Chapter 9
Microbes and the Arctic Ocean

Iain Dickinson, Giselle Walker, and David A. Pearce

Abstract It is surprising how little we really know about the microorganisms that live within the Arctic Ocean and in particular their role in the marine food web. A comprehensive food web study is yet to be conducted, and although many studies talk of an Arctic marine food web, publications normally focus on just one aspect of it. In some way, it mirrors our knowledge of the deep sea. We know it exists, we know the main interactions and pathways, but a great deal of the background information and detail is lacking. The single most important part of our research, therefore, is to understand the role and function of microorganisms in the environment. A fitting analogy is perhaps an iceberg. We know what it looks like, we know roughly what it does and how it behaves, we even know that the majority of the iceberg is hidden from view. However, we know very little about the effects of an iceberg on the general environment around it. Further, if we induce change in the behaviour of that iceberg, we have little idea what effect it might have. This is due to a combination of factors; (1) the complexity of the science, (2) the ambition, cost and logistics of conducting experimental work in these systems, (3) the fact that the existing, relatively simple model is sufficient for most purposes, (4) technological and methodological limitations and (5) research funding tends not to favour supporting ambitious long term ecological studies which can be very expensive. However, as with most questions in science, the harder we look, the more there is to

I. Dickinson
Northumbria University, Faculty of Health and Life Sciences, Ellison Building, Newcastle-upon-Tyne NE1 8ST, UK
e-mail: iain.dickinson@northumbria.ac.uk

G. Walker
The University Centre in Svalbard (UNIS), P.O. Box 156, 9171 Longyearbyen, Svalbard, Norway

D.A. Pearce (✉)
Northumbria University, Faculty of Health and Life Sciences, Ellison Building, Newcastle-upon-Tyne NE1 8ST, UK

The University Centre in Svalbard (UNIS), P.O. Box 156, 9171 Longyearbyen, Svalbard, Norway

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 OET, UK
e-mail: david.pearce@northumbria.ac.uk

C.J. Hurst (ed.), *Their World: A Diversity of Microbial Environments*, Advances in Environmental Microbiology 1, DOI 10.1007/978-3-319-28071-4_9

find, and for every question we answer, a number of new questions arise. In this chapter, we attempt to give an overview of what is known about the microbial community in the Arctic marine food web, assess why this knowledge is relatively limited and pose some of the questions that remain to be answered.

9.1 What Is a Food Web?

A food web describes feeding relationships in an ecosystem. A simple food chain describes a linear flow of energy from primary producers to consumers, eventually leading to the apex predator. Decomposers recycle material from the food chain back into the environment. However, in reality there are trophic links between many different producers and consumers of various sizes, so it is more appropriate to consider the whole food web rather than a simple chain.

9.2 What Is Special About the Arctic Ocean?

The Arctic Ocean and its environment encompass parts of Russia, Canada, Greenland, Norway, Alaska and Iceland. The Arctic Ocean is unique, due to its location on the planet and its relationship with the sun. North of the Arctic Circle beginning at 66°33′N, the region experiences 24 h daylight in the summer and 24 h darkness in the winter, and this, perhaps more than any other factor, drives the Arctic Ocean's unique ecology. As well as light, low temperatures may also have cascading effects on the interlinked and delicately balanced food web. The Arctic Ocean is relatively shallow and is mostly surrounded by land, unlike the Southern Ocean. Land masses surrounding the Arctic Ocean drain huge areas of land and contribute vast quantities of nutrients into the coastal ecosystem. As a result of the unique nature of the Arctic Ocean, the nutrients available and the long periods of daylight during the summer, the Arctic Ocean is rich in life. The presence of ice and its attendant snow cover, and total darkness during the winter months, means that this region has a distinctive ecology, in terms of the phytoplankton and zooplankton, the animal populations and their associated environmental factors. The Arctic Ocean ecosystem therefore has a distinct and complex food web, quite unlike those found elsewhere. Arctic marine species have adapted to the cold temperatures to take advantage of the nutrient-rich waters surrounding the ice edges and continental shelves. Indeed, the highest biomass occurs along the coastlines. This observation is consistent with river runoff, nutrient availability and increased stability along coastlines, as well as the convergence of Atlantic water and Arctic water in the Barents Sea (Smetacek and Nicol 2005). Examples of specialist species endemic to the Arctic Ocean are exemplified by the charismatic megafauna: the polar bear, the walrus and the

narwhal, all of which depend on sea ice for hunting, reproduction or protection (Stirling 1997; Tynan and DeMaster 1997). However, most of what we know about this ecosystem is based mainly on summer observations as expeditions to the remote Arctic in the winter are both difficult and expensive.

