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Diversity of planktonic microorganisms in the Arctic Ocean

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ABSTRACT

The present paper begins by reviewing recent developments in our understanding of the diversity of planktonic microorganisms in the Arctic Ocean, taking into account recent data from high throughput sequencing techniques. This data has enabled deeper analysis of the many thousands of different microorganisms present in natural samples. The Arctic Ocean is similar to the other oceans in terms of the abundance and general composition of microbial communities. However, some traits are unique. For example, there are essentially no cyanobacteria in the Arctic and their ecological role seems to be taken up by picoeukaryotic algae. Recent comparisons of the bacterial communities from the two Polar oceans with those from temperate waters showed that Polar communities were closer to each other than to the lower latitude ones. However, they only shared about 15% of the taxa. Newer data considerably increases the coverage of Arctic sites sampled and indicates that bacterial communities in the Arctic vary significantly across regions and seasons. In particular several recent cruises have provided access to the Arctic Ocean during the winter, the least known season and we review two instances of active microbes during the winter. First a bloom of Thaumarchaeota that may have been based on the use of urea as a source of carbon and reducing power, and second the increase in picoeukaryotic algae as soon as light reaches the ocean in February. Both examples show that there is considerable microbial activity during the Polar winter.

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1. Introduction

Similar to other oceans, the Arctic Ocean is dominated by microbial biomass and microbes are responsible for carbon, energy and nutrient cycling. In the past decade, there have been several excellent reviews on the microbiology of both the water column (Staley and Gosink, 1999; Hollibaugh et al., 2007; Lovejoy et al., 2010; Lovejoy, 2011, 2014; Boeuf et al., 2014) and sea ice (Deming, 2010; Caron and Gast, 2010; Arrigo et al., 2014) in the Arctic. The contribution of arctic microbes to element cycles has also been reviewed by Wassmann (2006, 2011), and there have been a number of publications on the ecology and character of marine microbes in the Arctic (Galand et al., 2006, 2008a,b; Sala et al., 2008; Alonso-Sáez et al., 2008, 2010; Estrada et al., 2009; Cottrell and Kirchman, 2009; Kirchman et al., 2009; Terrado et al., 2011). Microbes dominate the global diversity and can be found in all three domains of life, Bacteria, Archaea and Eukarya. While we will briefly comment on a few particular aspects of

Eukarya and Archaea, the main focus of this review will be on summer and early fall distributions of the Domain Bacteria where data is more complete; ships have better access to the Arctic after ice out and generally Bacteria are more well studied compared to Archaea and microbial eukaryotes. Because of the profound seasonality of the Arctic, we will also examine several examples of what is known about winter microbial communities.

2. Patterns of microbial community function and biodiversity

Firstly we review the evidence for general patterns in microbial assemblage composition that may be unique to the Arctic (or to the two Polar zones). Extrapolating from known concentrations and the volume of the Arctic Ocean the total number of bacterial and archaeal cells in the Arctic Ocean is 10^{27} , with a biomass of ca. 20 fg C per cell, or a total biomass is 2.9×10^{11} kg of wet weight. By way of comparison, a Beluga whale weighs 1600 kg, which means prokaryotes in the Arctic Ocean have a wet weight equivalent 18 million Belugas. To put this in context, the world population of Belugas is estimated at 75,000 individuals (Jefferson et al., 2008). Specific activity is also very high for smaller organisms, it is estimated that more than 95% respiration in the oceans is due to microorganisms (Williams, 1981; del Giorgio and Duarte, 2002). In addition, over 95% of the primary production in the

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oceans is due to photosynthetic microbes (de Vooy, 1979; Matrai et al., 2013). In the Arctic Ocean this figure is likely higher because of the limited distribution of macroalgae in ice scoured inshore regions (Daniëls et al., 2013). Flow cytometry studies indicate the total absence of *Prochlorococcus*, and almost complete absence of *Synechococcus* that dominate the smallest phytoplankton size class in much of the World Ocean (Li et al., 2009), and if only for this reason Polar Oceans differ markedly from other oceans. This size class is replaced by picoeukaryotes; microbial eukaryotes less than 3 µm in diameter (Lovejoy et al., 2007). There are also differences in the carbon flow that are examined in Maranger et al. (present volume).

