

## Microbiology in Polar Oceans

BY JAMES T. HOLLIBAUGH, CONNIE LOVEJOY, AND ALISON E. MURRAY

### THE POLAR OCEANS

Polar oceans are distinct from other oceanic environments in a number of ways, but the presence of sea ice is a major habitat difference. Sea ice affects polar microbial communities by limiting light penetration into the upper ocean and by providing a unique sea-surface habitat (Figures 1 and 2). Sea ice serves as a support matrix for a diverse and dynamic assemblage of microbes, including phytoplankton and prokaryotes, often referred to as the sea-ice microbial community, or SIMCO. Growth of ice-associated microalgae can lead to extreme carbon enrichment in the ice, fueling microbial production and providing a food supply for herbivorous metazoa. Brine exclusion during the formation of sea ice, coupled with summer melting, contributes to significant and persistent water-column stratification. This is especially the case in the Arctic Ocean where permanent ice cover con-

strains wind mixing and the land-locked geography of the basin restricts exchange with lower-latitude waters. Other characteristics of polar oceans, such as low temperature and intense seasonal variation in primary production and carbon flux, are often more extreme than in other oceanic habitats.

Unique differences between the two polar oceans are due to the circumstance that the Arctic Ocean is a land-locked

basin receiving ~10% of the global runoff of freshwater (Aagaard and Carmack, 1989), while the Southern Ocean surrounds an ice-covered land mass and is separated from lower-latitude waters by a well-defined circumpolar front. The rivers emptying into the Arctic Ocean drain lower-latitude terrestrial environments, including tundra and boreal forests. These rivers are quantitatively important sources of organic carbon to the Arctic

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Figure 1. This late-season sea ice is tinged brown from the growth of microorganisms and algae growing on the bottom and in the flooded pores of the disintegrating ice. Note the low ceiling and thick cloud cover, fairly typical of polar oceans for much of the year and further reducing the light available to water-column primary producers. Photo courtesy of Alison Murray

Ocean (Opsahl et al., 1999; Benner et al., 2005). The Southern Ocean receives no such terrestrial carbon subsidy.

### POLYNYAS

Limited areas of persistently open water provide habitats that contrast with areas that are ice covered during much of the year. These open-water areas, called polynyas, result from a variety of physical processes. There have been several studies focusing on polynyas in recent years, notably the Canadian-led North Water (NOW) Polynya study (Deming et al., 2002). The NOW polynya was occupied for over four months in 1998, from April through July, and also sampled in the late summer and early fall of 1997 and 1999 (Figure 3). These studies show that microbes in the polynya were more active than their counterparts under the adjacent ice cover. There is little overlap between the phytoplankton species found in adjacent sea ice and open waters and the distinct phytoplankton communities associated with different water masses that meet in the NOW (Lovejoy et al., 2002a, 2002b). Work in the NOW in 2005 using clone library analysis shows that the bacterial and archaeal communities found in open waters are more similar to other open oceans than to the specialized sea-ice communities (recent work of author Lovejoy and Pierre Galand, Université Laval).

### SEA-ICE ASSEMBLAGES

Sea-ice microbial communities have been the focus of polar investigations for many years, with some of the early characterizations going back to the work of John Bunt, Rita Horner, and



Figure 2. Close-up of sea ice containing a thick microbial community. Photo courtesy of Alison Murray

Max Dunbar in the 1960s. SIMCO are rich communities of prokaryotic and eukaryotic organisms found in sea ice at both poles. Brine channels that form as salts are excluded during the freezing process provide a major SIMCO habitat within the ice. Sea-ice brines are reservoirs of dissolved organic and inorganic nutrients, and are home to abundant bacterial populations. The diversity and ecology of SIMCO bacteria have been the subjects of numerous studies over the years, with recent efforts focusing on describing the phylogenetic composition of bacterial assemblages. Archaeal populations have not been characterized as thoroughly, though they have been detected in SIMCO in at least one study (Junge et al., 2004).

Bacteria were first observed in Antarctic sea ice in 1966 (Iizuka et al., 1966). SIMCO bacteria are often reported to be larger than pelagic forms, are capable of rapid growth rates (Kottmeier and Sullivan, 1987),

and can be found both free-living and attached to algal cells in the dense assemblages that form within the ice (Palmisano and Garrison, 1993). Sea-ice-associated bacteria are more likely to be true psychrophiles (optimal growth temperatures  $< 15^{\circ}\text{C}$ ) (Delille, 1992) than their planktonic counterparts, and produce more colony-forming units (CFU) per volume sampled than seawater populations (Bowman et al., 1997a; Brinkmeyer et al., 2003; Junge et al., 2002). Molecular taxonomic characterization of sea-ice bacterial diversity using 16S rRNA gene sequencing suggests that although there are some organisms in common between the sea ice and underlying seawater, many of the psychrophilic species appear to be unique to the sea-ice habitat (Bowman, 1997b). Most SIMCO bacteria are affiliated with the Proteobacteria (alpha- and gamma-Proteobacteria), Bacteroidetes, and Actinobacteria phyla. The question of marine microbial biogeography was