9.3 The Fundamental Importance of Sea Ice

Sea ice still covers significant portions of the Arctic Ocean, particularly in winter, forming at temperatures below the freezing point of seawater. In the polar regions, with an ocean salinity of 35 ppt, the water begins to freeze at −1.8 °C (NSIDC 2015). The formation and structure of sea ice is reviewed in detail by Petrich and Eicken (2009). With its high albedo, the ice and its snow cover reduce the amount of incoming solar radiation absorbed at the ocean surface by reflecting much of that radiation back into space. Changes in the timing of formation and extent of ocean coverage by the sea ice impose temporal and spatial variation in energy requirements and food availability for higher trophic levels. Mismatches in the patterns of climate and biology can lead to decreased reproductive success, lower abundances and changes in the distribution of organisms (Moline et al. 2008). Sea ice is critical for Arctic marine ecosystems in at least two important ways: it provides a habitat for photosynthetic algae and a nursery ground for both invertebrates and fish during times when the water column does not support phytoplankton growth. As the ice melts, releasing organisms into the surface water, a shallow mixed layer forms which fosters large ice-edge blooms important to the overall productivity of Arctic seas (Nielsen et al. 2002). Sea ice is one of the largest habitats in polar oceans and can cover up to 13 % of the world's surface in winter, so it has a massive influence on the Arctic marine food web (Eicken 1992). In winter, sea ice constitutes a thermal barrier against the cold winter atmosphere with the result that the interface between the ice and the seawater remains near the temperature of seawater (Krembs and Deming 2011).

Sea ice imposes a three dimensional structure on the Arctic Ocean microbial community. Sea-ice algal growth is limited by space availability within the sea ice itself rather than by nutrient availability, due to the high retention of nutrients in the sea ice and low abundance of prokaryote grazers (Becquevort et al. 2009). Frost flowers contain high concentrations of bacteria compared to other formations of sea ice; they can mediate long-range wind transportation of microbes, which can themselves influence atmospheric processes by influencing (e.g.) photochemistry (Bowman and Deming 2010). Bacterial–algal relationships in sea ice are also hindered by substrate and temperature limitations, limiting primary production through the microbial loop within the sea ice (Stewart and Fritsen 2004).

The Polar regions have, so far, shown the greatest sensitivity to rising global temperatures. Sea ice has shown a rapid decrease in both area and thickness over the

past 10 years (Comiso et al. 2008). Multilayer sea ice occurs when sea ice survives the summer months and refreezes, often increasing in thickness. Bowman et al. (2012) found unique microbes in multiyear ice not seen in first year ice, including *Cyanobacteria*, *Spartobacteria* and *Coraliomargarita* in sufficient numbers to suggest a niche occupation. However, the thickness of the sea ice has rapidly reduced in recent years (Serreze et al. 2007). Ongoing climate warming is causing a dramatic loss of sea ice in the Arctic Ocean, and it is projected that the Arctic Ocean will become seasonally ice-free by 2040 (Kedra et al. 2015). The thickness of sea ice can also drastically alter the activity and composition of marine microorganisms (Mock and Junge 2007). The common theory that the formation of first year sea ice acts as a selective pressure on microbial communities was found to be false by Collins, Rocap and Deming (2010), who sampled sea ice on a weekly basis over winter and only found a drop in microbial abundance rather than a change in community structure. High latitude changes in ice dynamics and their impact on polar marine ecosystems are reviewed by Moline et al. (2008). Whilst the effect of ice dynamics is easily visible when considering the impact on organisms higher in the food chain such as polar bears (through reduction in hunting grounds, etc.), the effect of changing ice dynamics is much less visible on microorganisms at the base of the food chain. Marine microorganisms play a vital role in global biogeochemical cycling (Helmke and Weyland 2004), and are important primary producers in polar environments (Legendre et al. 1992), a decline in microbial activity will have a direct influence on species higher up the food chain such as mammals, fish and birds.

