Microorganisms are numerous almost everywhere. Here is an epi-fluorescene micrograph from a northern Baffin Bay water sample. The sample was treated with a fluorescent probe which stains the DNA inside of the cells. Bacteria and the nucleus of single celled eukaryotic plankton appear in blue. The smaller points are bacteria and the larger are Eukarya. Photo: Connie Lovejoy.

5 µm

Chapter 11

Microorganisms

Author

Connie Lovejoy

Contents

SUMMARY

Microbes, defined here as Bacteria, Archaea and single-celled Eukaryota (protists) are ubiquitous and diverse members of all biological communities. In marine and many freshwater systems, photosynthetic microbes form the base of the food chain supporting higher trophic levels. Among the photosynthetic species are biologically diverse small flagellates that also graze on bacteria and other protists and hence are functional heterotrophs at times. Strictly phagotrophic protists are also diverse and contribute to the complexity of microbial food webs, with a multitude of trophic interactions. The fate of Arctic primary production emerges from the assembly of the entire microbial community. Heterotrophic bacteria break down fixed organic carbon and recycle nutrients, while other bacteria and Archaea with diverse metabolic capacities are active in the remineralization of carbon, nitrogen and other elements. There is a lack of long-term comprehensive baseline data on microbial biodiversity in terrestrial, freshwater and marine systems that largely impedes understanding ecosystem structure and resilience over both local and regional scales.

Because of their small size and often large populations, microbes in principle may have global distributions as they are transported by moving masses of air and water. Microbial communities are strongly selected for by their immediate environment, and successful global transport will be influenced by the ability of organisms to remain viable during transport between favorable environments. Species are more likely to have geographically restricted distributions if they lack a dormant stage or are specialists, and if their preferred environments are rare and distant from each other. Local communities may also resist invasions in the absence of physical or ecological perturbations that would give invading species or ecotypes an advantage. In the absence of ice cover, increased light availability and increased water column stratification can influence microbial community structure, affecting both phototrophic and heterotrophic species. Both the duration of the productive season and the species composition of protists have implications for higher food webs, thus ecosystem services by microbes are of direct relevance to wildlife and fisheries biologists as well as local communities. In addition, microbial community interactions largely determine the efficacy of the biological carbon pump.

The diversity of heterotrophic protists and other microbes is largely unknown, since for the most part they cannot be identified morphologically. Hence, sound historical records are lacking. New tools are being used to identify these heterotrophs from their DNA and RNA collected from the environment. Even among larger species of phytoplankton, cryptic species have been identified from DNA sequences. The small sub-unit ribosomal RNA (SS rRNA) gene is the most common target for gene surveys and enables the identification of microbes at the level of genus and even species and ecotype for some groups. In addition, genomic and transcriptomic signatures of microbes from the Arctic will provide valuable insight into the resilience and capacity of Arctic ecosystems. The recent rapid advances in sequencing technology will enable the expansion of microbial surveys, facilitating the integration of microbial biodiversity data into coupled biogeochemical climate models. Further, monitoring could provide the means to test whether there are linkages between climate change, environmental perturbation and the emergence of southerly species, enabling robust projections about dynamic shifts in ecosystem structure over time. For these reasons there is an urgent need to increase knowledge of microbial communities at the finest taxonomic and functional levels.

11.1. INTRODUCTION

Microbes represent the majority of biodiversity on Earth and are integral components of all ecosystems. In terms of numbers, microbes also dominate with c. one million cells per milliliter (ml) of seawater and most freshwaters. Marine sediments host an even more impressive number of bacterial cells per ml (in the order of 1 billion). Sea ice also harbors distinct microbial communities that live within brine channels and at high local concentrations (Deming 2002). Distinct communities can be found attached to the bottom of first year ice and occurring in surface melt ponds (Mundy *et al.* 2011). Concentrations of bacteria in Arctic soils are less than in temperate soils, but can still reach substantial numbers in key microhabitats (Yergeau *et al.* 2010, Wilhelm *et al.* 2011). Although heterotrophic protists and other microbes are the primary drivers of marine food webs and play key roles in freshwaters and soils, they are rarely included in general assessments of biodiversity (Archambault *et al.* 2010).