Figure 3. Ice-covered oceans present a special challenge for sampling, as well as unique environmental conditions. Here, the Canadian icebreaker *Radisson* occupies a station during the North Water Polynya study. Photo courtesy of Connie Lovejoy

first introduced and examined by studying gas vacuolate psychrophiles isolated from both poles (Staley and Gosink, 1999). Gas vacuolate bacteria are postulated to be adapted to a SIMCO lifestyle because their buoyancy would ensure inclusion in forming sea ice. Commonly isolated gamma-Proteobacteria phylotypes from both poles fall into the genera *Glaciecola*, *Psychrobacter*, and *Colwellia*; the alpha-Proteobacteria into the genera *Octadecabacter* and *Sulfitobacter*; and Bacterioidetes into the genera *Polaribacter*, *Flavobacterium*, and *Psychroserpens*. (Brown and Bowman, 2001; Junge et al., 2002).

### PICOEUKARYOTES

López-García et al. (2001a, 2001b) provided one of the first reports of novel, uncultivated picoeukaryotes in the open ocean from samples collected in deep waters of the Antarctic polar front. Their analysis of an 18S rRNA clone library

uncovered three major new clades of marine eukaryotes: group I and II alveolates and marine stramenopiles (MAST) that have since been reported from throughout the world's seas and ocean. The largest survey of picoeukaryotes in the Arctic to date reports that 42% of the sequences retrieved are less than 98% identical to sequences from other oceanographic regions (Lovejoy et al., 2006). Two clades of small radiolarians within the family Spongodiscidae and class Polycystinea found among these sequences had closest matches to Antarctic sequences. This could indicate bipolar distribution of these organisms and their importance in polar waters. That study also revealed at least one clade of heterokont algae (a major line of eukaryotes) that was distinct from either diatoms or bolidophytes. Lovejoy et al. (2006) speculate that the sequences could be candidates for the polar *Parmales*, a group of algae known only

from electron microscopy examinations of polar ocean samples.

With additional environmental rRNA sequence data now available from many oceanic regions, it is becoming feasible to distinguish biogeographies of these uncultivated eukaryotic microbes. For example, Massana et al. (2006) found that among 12 MAST subclades, at least one (MAST 4) is absent from polar waters, and Lovejoy et al. (2007) recently described a polar ecotype of the small prasinophyte *Micromonas* with pan-Arctic distribution. This 1–2 µm cell is ubiquitous throughout the Arctic basin and, as the persistent dominant of the deep chlorophyll maximum layer, is a major contributor to primary production in the Arctic Ocean. The physiological adaptation of this ecotype to low temperatures and light may well be widespread among polar protists.

### BACTERIOPLANKTON

Bacterioplankton, including organisms in the domains Bacteria and Archaea, dominate the picoplankton in both the Arctic and Southern Oceans. The function of these organisms in polar oceans is similar to their function in lower latitudes: to grow, heterotrophs and photo-heterotrophs use organic carbon produced by phytoplankton and sea-ice algae. Chemolithoautotrophic bacteria appear to be widespread in polar oceans and to mediate inorganic nitrogen (Hollibaugh et al., 2002) and sulfur transformations. Secondary production rates in polar waters during summer are similar to those in lower latitudes, despite much colder ocean temperatures (Fuhrman and Azam, 1980; Hollibaugh et al., 1992). Winter

rates are much lower, however, likely due to carbon limitation. Bacterioplankton blooms have been detected in the sub-Antarctic (Delille et al., 1996) and in the Ross Sea during late summer (February) (Ducklow et al., 2001), lagging, rather than being directly coupled to, seasonal spring phytoplankton blooms as they are at lower latitudes. In addition to strong seasonal dynamics in bacterioplankton abundance and activity, bacterial species composition in coastal Antarctic Peninsula waters shifts. Phylogenetic analyses based on 16S rRNA genes suggest over 50% turnover in community composition between winter and summer (Murray and Grzyski, 2007; Murray et al., 1998). Hodges et al. (2005) and Yager et al. (2001) report similar seasonal shifts in the Arctic Ocean.