Sea ice can be divided into four distinct parts: ice surface, ice matrix, under the ice and brine channels and pockets. When sea water freezes and sea ice forms, dissolved air, inorganic and organic matter are expelled into concentrated brine which forms pockets and channels in the ice depending on the temperature of the ice (Eicken 1992). Temperature affects the salinity of the pockets, with colder temperatures forcing a higher salinity into a smaller volume of brine. In columnar ice, −5 °C is the tipping point between permeable and impermeable ice, allowing channels to form between brine pockets. This is because warmer ice has a higher volume of brine in the channels (above 5 %) allowing for more convective flow within the sea ice (Golden et al. 1998). Conditions within these pockets and channels can vary greatly depending on their depth in the sea-ice column. Virus-containing bacteria that were isolated from brine pockets in sea ice had a much greater viral load than those isolated from sea water (Wells and Deming 2006). Typically, the ice closer to the ice–air interface is much colder than the equivalent ice–sea water boundary, reducing surface ice volume and increasing its salt concentration. Conversely, irradiance will be higher at lower depths in the ice since the light has less ice to travel through than to deeper ice layers. When sea ice begins to freeze, diverse mixed populations of microorganisms are forced into a new cold, dark, hypersaline environment and must possess the correct adaptations to survive and remain active. As the season progresses, there is a gradual transition from a microbial population similar to that of the open seawater to a new psychrophilic heterotrophic population (Thomas and Dieckmann 2002) which is fuelled by the

organic carbon released from the death and lysis of microorganisms less adapted to survive (Thomas et al. 2001).

The Arctic marine food web relies heavily on the availability of organic carbon within the sea ice. Microbial heterotrophs rely on dissolved or organismal organic carbon, provided by marine autotrophs or indirectly via the microbial loop (Fenchel 1982; Sanders et al. 1992). The melting or thinning of sea ice in spring releases a vast number of microbes into the water column under the sea ice, and coupled with the phytoplankton bloom brought about by increasing light availability, this melting provides a high concentration of organic matter into the underlying seawater (Sherr and Sherr 2007). There are two main beneficiaries of this influx of organic matter. Cells avoiding high-wavelength radiation, and dead cells, quickly sink and provide nutrients to the benthic community such as crustaceans and molluscs. Cells growing in surface waters provide a food source to pelagic zooplankton. The water column directly below the sea ice of both poles is dominated by calanoid copepods, along with pteropod gastropods, siphonophores, appendicularians, chaetognaths, hyperiid amphipods, mysids and benthic invertebrate larvae (Schnack-Schiel 2003). The high concentration of these organisms provides the perfect feeding ground for polar fish including the polar cod, a species that represents the bridge between the upper and lower trophic levels (Gradinger and Bluhm 2004).

Higher trophic level organisms such as seals and birds must rely on polynyas to access the rich pelagic zone below the sea ice. Polynyas are characterised by an open water source surrounded by sea ice (Stringer and Groves 1991), and allow diving mammals and birds to hunt for polar cod and other fish, which in turn feed on pelagic and benthic invertebrates. The sea ice also provides nesting grounds for these birds and mammals, which in turn provides larger predators such as Polar bears and Arctic foxes with an opportunity to hunt for these animals as food. Seasonal sea ice can have a great effect on primary production in an area. However, the decline in primary production associated with sea ice formation may not have as great an effect on species at it does at higher trophic levels, who can change their diet from fresh algal material to detritus when primary production drops (Norkko et al. 2007).

9.4 Structure of the Arctic Marine Food Web

In its simplest form, the Arctic marine food web starts with primary producers, which comprise photosynthetic microbes that use either chlorophyll or bacteriorhodopsins to convert light into carbon (Béjà et al. 2000). Microorganisms exist within the sea ice in pockets and channels containing high concentrations of salt and other elements such as carbon, nitrogen, silica and iron. The cycling of these elements by microorganisms plays a vital role in the initial food chain, altering the abundance of microorganisms available to grazers between summer and winter. Carbon dioxide, ammonium, silicic acid and iron are all mass utilised in summer months by photosynthesising microalgae, which in turn provide organic carbon and