As reported in other chapters, climate and environmental change is rapidly reshaping northern ecosystems. These perturbations include the loss of summer ice, changes in the annual production cycle and changes in the depth of the most biologically active layers in both pelagic water columns and soils. Such environmental changes will have a direct effect on visible animals and plants (Falk-Petersen *et al.* 2009) and also have direct impact on the microbial food webs that support higher trophic levels.

In addition, as mentioned in other chapters, terrestrial and aquatic habitats merge over much of the sub-Arctic and Arctic. Distinct ponds and lakes are formed in polygons and runnels surrounding polygons within the permafrost, and in the high Arctic water increasingly remain as ice over the year. Deeper lakes are also scattered throughout the Arctic, and the microbial community structure of ponds and lakes is influenced by their depth, catchment area, orientation and underlying basin geology. Freshwater microbes are poorly studied with only sporadic reports of species. Most surveys of soil microbes have focused on disturbed sites with few reports on the microbes from pristine regions (Steven *et al.*

2008a, Martineau *et al.* 2010, Niederberger *et al.* 2010, Wilhelm *et al.* 2011). In this chapter, I provide a brief summary of existing knowledge, identify key gaps and suggest strategies for monitoring microbial biodiversity.

11.2. STATUS AND KNOWLEDGE

11.2.1. Bacteria

Prior to the application of molecular techniques, all that was known about the identity of bacteria in the Arctic was from culture studies of isolates. This approach continues to be valuable and provides unique insights into the metabolic capacity of microorganisms, especially those from extreme environments (Steven *et al.* 2008b, Niederberger *et al.* 2009a, 2009b). Sea ice bacteria are also represented in culture collections (Junge *et al.* 2002, 2003), but few unequivocally planktonic polar bacteria have ever been cultured. An alternative approach to culture studies are gene surveys, where the taxonomically informative gene coding for 16S ribosomal RNA (rRNA) is amplified by polymerase chain reaction (PCR), cloned and sequenced (Crump *et al.* 2003, 2009, Hollibaugh *et al.* 2007, Kellogg & Deming 2009, Jungblut *et al.* 2010, Harding *et al.* 2011, Lovejoy *et al.* 2011). The combination of culture studies and environmental gene surveys can reveal greater diversity than either alone (Wilhelm *et al.* 2011). Recently, high throughput sequencing technologies have been used to tag samples and enable massive parallel sequencing without cloning. This technique was first applied to marine Arctic water samples as part of the International Census of Marine Microbes (ICOMM; Galand *et al.* 2010, Kirchman *et al.* 2010). Those results indicate, as with most open ocean systems, that bacterial diversity has been underestimated by earlier approaches and showed that biogeography, history and water mass distribution were important determinants in the makeup of pelagic microbial communities. Similar studies of soil systems and freshwater have also indicated that bacterial diversity is much greater than previously thought (Yergeau *et al.* 2010, Wilhelm *et al.* 2011, Comeau *et al.* 2012a).

Salinity and oxygen are primary environmental drivers that select for microorganisms at the level of phyla. Freshwaters are dominated by *Betaproteobacteria* and freshwater clades of *Bacteroidetes*. *Bacteroidetes* are also commonly found in sea ice and marine Arctic surface waters along with *Gammaproteobacteria*. Sea ice communities vary within ice core horizons, and multiyear ice may be distinct from more biologically active first year ice (Staley & Gosink 1999, Bowman *et al.* 2012, Comeau *et al.* 2012b). *Alphaproteobacteria* are more frequent dominants in marine pelagic waters (Galand *et al.* 2008, 2010). *Gammaproteobacteria*, *Deltaproteobacteria*, *Actinobacteria* and *Alphaproteobacteria* are the most common classes in Arctic marine sediments (Ravenschlag *et al.* 1999, Li *et al.* 2009, Teske *et al.* 2011, Bienhold *et al.* 2012). *Acidobacter* and *Actinobacteria* have been reported from sub-Arctic and Arctic freshwaters and may be selected