Although multicellular plants and animals can usually be identified by their morphology the majority of microorganisms require some form of genetic characterization to be identified. In recent years the most common proxy in use for taxonomic identification of microbes are genes coding for ribosomal RNA (rRNA). The utility of these genes is that their core functions are fundamental to protein synthesis and so active portions of the gene are conserved across all domains of life. Importantly however, ribosomal genes also contain variable nucleotide regions that have drifted over time and reflect the phylogeny of organisms. With accurate reference databases, uncultured microorganisms from an environment can be identified even to the level of ecotype. The gene that codes for the small subunit of rRNA (16S rRNA for Bacteria and Archaea and 18S rRNA for Eukarya) is by far the most frequent gene used in environmental microbiology surveys. However, arbitrary levels of sequence similarity used for defining a bacterial (97%) or microbial eukaryotic (98%) species may underestimate species diversity (Amato et al., 2007; Coleman, 2000) and diversity estimates based on SS rRNA will be on the conservative side. A good example is *Micromonas pusilla*, in the green algal family Mamiellophyceae. This unicellular phototroph was recorded in Arctic waters for decades; both through light microscopy (Sherr et al., 2003; Lovejoy et al., 2007) and culture studies based on most probable number counts (Thronsen and Kristiansen, 1991) indicating it was an abundant member of the phytoplankton community. Initially this identification was based on the morphology since the organism is a small bean shaped cell with one chloroplast and a single short flagellum, which is fairly distinctive. Early molecular based studies also showed that there was widespread distribution of *M. pusilla* (Not et al., 2005). However, when more detailed phylogenetic studies were carried out on *M. pusilla* strains isolated from different oceans and seasons, they formed at least five distinct clusters (Slapeta et al., 2006). *M. pusilla*, therefore, is an example of a cryptic species complex: a group of morphologically indistinguishable microorganisms that are genetically different. This phenomenon is extremely common among microorganisms, where similar morphology may hide profound genetic divergence. Indeed, in the case of *M. pusilla* Lovejoy et al. (2007) reported that one distinct cluster (and only one) was found exclusively in the Arctic Ocean, while the other clusters were extremely rare or absent from the Arctic. This particular Arctic endemic has specific adaptations to live at low temperatures and low light intensities (Lovejoy et al., 2007), which will be discussed further in the “Microbial dynamics during the polar winter” section below.

Rank abundance curves are used to visualize the contribution of different members to the total community (Fig. 1). Usually, a few taxa are very abundant while most other taxa are rare. In the case of bacteria this rare part of the curve can be particularly long (Pedrós-Alió, 2012; Amaral-Zettler et al., 2010). This is partly because bacteria do not have a sexual reproductive cycle and in the absence of mutations daughter cells are genetically identical. Assuming a doubling time of once a day, a single cell could arrive in the Arctic and continue to divide filling the whole basin with a single bacterial lineage in three months. However, because of rapid

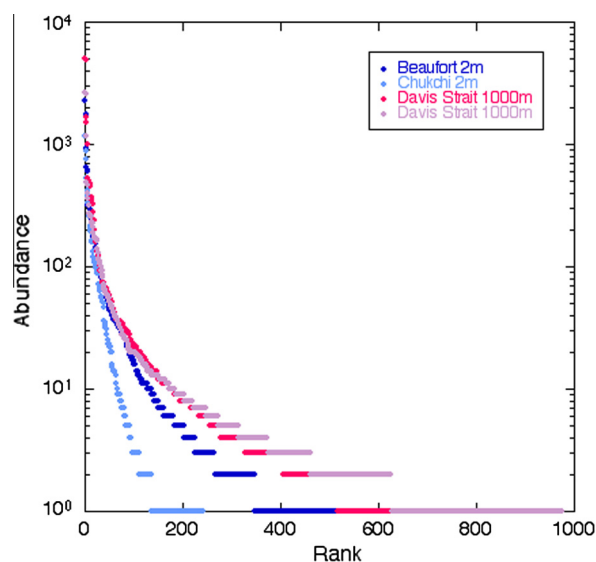


Fig. 1. Rank–abundance curves for bacterial assemblages from the Arctic Ocean. Light blue: Surface coastal Beaufort Sea, Bacteria. Dark blue: Surface coastal Chukchi Sea, Bacteria. Red: Deep sample from Beaufort Sea, Bacteria. Purple: Deep sample from Beaufort Sea, Archaea. These curves were obtained by pyrosequencing within the ICoMM project. There were between 18,000 and 22,000 sequences per sample. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

losses due to grazing and viral lysis (Vaqué et al., 2008) this does not occur. But given the capacity for rapid growth even over a few days a genetically distinct microbe can reach relatively high numbers; a few representatives of these microbial lineages may persist when the environment becomes less than favorable, these persistent relics of past blooms contribute to the long tail of the rank abundance curve (Fig. 1). This concept of propagation and persistence has given rise to the notion that the whole diversity of microorganisms on the Planet could possibly be found in the long tail of the rank–abundance curve of any given ecosystem. The huge reservoir of diversity has been named “the rare biosphere” (Sogin et al., 2006). Since growth conditions in laboratories all over the world, often select the same microorganisms, the statement that “everything is everywhere, but the environment selects” (L. G. M. Bass – Becking, see de Wit and Bouvier, 2006) also suggests no limit to microbial dispersal and a strong role for environmental selection. Gibbons et al. (2013) compared the diversity in the whole International Census of Marine Microbes (ICoMM, see next paragraph) data set with that of a fixed marine station and found a considerable proportion (at least ca. one third) of the operational taxonomic units (OTUs) from any particular marine data sets were also retrieved at the single site which had been resampled over several years. However, this analysis ignored the limitations of the short reads and the use of just one 16S rRNA variable region targeted by ICoMM, but nonetheless highlights how a proportion of bacteria may have very broad distributions. At least some of this global distribution is likely due to some bacteria having very robust resting stages, for example thermophilic endospores reported from the Arctic (Hubert et al., 2009).

The relatively recent development of high throughput sequencing techniques has increased our sequencing capacity by two or more orders of magnitude (Fig. 2). The International Census of Marine Microbes pioneered this approach applying 454 pyrosequencing to samples from all the oceans, including the Arctic (Fig. 3). This effort used the same sequencing methods and bioinformatics pipelines with DNA from almost 800 different samples. Over 18 million sequences of the target single variable regions of

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