oxygen for heterotrophic bacteria during the winter, which provides a large biomass for grazers during spring melts. The two main sources of primary production in Arctic ecosystems are sea-ice algae and phytoplankton in the water column (Søreide et al. 2006). These are then consumed by primary consumers, heterotrophic protists, other small eukaryotes, larvae and also bacteria (Fenchel 1988; Sanders et al. 1992; Sherr and Sherr 2007). Ice algae are a very important part of the marine food web, contributing on average 57 % to the total Arctic marine primary production (Gosselin et al. 1997). The organisms that eat algae, called zooplankton grazers (such as *Gammarus wilkitzkii*), seek not only food in this algal-rich ice but also protection from their own predators. Arctic cod (*Boreogadus saida*), an important food source for many marine mammals and birds, use the same habitat as nursery grounds (Krembs and Deming 2011), and their larvae feed on single-celled protists (i.e. algae and protozoa). The protists and bacteria are also lysed by the virus community, known to be about 10× as numerous as the bacteria. Large phytoplankton cells, such as diatoms and dinoflagellates, are the primary food of the zooplankton. Secondary consumers, largely fish species including polar cod, feed on these zooplankton, acting as a bridge between lower trophic levels and apex predators such as seabirds, whales, arctic foxes and polar bears. Excretions of metabolic products and debris from dying cells contribute to an increasing pool of organic material. As the ice melts in summer, this material releases into the water column, where it contributes to the vertical flux of material that fuels both pelagic and benthic food webs (Krembs and Deming 2011). However, this simplified description does not take into account the huge number of species involved, estimated to be between 9500 and 54,500 taxa (Archambault et al. 2010). In a recent study, Lovejoy and Potvin (2011) estimated that the number of picoplankton (plankton species less than 2 μm in diameter) operational taxonomic units (considered as roughly analogous to species) was ~45,000 (which include the archaea, picoeukaryotes and bacteria) in the Arctic Ocean. The food web is complex: species of different sizes can compete for the same sources of food, and losses of energy (through e.g. death, viral lysis, leakage of nutrients) at each trophic level can be picked up by heterotrophs at lower trophic levels (Azam et al. 1983). This makes the complexity absolutely staggering and our knowledge of the detailed interactions limited. To add to this, at least 10 % of the prokaryote population is as yet unknown. Many studies of distinct aspects of the Arctic food web now exist. Indeed, a number of very good reviews cover what is known of the topic in some detail: Bluhm and Gradinger (2008), Gradinger (2009), Darnis et al. (2012) and Kedra et al. (2015).

9.5 Viruses

Viruses are an important and often overlooked component of the marine food web (Fuhrman 1999; Suttle 2005, 2007), and they have been known to exist in the Polar regions for some time (see review by Pearce and Wilson 2003) where high viral infection rates have been observed (Säwström et al. 2007). Genome size

distributions indicate variability and similarities among marine viral assemblages from diverse environments (Stewart and Possingham 2005). Sequence analysis of marine virus communities reveals that groups of related algal viruses are widely distributed in nature (Short and Suttle 2002). Global diversity is very high, presumably encompassing several hundred thousand viral species, and regional richness varies on a North-South latitudinal gradient. The marine regions have been shown to have different assemblages of viruses, e.g. prophage-like sequences are most common in the Arctic (Angly et al. 2006), following similar patterns to other Polar environments (Aguirre de Cárcer et al. 2015). However, ubiquity has also been described. To this end, nearly identical bacteriophage structural gene sequences are widely distributed in both marine and freshwater environments (Short and Suttle 2005), with marine T4-type bacteriophages found to be a ubiquitous component of the dark matter of the biosphere (Filée et al. 2005). Regional differences include the abundance and production of bacteria and viruses in the Bering and Chukchi Seas (Grieg et al. 1996). These communities are not static and can be quite dynamic, over time (Wells and Deming 2006). Studies exist which target specific aspects of the microbial ecology of Arctic marine viruses, such as those that infect psychrophiles (Borriss et al. 2003) and whether there is a cost associated with virus resistance (Lennon et al. 2007). High-throughput sequencing will allow better studies of specific microbiomes, such as the highly divergent picornavirus found in marine mammals (Kapoor et al. 2008), and lead us to better understand the natural role of viruses in gene exchange (Hambly and Suttle 2005). Going forward, we are sure to gain a better understanding of what shapes viral distribution, including how viral activity controls both prokaryotic and eukaryotic populations, their activity and other interactions within the Arctic food web. However, the cultivation of key viral groups and an understanding of the activity of specific virus populations in biogeochemical cycling remain as key challenges in this field.