for by particular environmental characteristics (Liebner *et al.* 2008). *Actinobacteria*, *Alphaproteobacteria* and *Bacteroidetes* tend be most abundant in the high Arctic, however as in other soil environments bacteria are very patchy both in terms of abundance, species composition and species turnover (Pellerin *et al.* 2009, Wagner *et al.* 2009). Seasonal changes in bacterial communities have also been reported with one sulphur-oxidizing species in the genus *Thiomicrospira* forming macroscopic streamers during winter and disappearing during the Arctic summer (Niederberger *et al.* 2009a). Similar species and associated communities are also reported from Svalbard thermal springs (Reigstad *et al.* 2011) indicating the importance of specialized micro-environments harboring microbial biodiversity. Recent metagenome analyses revealed that during transition from a frozen to a thawed state there are rapid shifts in many microbial, phylogenetic and functional gene abundances and pathways (Mackelprang *et al.* 2011).

Polar seas are well oxygenated, and bacterial chemosynthetic primary production has not been widely studied, although methane production is reported from ice covered waters (Damm *et al.* 2010) suggesting microbial activity apart from heterotrophy. Energy availability in the form of phytodetritus was suggested to be a main driver of diversity and activity for benthic bacterial communities at the Laptev Sea continental slope, which implies that changes in primary production and subsequent flux to the benthos will likely influence bacterial community structure and activity, with subsequent impacts on ecosystem functioning, such as C-cycling (Bienhold *et al.* 2012).

Ponds formed by permafrost thaw and polygon collapse may be major contributors to greenhouse gases via respiration of ancient carbon: both CO_2 and methane can be released from these systems (Rivkina *et al.* 1998, Wagner *et al.* 2009). Methane production may also be balanced by methane oxidation, where methanotrophs use methane as a source of carbon and energy (Liebner *et al.* 2009, 2011). Gene sequences of 16S rRNA associated with these methanotrophs, though rare, have also been recovered from polar seas (Galand *et al.* 2010, Kirchman *et al.* 2010). Overall, the dynamics and community composition in these systems is poorly understood. The suite of rare and occasional abundant taxa found in water columns, marine benthos and soil are likely involved in other diagenetic processes and require further study.

11.2.2. Archaea

Archaea are a separate domain of life apart from Bacteria and Eukarya. When they were first discovered, Archaea were thought to be uniquely extremophiles, inhabiting hot springs, supersaturated saline waters and highly acidic environments. They are now recognized as being ubiquitous in all marine waters and frequent members of freshwater microbiota (Galand *et al.* 2006, Pouliot *et al.* 2009). In terms of numbers, Archaea may be more important in polar seas compared with other systems

and are especially abundant in winter (Alonso-Saez *et al.* 2008). The two most abundant archaeal phyla in the ocean belong to the Euryarchaeota (Marine Groups: MGII, MGIII and MGIV) and Thaumarchaeota, also referred to as Marine Group I (MGI) and originally classified with Crenarchaeota (Spang *et al.* 2010). The only free living cultivated representative of MGI, *Nitrosopumilus maritimus*, is able to oxidize ammonia and fix inorganic carbon (Konneke *et al.* 2005, Walker *et al.* 2010), and the majority of Thaumarchaeota in the oceans appear to have the ammonia monooxygenase gene (*amoA*) involved in ammonium oxidation and nitrification (Francis *et al.* 2007). Thaumarchaeota and the Archaeal *amoA* gene have been widely reported from soils generally (Leininger *et al.* 2006) and specifically from Arctic soils (Wilhelm *et al.* 2011) as well as Arctic freshwaters (Pouliot *et al.* 2009). Thaumarchaeota and the *amoA* gene are found throughout the marine Arctic (Hollibaugh *et al.* 2007).

