal, respiration rates, and transfer from particulate to dissolved states. The physical structure of the DOM-POM continuum may mechanistically link microbial diversity to this heterogenous lability. Microscale patchiness in DOM lability is likely due in part to physical aggregation and polymerization processes, as larger scaffolding structures are preferentially colonized and metabolized by microbes (Amon and Benner 1996). These physical hotspots may represent the intersection between microbial community structure and organic matter lability, as complex consortia may accelerate rates of organic use and rates of local diversification, allowing enhanced community growth efficiency and potentially supporting the transfer of nutrients to higher trophic levels (Seymour et al. 2009).

Scaling community adaptation and resource use efficiency—In dynamic aquatic environments, such as the coastal ocean or snowmelt-dominated lakes, the organic matter pool is likely derived from multiple, transient sources and thus is composed of substrates of higher compositional complexity than in more stable regimes. Within a heterogeneous resource pool, certain substrates may be accessible only to distinct bacterial clades (e.g., methane and methanotrophs, DMSP, and *Roseobacter*). In response to increases in these substrates, specialized taxa may immigrate or increase in abundance through species-sorting processes (Leibold et al. 2004).

Other organic compounds may be metabolites for a wide range of heterotrophic bacterioplankton; for example, protein-containing Coomassie-stained particles are likely metabolized by bacteria with extracellular proteases. In highly dynamic regimes, such as the coastal oceans, generalist copiotrophs such as *Vibrio* and *Roseobacter*, with diverse metabolic capabilities and short generation times, can rapidly respond to substrate changes and enhance degradation rates of organic matter (Polz et al. 2006). However, generalist-dominated communities are associated with a buildup of "refractory" low and medium molecular weight DOM (Amon and Benner 1996), due to a combination of inefficient consumption of small size fractions and the production of smaller degradation byproducts.

In less dynamic systems, such as the surface waters of oceanic gyres, microscale resource depletion or adaptation to slow growth may be the cause of observed DOM buildup throughout the summer months, where free-living oligotrophs such as SAR11 Group Ia dominate. Macronutrient additions do not appear to enhance the removal of this organic matter (Carlson et al. 2004), indicating either that the DOM is highly refractory or that highly adapted communities of oligotrophs are limited by an alternate resource. In this example, winter mixing introduces additional nutrients and mesopelagic DOM, resulting in enhanced labilities with concomitant shifts in population structure toward SAR11 Group II (Carlson et al. 2004; Carlson et al. 2008).

Although anecdotal, these examples underscore the potential interaction between community composition, resource use, and environmental heterogeneity. If similar heterogeneity exists at the scale of the DOM-POM continuum we can expect analogous processes of ecotype differentiation and niche par-

titioning to generate fine-scale variation in DOM metabolism and remineralization relevant to ecosystem-scale processes. In metazoans and phytoplankton, diverse communities have been found to use resources more efficiently (Tilman 1994; Loreau et al. 2001; Cardinale et al. 2006; Ptacnik et al. 2008). However, the low fraction of cultivable bacteria, the metabolic diversity of heterotrophs, and the complexity of aquatic organic matter pools render it difficult to develop simple relationships between bacterial community structure and resource use efficiency. Moreover, the field lacks a strong conceptual framework for predicting differential organic remineralization rates of heterotrophic taxa within an assemblage; nor do we know how membership in a given assemblage may influence those rates due to synergistic or antagonistic interactions.

In bacterioplankton communities, the byproducts of organic substrate transformation by one population may be directly used by another population of the same "trophic status" (bacteria that may also compete for organic substrates or other nutrients). Examples of these consortia interactions abound in the microbial literature from sediment habitats (e.g., the anaerobic oxidation of methane), but these links are muddied in oxygenated pelagic waters because most taxa have complex metabolic capabilities and heterogeneous DOM pools. For example, the ultraoligotrophic SAR11 clade requires reduced sulfur, which may be a waste byproduct of another bacterium (Tripp et al. 2008). It is assumed that reduced sulfur is not growth limiting, but how SAR11 acquires this resource may dictate completion or association with other organisms. Advances in microscopy (Malfatti and Azam 2009; Malfatti et al. 2010) and coculturing (Morris et al. 2008) can provide the first steps toward understanding microbial consortia resource use by demonstrating the frequency of physical associations between bacterial taxa in aquatic environments. These interactions are likely to determine resource use efficiency and allow scaling of community structure to ecosystem metabolism.