9.6 Prokaryote Microbial Diversity

Much more is known about the diversity and phylogenetic relationships of the prokaryote community in Arctic marine food webs. In particular, there are several studies dealing with total prokaryote diversity and its limits (Curtis et al. 2002), diversity in permanently cold marine sediments (Ravenschlag et al. 1999) and the water column (Bano and Hollibaugh 2002), the differences between Arctic and Antarctic pack ice (Brinkmeyer et al. 2003), the abundance and production of bacterial groups in the western Arctic Ocean (Rex et al. 2007) and the ecology of the rare microbial biosphere of the Arctic Ocean (Galand et al. 2009). Indeed, global patterns have been recognised in the diversity and community structure in marine bacterioplankton (Pommier et al. 2007), and a latitudinal diversity gradient has been observed in planktonic marine bacteria (Fuhrman et al. 2008). It has recently been suggested that hydrography shapes the bacterial biogeography of

the deep Arctic Ocean (Galand et al. 2010), and new insights emerge frequently, into specific bacterioplankton groups, for example, the alpha-Proteobacteria in coastal seawater (González and Moran 1997). Psychrophiles are clearly important in the polar regions (Deming 2002), and a great deal of work has been done on the diversity and association of psychrophilic bacteria in sea ice (Bowman et al. 1997). However, biodiversity of many taxonomic groups remains relatively unknown (Archambault et al. 2010), including areas of the High Arctic where biological data are almost non-existent (Piepenburg et al. 2011).

Unlike the virioplankton, great strides have been made in the cultivation of marine bacteria, including the numerically important Arctic sea-ice bacteria cultured at subzero temperatures (Junge et al. 2002). High-throughput methods for culturing microorganisms in very-low-nutrient media have yielded diverse new marine isolates (Connon and Giovannoni 2002) enabling researchers to focus their attention on specific groups such as the ubiquitous SAR11 marine bacterioplankton clade (Rappe et al. 2002) or the oligotrophic marine gamma-Proteobacteria (Cho and Giovannoni 2004). Such amenability to culture also permits bioprospecting for cold-active enzymes such as the lipases, amylases and proteases, from culturable bacteria, for example from Kongsfjorden near Ny-Ålesund in Svalbard (Srinivas et al. 2009). The cold-active glutaredoxin enzyme was discovered in a sea-ice bacterium *Pseudoalteromonas* sp. AN178 (Wang et al. 2014).

Studies of the prokaryote community in the Arctic Ocean have included activity measurements, for example, the bacterial contribution to respiration in the water column may be substantial: 3–60 % in the Chukchi Sea and Canada Basin and 25 % on average in the Arctic (Kirchman et al. 2009). Bacterial activity has also been studied at −2 to −20 °C in Arctic wintertime sea ice (Junge et al. 2004). Specific functional activity has been studied relating to biogeochemical cycling such as the analysis of the sulphate-reducing bacterial and methanogenic archaeal populations in contrasting Antarctic sediments (Purdy et al. 2003) and the fact that anaerobic ammonium-oxidising bacteria in marine environments are of widespread occurrence but low diversity (Schmid et al. 2007), although progress in this area is far more restricted compared to other bacterial groups.

9.7 Eukaryotic Microbial Diversity

Single-celled eukaryotes, or protists, a category largely comprised of protozoa and micro-algae, make up most of the diversity of eukaryotes. Typically, the first classification applied in microbial ecology is that of size classes. Protists typically range in size from 0.2 to 200 μm (some are larger) and are usually segregated into the pico- (<2 μm), nano- (2–20 μm) and micro-sized fractions (20–200 μm) of the scaling plankton nomenclature (Murphy and Haugen 1985). These size classes may be referred to as “picophytoplankton” or “nanozooplankton”, etc. according to whether the groups under study are photosynthetic or heterotrophic, though

many taxa include heterotrophs, autotrophs and mixotrophs, due to the complex evolutionary history of gains, transfers and losses of chloroplasts among microbial eukaryotes.

During the classification of the eukaryotes, what has recently emerged is a tree that splits into mostly previously unknown large groups, dubbed "supergroups": Opisthokonts (including animals and fungi), Amoebozoa (amoebae and slime moulds), Excavates (e.g. trypanosomes, amitochondriate parasites), Archaeplastida (green algae and plants, red algae), Stramenopiles (brown algae and kelps), Alveolates (ciliates, apicomplexa, dinoflagellates), Rhizaria (foraminifera, radiolaria, cercozoans) and several smaller groups such as the clade containing the haptophyte algae (all reviewed in Walker et al. 2011). These groups are now widely accepted and are increasingly referred to in ecological literature, meaning that the taxa discussed in recent ecological analyses of particular environments (e.g. Massana et al. 2004) have different affiliations from their former placements as "protozoa" or "algae" in classical literature (Van den Hoek et al. 1996).