Marine Group II Euryarchaeota are widespread and reported from throughout the world oceans, but they have remained uncultivated. Although some are reported to take up amino acids (Ouverney & Fuhrman 2000), and a recent study using enviromental gene assembly found evidence of a heterotrophic capacity (Iverson *et al.* 2012), some groups are likely chemolithotrophic[1] as well (Martin-Cuadrado *et al.* 2008). Even less is known about Marine Group III Euryarchaeota, which are rare in the global oceans, but appear to be common in the mesopelagic zone of the Arctic (Galand *et al.* 2009a). As with MGII, there is no clear understanding of the functional role of these microorganisms in the sea, but if they are chemolithotrophic, their sheer numbers suggest they could contribute to oceanic inorganic carbon fixation.

11.2.3. Heterotrophic and mixotrophic protists (Eukarya)

Protists are morphologically more diverse than Bacteria and Archaea. They are also phylogenetically and functionally diverse; the term protist is for convenience, not a valid taxonomic classification (Adl *et al.* 2005, 2007), and evolutionary relationships at the highest taxonomic ranks remain controversial. While larger protists such as ciliates, testate amoeba and dinoflagellates have a well-defined taxonomy based on morphology, the diversity of smaller flagellates is underestimated, and the lack of qualified taxonomists working on specific groups is problematic. As with Bacteria and Archaea, investigations using high throughput sequencing technology will facilitate comparisons among sites and seasons (Comeau *et al.* 2011). The need for taxonomic verification of samples to match historical records to their genetic signature remains a major challenge.

Photosynthetic microalgal groups are reported in the chapter on plants (Daniëls *et al.*, Chapter 9). However, it is important to reiterate that these are not plants; many

of these algae are also mixotrophic, supplementing their energy and nutrient requirements via phagotrophy[2] and sometimes osmotrophy[3]. Mixotrophic Chrysophyceae are particularly common in Arctic freshwaters (Kristiansen 2008, Charvet *et al.* 2012) and are also reported from sea ice and Arctic marine waters (Lovejoy *et al.* 2002, Rozanska *et al.* 2008) and include everything from small free living flagellates to large tree shaped colonies of *Dinobryon balticum* and other colonial species. In addition to Chrysophyceae, other mixotrophs among the stramenopiles[4] (Heterokonta) include members of the Dictyophyceae, Pelagophyceae, Raphidophyceae (Scott & Marchant 2005, Poulin *et al.* 2011) and Bolidophyceae, which are all frequently recovered in marine Arctic 18S rRNA gene surveys (Lovejoy *et al.* 2006, 2011).

Recent work suggests that the Parmales, which have siliceous walls and have been reported from electron microscopy studies of polar waters (Kosman *et al.* 1993), are closely related to or within the flagellated bolidophytes (Ichinomiya *et al.* 2011). In Antarctic sediment cores, Parmales have been considered paleoenvironmental indicators of cold water (Franklin & Marchant 1995), but to my knowledge have not been reported as such in the Arctic. Other major phyla level groups, which are mixotrophic, are also commonly reported from Arctic seas, sea ice and freshwaters, including Euglenozoa, Cryptophyceae, Haptophyceae and many small dinoflagellates (Lovejoy *et al.* 2002, 2006, Poulin *et al.* 2011, Charvet *et al.* 2012). Chloroarchniophytes, which are Cercozoa with chlorophyll *b* (derived from a green algal secondary endosymbiosis), have been recovered from most surface marine 18S rRNA gene surveys (Lovejoy *et al.* 2006, 2011, Lovejoy & Potvin 2011).