Similar groups of bacterioplankton inhabit polar seas and lower-latitude waters, with dominance of organisms related to alpha-Proteobacteria, gamma-Proteobacteria, Actinobacteria, and Bacteroidetes (Bano and Hollibaugh, 2002; Bowman et al., 1997b; Murray and Grzyski, 2007). Though comprehensive studies comparing the levels of diversity in polar waters to other oceanic systems have not been conducted, it appears that they are comparable. The most notable difference is the lack of cyanobacteria (especially *Prochlorococcus*) in polar waters (Letelier and Karl, 1989; Zubkov et al., 1998; Johnson et al., 2006). Garneau et al. (2006) detected *Synechococcus* in Arctic waters; however, they are related to freshwater clades and their occurrence seems to be the result of freshwater input (Waleron et al., 2007). Most research concerning the diversity of polar marine bacteria has focused

on cultivated organisms. Recent reports of studies in Terra Nova Bay (Maugeri et al., 1996; Michaud et al., 2004) and McMurdo Sound (Webster et al., 2004) reported high diversity, while another study comparing strains isolated from both poles (Mergaert et al., 2001) reports that five of eight clusters derived using numerical taxonomy were common to both poles. Diversity studies of the 16S rRNA gene sequence provide similar findings in which polar species (from either pole) are the nearest relatives (Murray and Grzyski, 2007).

Many cosmopolitan marine groups have been detected in waters from both poles. Organisms in the SAR86 (Béjà et al., 2002), SAR11 (Mullins et al., 1995; Giovannoni et al., 2005), and Flavobacteria groups (Gómez-Consarnau et al., 2007) are found in both Arctic (Bano and Hollibaugh, 2002) and Antarctic (Murray and Grzyski, 2007) samples, suggesting the importance of these organisms in these ecosystems. Members of these groups are known to produce proteorhodopsin

but more details can be found in reviews such as Murray and Grzyski (2007) for the Antarctic and Bano and Hollibaugh (2002) for the Arctic.

Psychrophilic marine bacteria are phenotypically and genotypically divergent in comparison to their mesophilic relatives. Psychrophile genomes may contain specific genes that facilitate cold adaptation, such as the nucleic-acid-binding proteins found in methanogenic archaea from an Antarctic lake (Saunders et al., 2003), though the current paradigm is that highly active enzymes are strongly selected and have undergone significant modifications in amino-acid usage (Feller and Gerday, 2003). With the recent completion of several genome sequences, themes in cold adaptation are becoming more evident. Adaptation to permanently cold conditions has been investigated through analysis of amino-acid usage in bacterial genomes. Adaptations presumed to increase cold tolerance, such as a reduction in charged amino-acid residues forming salt bridges, a bias towards asparagine residues, and a reduction in

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and thus they may benefit from energy obtained from proteorhodopsin-proton pumping actions. Aerobic anoxygenic phototrophs related to the Roseobacter clade also appear to be abundant in both polar coastal and oceanic systems (Selje et al., 2004). A detailed description is beyond the scope of this article,

proline and hydrophobic clusters, have been reported (Grzyski et al., 2006; Medigue et al., 2005; Methe et al., 2005).

#### ARCHAEOPANKTON


Planktonic archaea in polar waters appear to be dominated by the marine Group I Crenarchaeota (Bano et al.,



2004; Church et al., 2003; DeLong et al., 1994; Galand et al., 2006; Massana et al., 1998; Murray et al., 1998; Wells et al., 2006; Wells and Deming, 2003). Group II marine Euryarchaeota have also been detected (DeLong et al., 1994), as have GIII and GIV Crenarchaeota in the deep polar frontal waters of the Antarctic (López-García et al., 2004) and in Arctic waters (Bano et al., 2004; Galand et al., 2006). The marine Group I Crenarchaeota are unique in their distribution as they have been detected in winter surface waters in high relative abundance (~ 20% of total rRNA) in comparison to other lower-latitude waters where they are rarely detected in surface waters (Murray et al., 1998). They are abundant in deeper polar waters as in other regions of the ocean (Church et al., 2003; Karner et al., 2001). Activities of these archaea remain to be demonstrated in polar waters, though some of them may play roles as ammonia oxidizers, as has been suggested for other Crenarchaeota affiliated with this lineage (Francis et al., 2005; Konneke et al., 2005). In addition, a relative of the Group II Euryarchaeota is reported to contain a proteorhodopsin ortholog, suggesting that this group of archaea, whose distribution is mostly restricted to surface waters, can use the light-driven rhodopsin proton pump to generate a proton motive force (Frigaard et al., 2006). Marine archaea have not been cultivated from the poles; thus, knowledge of this domain has been solely through environmental molecular surveys, fluorescent in situ hybridization studies, and environmental genomic sequencing (Béjà et al., 2002). Several genomic fragments identified and par-

tially sequenced by Béjà et al. (2002) suggest a lack of synteny (preservation of gene order between related species), indicating genomic complexity beyond that seen in the 16S rRNA gene sequence of the marine Group I Crenarchaeota.

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