In the Arctic, protists have mostly been described from the upper water column in coastal and oceanic areas or in ice-associated (sympagic) communities (Poulin et al. 2011). Arctic marine protists in the water column contribute about 98 % of primary production in coastal regions, while in the mid-Arctic ocean about 57 % of primary production is in ice-associated protist communities (Gosselin et al. 1997). Poulin et al. (2011) estimated that 1874 taxa of phytoplankton organisms and 1027 of sympagic unicellular eukaryotes had been described by microscopical methods from Arctic samples. Protists are important as primary producers and as consumers of prokaryotes such as the cyanobacteria. They are key to the "microbial loop", the set of trophic interactions that operates below the level of classical food chains, from dissolved organic carbon through to unicellular organisms that are eaten by invertebrates (Azam et al. 1983; Fenchel 1988).

The microbial food web sustains the Arctic Ocean under most circumstances, dominating where there is not a large phytoplankton bloom. Energy is released as Dissolved Organic Matter from phytoplankton (either through death of cells, viral lysis or "leaky" photosynthesis) and taken up by bacteria and the smallest eukaryotes, who are then eaten by heterotrophic or mixotrophic protists, who are in turn eaten by larger protists and zooplankton, with energy losses at every stage permitting blooms of smaller taxa and heterotrophy permitting blooms of larger taxa (Sheldon 1972).

9.8 Adaptations

Abiotic extremes characterise the Arctic Ocean. These extremes include the intensity, duration and wavelength of incoming solar radiation, the extent, thickness and duration of ice cover, temperature extremes, stratification of the water column and structures associated with the sea ice (Gosselin et al. 1997). Temperatures within the sea ice form a depth gradient, where temperatures at the surface can be −20 °C

and temperatures within the sea ice itself around −2 °C. There are several mechanisms employed by microorganisms to survive this rapid decline in temperature. Mykytczuk et al. (2013) describes the mechanisms used by *Planococcus halocryophilus* to grow and divide at −15 °C, the lowest temperature recorded to date, suggesting cryoenvironments harbour a more active microbial ecosystem than previously thought. One mechanism sea-ice diatoms employ to thrive in the sea-ice environment is the production of ice binding proteins, which act as a cryoprotectant (Janech et al. 2006). These ice binding proteins have both strong recrystallisation inhibition activity and act to slow the drainage of brine from sea ice, allowing them to maintain a liquid environment around the diatom (Raymond et al. 2009). A method often employed by algae and protozoans in particular is to form a robust stress resistant cyst, triggered by low temperature or a lack of nutrients—depending on the species (Stoecker et al. 1998). Whilst a viable method of survival the cyst is often dormant, not contributing to nutrient cycling or affecting the microbial population. Similarly, some bacteria may become associated with particles such as soil already present in the seawater before freezing occurs (Junge et al. 2004). This allows the bacteria to survive in the slightly less harsh microenvironment of the soil (higher temperature, less salinity, etc.) until the sea ice thaws in spring.

However, in order to continue population growth and metabolic activity, microorganisms need to possess two key adaptations: the ability to maintain membrane fluidity in order to allow nutrients and waste to enter and leave the cell (Thomas and Dieckmann 2002) and cold functioning enzymes. Membrane fluidity at sub-zero temperatures can be achieved in three ways; by an increase in the proportion of unsaturated fatty acids, a decrease in membrane chain length and an increase in polyunsaturated fatty acids (Russell 1997). The increase in polyunsaturated fatty acids is brought about by an increase in the activity of the polyketide synthase group of enzymes (Metz et al. 2001) and as well as being important to the microorganism, it plays an important part in the diet of grazers (Thomas and Dieckmann 2002). Another limiting factor is the reduced affinity for substrates due to enzyme denaturation. Psychrophilic bacteria must maintain high catalytic activity at low temperatures, which is best achieved by either maintaining enzyme structure or increasing enzyme concentration. Psychrophilic bacteria have been found to contain cold-adapted proteases, β-galactosidases, phosphatases and amylases (Pomeroy and Weibe 2001). Maintaining enzyme structure allows for a higher proportion of substrate–active site binding and allows the microorganism to maintain its function. If the microbe does not possess psychrophilic enzymes, it can maintain catalytic activity by increasing the concentration of the enzyme, an option which allows more active sites for substrates to bind to, although with less specificity. This increase in total activity at the cost of specificity can be seen in some microalgae with the photosynthetic enzyme, Ribulose-1,5-biphospate carboxylase/oxygenase (Devos et al. 1998).