There have been fewer studies on primarily heterotrophic protists that depend on bacteria and other protists for energy (nutrition). Key non-marine, larger heterotrophic protists from Arctic freshwater habitats were treated in the chapter on terrestrial invertebrates, where it was noted that ciliates and testate amoebae are common (Hodkinson, Chapter 7). Smaller heterotrophic protists can be assumed to be common in sub-Arctic to high Arctic ponds and lakes, but very few reports are available. One recent 18SrRNA gene survey found that ponds and lakes have typical freshwater phylotypes of non photosynthetic heterokonts, as well as choanoflagellates, Cercozoa and bodinids (Charvet *et al.* 2012). Extensive surveys of smaller protists in Arctic soils using molecular techniques are planned but have not been undertaken (S. Adl pers. com.)

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1 Organisms that obtain energy from the oxidation of inorganic compounds.

2 Particles such as bacteria that are engulfed by a cell; protists are often phagotrophic feeders.
3 The uptake of dissolved organic material by an organism, where the solute permeates the membrane. Fungi and bacteria commonly use osmotrophy to obtain energy.
4 The collection of organisms that either currently or ancestrally had two different types of flagella, specifically a flimmer flagella and a smooth flagella; these include the diatoms, brown algae, chrysophytes and related phyla.

Compared with freshwaters, marine waters have been better investigated both by way of microscopy (Appendix 11; Vørs 1993, Ikävalko & Gradinger 1997, Lovejoy *et al.* 2002) and more recently using molecular 18S rRNA gene surveys. Such surveys have highlighted the diversity and distribution of small heterotrophic protists (Lovejoy & Potvin 2011, Terrado *et al.* 2011), many of which have never been brought into culture (Appendix 11). Among the small marine flagellates are choanoflagellates, Katablepharidia, *Telonemia*, cerozoans, diplomonads[5] and diverse marine stramenopiles (MASTS; Massana *et al.* 2006). MASTS are only known from their 18S rRNA gene sequences, but most are thought to be phagotrophic (Massana *et al.* 2004). One group, MAST 3, is reported to be related to an epibiont[6] of marine algae (Gomez *et al.* 2011). Also among heterotrophic flagellates are un-cultured flagellates that were designated picobiliphytes or biliphytes (Not *et al.* 2007). These cells are phylogenetically distant from other protist groups, and recent genome sequencing of an enviromental cell population indicates that they are probably heterotrophic (Yoon *et al.* 2011). The biliphytes are nearly always recovered in Arctic clone libraries (Lovejoy *et al.* 2011) and appear to be most common in winter (E. Medrinal and C. Lovejoy unpubl.).

In marine waters, classic Rhizaria (Polycystinea, Acantharia) are also frequently recovered from 18S rRNA gene libraries from the Arctic; often the sequences are most similar to sequences from the deep ocean (Lovejoy & Potvin 2011). These fragile cells are not well preserved from net or bottle samples, but their frequency in environmental gene surveys suggest they may be important phytoplankton predators in polar waters. As in other oceanic regions, alveolates, which include dinoflagellates, ciliates and uncultivated groups, are common and very diverse. Dinoflagellates and ciliates have long been noted in microscopic surveys (Okolodkov & Dodge 1996, Okolodkov 1999, Lovejoy *et al.* 2002) and are also frequently recovered in 18S rRNA gene surveys. While about half of known dinoflagellates are photosynthetic, it is likely that all prey on phytoplankton and other protists (Taylor *et al.* 2008). Ciliates also graze on phytoplankton, other protists and each other (Montagnes *et al.* 2010).

Gene surveys have also revealed uncultivated alveolates mostly falling into two major clades (Group I and Group II Alveolates; Lopez-Garcia *et al.* 2001). These two groups are found in nearly all marine samples including the Arctic (Lovejoy *et al.* 2006). These uncultivated alveolates are within or related to the parasitic Syndiniales (Skovgaard *et al.* 2005, Guillou *et al.* 2008). The most commonly recovered clade in the Arctic belongs to Syndiniales Group II, which contains the dinoflagellate parasitoid, *Amoebophyra*. Others are related to fish parasites (Skovgaard *et al.* 2009). All known representatives of the Syndiniales have complex life stages and are either parasitoids, parasitic or commensally dependent on a host.