Ecosystem implications of microscale diversity, coexistence, and community stability—Ecological theory suggests that the high diversity and dispersal potential of bacterioplankton act to minimize the influence of microscale interactions on ecosystem-scale biogeochemical processes because of widespread functional redundancy (Griffen et al. 2010, this volume). This concept is supported by the argument that environmental conditions largely determine microbial community structure and metabolic potential through selection of widely dispersed taxa via species sorting (Fierer and Jackson 2006; Crump et al. 2007; Nelson et al. 2009). Here we argue that microscale phylogenetic and functional heterogeneity is a fundamental aspect of bacterioplankton communities, and that these small-scale properties have significant influence on rates of biogeochemical cycling.

Metacommunity and dispersal processes influence bacterioplankton community structure and ecosystem biogeochemistry by modulating community resource use efficiency, community stability, and response to environmental change. Microenvironmental and temporal niche partitioning may mediate the coexistence of bacterial ecotypes that have similar metabolic capabilities (Koeppel et al. 2008), and this enhanced diversity is suggested to increase community functional stability and resilience to disturbance (Naeem and Li 1997; Loreau et al. 2001); but see also (Curtis and Sloan 2004). Surprisingly, results of most studies that have tested stability and resilience indicate that microbial communities are neither taxonomically resilient nor functionally stable in response to environmental change (Allison and Martiny 2008). However, most investigation of resiliency involves relatively coarse phylogenetic analyses in soil habitats, where microhabitat partitioning is arguably higher than in pelagic environments. Additionally, bacterioplankton may not be resilient to perturbations in temperature (Allison and Martiny 2008), which require genome-wide adaptation of enzyme activity and protein folding, but may be more plastic in response to the addition of novel chemical substrates, as during a phytoplankton bloom. As a less structured system with fewer confounding influences (milder environmental gradients, no geographic barriers, enhanced diffusion and mixing rates) marine ecosystems represent a simplified natural environment for the study of microbial resource partitioning and functional redundancy (Polz et al. 2006). Whether or not microscale diversification of bacterioplankton in response to resource heterogeneity influences community stability, partitioning at ecologically relevant microscopic scales is likely to influence community metabolism and response to environmental changes.

To the extent that resource heterogeneity and the structure of the organic matter size continuum may influence bacterioplankton metacommunity dynamics, more studies should investigate the idea that small-scale effects on dispersal and persistence can translate into larger impacts on ecosystem processes. Recent modeling efforts have suggested that microbial diversity can have profound effects on organic matter remineralization and particle sinking by enhancing community adaptability (Miki et al. 2008; Stocker et al. 2008). High-throughput sequencing in pelagic systems has revealed the presence of a diverse microbial community of fairly abundant sequence types and a highly diverse "rare biosphere" (Sogin et al. 2006; Hofle et al. 2008). These rare taxa may increase the resiliency of the community to changes in substrate availability or other environmental factors by becoming more active/abundant following environmental change. Aquatic microenvironments may enhance the persistence of these rare populations. However, if these rare ribotypes represent dormant cells (which are unlikely to ever thrive in the environment) or taxa that grow well but are steadily grazed to rarity, the rare biosphere may not enhance community resilience or opportunistic response to environmental change.