11.3. STATUS AND TRENDS

11.3.1. Endemic species, population sizes and genetic diversity

While there are phylum-level similarities among communities from the different habitats, at the genus and species levels there is strong environmental selection with freshwater, brackish, sympagic and marine species very distinct from one another. Despite this, it has been strongly debated whether or not microbes have a biogeography or if endemic microbes even exist (Finlay & Fenchel 2004, O'Malley 2007). The debate centers on major differences between single-celled, mostly asexual-reproducing organisms and multicellular, mostly sexual species (Medlin 2007, Yang *et al.* 2010). The frequency of genetic exchange is the major difference; in addition microbes can attain very high populations via clonal division, which in combination with their small size could lead to global transport by winds and water given sufficient time. The original proposition that, for microbes, everything is everywhere came with an important proviso; the environment selects (de Wit & Bouvier 2006 citing Beijerinck 1913). In addition, as with plants and animals, some groups of microbes are better able to disperse between favorable environments and maintain viability over long periods.

The bipolar distribution of several sea ice bacteria (Staley & Gosink 1999) and protist taxa has been used to argue for lack of endemism among microbes; e.g. the cyst-forming dinoflagellate *Polarella glacialis* is found associated with ice in both the Arctic and Antarctic (Montresor *et al.* 2003). Until recently, this debate was largely semantic based on expert opinion on the definition of species, as most microbes are not in cultivation and type specimens do not exist. As more sequences from widely dispersed regions become available, biogeographic studies are becoming more common, and a level of similarity among taxa from different regions can by defined at levels from genera to strain, depending on the resolution of the marker (Koester *et al.* 2010). Cloning and sequencing studies of the 18S rRNA gene suggest a certain level of, if not endemic, then certainly restricted distribution of several marine Arctic protists (Lovejoy & Potvin 2011). A recent survey of over 2,500 sequences of small potential mixotrophs originating from Arctic 18S rRNA gene clone libraries indentified 14 potential Arctic taxa. Since most are not cultivated these were refered to by their designated type clone names (in parenthensis). Specifically these were: one Prasinophyceae (NPK2_194), two Haptophyceae (NOR50.28 and CFL133DA03), one Cryptophyceae (MD65.37), one Dictyochophyceae (05M80r.07), three Pelagophyceae (NW614.28,

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5 Organisms that belong to the Diplomonadida, which are mostly parasites and include Giardia and other vertebrate parasites.

6 An organism that grows on the surface of other organisms.

05M80r.43, and CB1901L07) two Chrysophyceaceae (ES069_E8 and AN0678L07) and finally three distinct taxa withing the bolido-parmales (CB1901S35, NW617.26 and NW614.34). All of these sequences were retrived from at least two independent studies and are therefore probably common and widespread in the Arctic Ocean (Terrado *et al.* 2012). Among other protists with possible restricted distributions are several ciliates, dinoflagellates and Acantharia (Lovejoy & Potvin 2011). Bacterial and Eukaryote SS rRNA gene sequences with best matches to sequences previously reported from freshwater and marine Arctic sites have been recovered from Arctic snow and air suggesting the importance of local transport reinforcing species distribution patterns (Harding *et al.* 2011). It is also important to emphasize that DNA based analysis can only record the historic input of microbes into a system. For example, Hubert *et al.* (2009) report on the occurrence of thermophilic bacteria in Arctic sediments, showing the importance of cold, deep sediments as archives of bacterial diversity.

Environmental gene surveys can be carried out on archived samples where DNA has been preserved, and on new samples collected specifically for monitoring. The application of high throughput sequencing will enable much more extensive comparisons of different regions and habitats (Comeau *et al.* 2011). Since species-specific identification is only as reliable as the reference data base, the need for ongoing studies using culturing and cloning and sequencing the entire SS rRNA gene and other taxonomically useful markers will remain. Global comparisons of the bacterial and archaeal sequences from many different sites are also underway by a group of polar ICOMM researchers. A recent bipolar comparison of marine surface and deep sea bacteria from this data revealed that the communities from the Arctic and Antarctic, while more similar to each other than to communities from the temperate oceans, grouped apart, suggesting isolation at time scales relevant to bacterial evolution (Ghiglione *et al.* 2012).

Knowledge of transcriptomes[7] of isolated species and metatranscriptome[8] data can be used to identify key genes in the environment. At the functional level of the gene, bipolar distributions seem clear at least among Archaea. For example, ammonia monooxygenase gene sequences, which are > 99% similar, occur in both Polar regions (Kalanetra *et al.* 2009). However, whether this reflects species and implied genetic exchange or the conserved nature of the genes being investigated will require single cell sequencing and further cultivation of isolates from both poles. Finally, there is some disagreement on the nature and definition of microbial species. Comparative studies at fine taxonomic levels will require agreement on the definition of a species or ecotype

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7 The sum of mRNA transcripts found in an organism. Transcripts of genes are used as evidence that a functional gene is being expressed.
8 The sum of transcripts from a community of organisms, for example all of the microbes in a soil or water sample.

and well-thought-out global surveys. Even putatively closely related species may have vastly different capabilities and be much less similar at the whole genome level compared with higher animals and plants (Bapteste *et al.* 2009, Worden *et al.* 2009). This implies that Arctic ecotypes may be a unique genetic resource regardless of taxonomic assignment, and loss of genetic diversity will be a consequence of habitat loss. In particular, specific adaptations to subzero temperatures at the enzymatic level could be of interest for biotechnology applications (Deming 2002, Varin *et al.* 2012). Bioprospecting for both genes and the bacteria that harbor them is already occurring in the Arctic and is an issue that needs to be considered (UNU-IAS web).

11.3.2. Trends

Microbial communities are expected to be influenced by environmental changes that are now underway. General projections of the effect of global environmental changes on microbes in Arctic ecosystems are generally based on the predicted increase in temperature and potential changes in primary production (Kirchman *et al.* 2009, Vincent *et al.* 2009, 2010, Kritzberg *et al.* 2010). According to a study based on data from the western Canadian oceanographic region, recent changes in ice cover have influenced microbial community structure (Comeau *et al.* 2011), likely caused by increased light availability and increased water column stratification (Michel, Chapter 14). Both phototrophic and heterotrophic species are vulnerable to change, as the seasonal open water increases over time and space. There is accumulating evidence that species assemblages among Bacteria, Archaea and Eukarya co-occur, and distinct communities re-appear annually in the same region (Beman *et al.* 2011, Steele *et al.* 2011). There is a need to identify existing patterns in the Arctic to facilitate efforts to predict ecosystem changes and microbial community structure following anthropogenic and climatic forcing (Lovejoy 2011). The timing and extent of the spring surface bloom will change, along with the timing and geographical extent of ice edge blooms with consequences for zooplankton and higher food webs (Soreide *et al.* 2010). Changes in primary productivity and subsequent export to the benthos (Michel, Chapter 14) will also likely have an impact on benthic bacterial community structure and activity (Boetius & Damm 1998, Bienhold *et al.* 2012, see also Josefson & Mokievsky, Chapter 8). Day length can influence food quality as well as species composition (Leu *et al.* 2010). Ongoing loss of ice and earlier blooms could result in a rearrangement of food webs in the Arctic, since annual light availability at high latitudes remains fixed and there is an increased probability of decoupling production patterns from annual animal cycles resulting in major ecosystem shifts (Grebmeier *et al.* 2006).