Our emerging understanding of organic matter in aquatic habitats paints a complex picture of a dynamic and heterogenous physical and chemical environment. The relevance of the phylogenetic and metabolic diversification of het-

erotrophic microbial communities interacting with this organic matter grows as we learn more about the ecology of bacterioplankton at small scales. Resource acquisition and transformation, population growth and differentiation, and microbial behavior and distributions are all likely to be fruitful avenues of research at micron scales. Because these small-scale dynamics potentially influence community stability, resource use efficiency, gross remineralization rates, and transfer of dissolved materials to higher trophic levels, scaling these microscale processes upward may help to explain much complexity in biogeochemical cycling. In addition, such fundamental ecological investigations will clarify key linkages between community structure and heterotrophic metabolic properties, which is emerging as one of the most critical areas of research in global ecosystem function.

IV Future directions

Understanding the microscale ecology of bacterioplankton and their interactions with organic matter will require a creative integration of technological advances and inspired applications of those technologies. We envision three key research areas that will yield important advances in our understanding of microscale ecology and its relevance to larger ecosystem processes and biogeochemical cycling: characterization of organic matter composition and spatiotemporal dynamics; understanding microscale partitioning of populations, communities and metabolic potential (genomics); and determining the relevance of microscale processes and diversity to resource use and biogeochemical cycling.

The most challenging of these three proposed areas of research is the development of new methods to analyze the composition of aquatic organic matter at the appropriate spatial scales. Cost-effective techniques to simultaneously analyze DOM composition and microbial community phylogenetic/metagenomic composition will permit analyses linking genotype to phenotype. Recently, scanning fluorometry to trace organic carbon sources has proved a low-cost and sensitive technique that allows characterization of organic matter in broad areas of the ocean (Murphy et al. 2008; Yamashita and Tanoue 2008), and advances in remote sensing allow time series measurement of particulate organic carbon, chromophoric matter absorption, and phytoplankton biomass (Siegel et al. 2002; Platt et al. 2008). Coupling these measurements with high-throughput "omics" techniques would allow correlations that then could be applied to microscale investigations. For example, finding high expression of specific genes during late phases of a diatom bloom might suggest that those same genes would be expressed by bacteria clustering around a dying diatom. However, metagenomic analyses suffer due to the fact that many genes cannot be linked to a known function nor can environmental perturbations be tied to microbial ecology (Mou et al. 2008).

Understanding the ecological distributions of bacterial populations in natural environments will aid both in understanding carbon cycling and developing an ecological species concept for bacteria. Recent work has identified ecologically and phylogenetically coherent groups associated with distinct habitats (Hunt et al. 2008; Koeppel et al. 2008). Careful study of the biogeochemical metabolism of bacterial communities in conjunction with the metabolic potential of a community (via metagenomics) in controlled ecological contexts will help constrain how diversity and resource use are coupled in natural environments. Genomic analysis can also be used to gain insight into distinct ecologies of bacteria on the oligotroph-copiotroph continuum (Lauro et al. 2009), offering hypotheses that can be tested with environmental data. Using microscale bacterioplankton ecology to inform models of resource use efficiency, food-web interaction strengths, and overall system metabolism will strengthen our knowledge of biogeochemical linkages as well as the basic ecological principles linking diversity to ecosystem function.

Finally, we wish to link these dynamic pools of organic matter and genotypes to biogeochemical cycling. Metagenomic and metabolomic approaches will certainly help to elucidate how bacteria functionally, spatially, and temporally partition resources in aquatic environments. Experimental approaches to tracking metabolism of specific compounds (stable isotope probing, 5-bromodeoxyuridine [BrdU] immunoprecipitation) should be applied to determine the relevant scales at which metabolic and taxonomic differentiation overlap (Behrens et al. 2008). In situ experimentation with natural communities and cultured representatives will rely on a suite of approaches to unravel microscale ecology, including motility, signaling, and other inter- and intraspecific interactions. Together these approaches will help to clarify the degree to which the heterogeneity of the bacterioplankton microenvironment may play a role in dictating the diversity of microbial life and the dynamics of pelagic biogeochemical cycles.

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