In addition, microbial community interactions and dominant species largely determine the efficacy of the biological carbon pump where CO_2 is drawn down from the atmosphere and sequestered in the deep ocean. This

absorption of CO_2 by the global ocean is now affecting the pH of oceanic waters and the biological availability of carbonate and aragonite minerals. There are already signs of such changes in the Arctic Ocean (Carmack & McLaughlin 2011), and these pH effects will add to the selection pressures on microbial community structure including effects on organisms with calcium and aragonite scales and structures (see also Josefson & Mokievsky, Chapter 8, and Michel, Chapter 14). Although the main marine microalgae with carbonate scales, coccolithophores, are rare in the Arctic, other calcifying species including some cyst-forming dinoflagellates could well be affected. The influence of pH on the metabolism of microbes in the ocean has been little explored, but a recent study suggests that ocean acidification could have an effect on microbial ammonia oxidizing communities (Kitidis *et al.* 2011). Such communities are key players in the Arctic nitrogen cycle, which is strongly linked to circulation patterns in the Arctic Ocean (Galand *et al.* 2009b), which in turn will be affected by climate change. There is an urgent need to acquire sufficient understanding of community assemblages and functions to predict how these factors will interact.

In sum, there will always be microbial communities, but there will be taxonomic adjustments to new circumstances. Such ecosystem changes may have unforeseen consequences on global biogeochemical cycling and higher trophic levels in the Arctic.

11.4. CONCLUSIONS AND RECOMMENDATIONS

11.4.1. Sensitive areas and hotspots

In the terrestrial and freshwater habitats, areas identified either as sensitive or as hotspots for animals and plants should also be considered as microbiologically significant regions. In addition, unique or rare habitats such as saline springs should be protected to preserve unique biomes and specialized microbiota. In coastal and oceanic regions, areas where mammals and birds congregate should also be monitored. For example, marine productivity is related not only to the quantity of photosynthetic biomass produced but also the quality. In oceanic regions, the diversity and stability of microbial food webs dictates lipid concentrations in the zooplankton that support higher trophic levels. As longer ice free periods become the norm, microbial food chains are predicted to lengthen, and less energy will be available to the highest trophic levels in the oceans (Lovejoy 2011). Such changes will also have major impacts on benthic communities and on the carbon and nutrient cycling that occurs in the benthos (see also Josefson & Mokievsky, Chapter 8). The potential loss of multiyear ice as a habitat and changes in the duration and type of sea ice with different communities (Comeau *et al.* 2012b) will have consequences for biodiversity and carbon cycling. More research is needed to better estimate which communities may be lost as a result of the loss of summer sea ice. These changes are likely to have significant effects on the diversity and functioning of Arctic ecosystems. In terrestrial based systems, increased liquid water, higher temperatures and longer growing seasons will affect all biological activity, and northward expansion of species can be expected. Although at present much of the Arctic appears poor in life, microbial communities are active and complex, and 'non-hotspot' regions need to be monitored as well as highly productive regions in order to anticipate new distributions and community associations. Microbes will respond to ecosystem changes much sooner than higher plants and invertebrates and are thus sensitive indicators of directional changes.

11.4.2. Key knowledge gaps and recommendations

Ecosystem assessments and the role of complex interacting factors, which may influence ecological patterns, can only be explored through long time series of biological collections and surveys at local to regional scales. The only open-ocean long-term observatory in the Arctic is HAUSGARTEN, coordinated by the Alfred Wegener Institute for Polar and Marine Research (Soltwedel *et al.* 2005; see also Josefson & Mokievsky, Chapter 8). The Arctic is vastly under-sampled and heterotrophic protists, Bacteria and Archaea play a critical role in ecosystem support. Currently, there are only a small handful of researchers interested in microbial biodiversity and how it directly relates to ocean ecosystem function. There is a need to foster greater interest in microbial ecology among Arctic researchers. Microbial communities must be included in any Arctic monitoring effort aimed at understanding biodiversity and ecosystem function.

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Appendix 11: www.abds.is/aba-2013-appendix-11