Tolerance to salinity is an important characteristic for sea-ice microorganisms. They must be able to survive both the high salinity of the brine pockets and channels and the sudden exposure to hypo saline conditions that occur when the sea ice melts in spring (Thomas and Dieckmann 2002). The hyper-saline conditions

of brine pockets can cause severe dehydration stress, as they can contain up to three times the salinity of open seawater (Eicken 1992). In order to cope with this stress, microorganisms must carefully regulate the uptake of osmolytes such as proline, mannitol and inorganic ions to restore osmotic balance (Thomas and Dieckmann 2002). Alongside, salt-tolerant enzymes have been described in psychrophilic isolates (Nichols et al. 2000) as has the regulation of fatty acid proportion for temperature tolerance.

Low light conditions primarily affect photosynthetic algae, and as they are important primary producers, their success affects the whole food chain. In order to continue to carry out photosynthesis within brine pockets, algae must be able to carry out extremely efficient photosynthesis reactions to maximise the little light they receive. The algae may also contain pigments that absorb those wavelengths which can penetrate sea ice. One such pigment, Fucoxanthin, is highly effective at absorbing said wavelengths and shows an increase in concentration during winter months (Lizotte and Priscu 1998). The early bloom depends on light, as is the case for the spike in photosynthetically active radiation which affects the prasinophytes in late January when sun comes back (Terrado et al. 2008).

The analysis of nutrient concentrations and the pulse-amplitude-modulated fluorescence signal of ice algae and phytoplankton suggests that nutrients are the prime limiting factor for sea-ice algal productivity (Gradinger 2008). Over much of the Arctic Ocean's vast shallow continental shelf, brine rejection during sea-ice formation triggers convective mixing that replenishes nutrients into surface waters (Stabeno et al. 2010). The traditional bloom depends on nutrients (Lovejoy et al. 2004), but very early and late seasonal blooms are light-dependent (Massana et al. 2007; Seuthe et al. 2011). Such strong dependence on light, and dominance by successive blooms of photosynthetic taxa (and in turn heterotrophic taxa), also suggests that the Arctic Ocean may have a different ecology from those of other oceans. However, as sampling intensity increases, it may become apparent that the ecology of the Arctic Ocean is similar to that of other oceans (Seuthe et al. 2011).

Marine psychrophiles form the base of the Arctic Ocean food web, and their population and species distribution is affected by the presence of organic and inorganic compounds. The cycling of carbon, nitrogen, silica and iron is responsible for the waxing and waning between population groups that influence species higher up in the food web.

Light availability plays the most important role in the sea-ice carbon cycle, with seasonal changes in light having an effect on autotroph/heterotroph dominance. During the summer, light availability is at its highest and at some latitudes photosynthesis can occur for 24 h a day. This leads to an increase in the autotrophic population both within the sea ice and in sea water (Horner and Schrader 1982). Pre-bloom to post-bloom algal cell concentrations can go from $<10^4$ cells to $>10^9$ cells within some brine pockets (Arrigo et al. 2010). The high populations of autotrophic microorganisms exhaust a lot of CO_2 from the brine pockets, causing a supersaturated O_2 solution of up to 932 μmol kg^{-1} (Skidmore et al. 2012).

During the transition to winter, the population switches to a dominant heterotrophic one. Free sea water autotrophs are forced into brine channels during sea-ice

formation and those not adapted die releasing organic carbon into the sea ice. Within the sea ice, autotrophs go into a dormant state, and the high O_2 concentration coupled with the readily available organic carbon allows a heterotrophic population increase. The increase in the heterotrophic population uses up O_2 and replenishes CO_2 inside the ice pockets. During the following spring, the increase in light availability and high CO_2 concentration allow another autotroph bloom. The melting sea ice also releases a high concentration of microbial cells into the water column, providing a food source for grazers.

The uptake of nitrogen happens in two distinct ways; through nitrification (oxidation of ammonium (NH_4^+) to produce NO_2 or NO_3) or assimilation (absorption of nitrites or ammonium, followed by reduction and incorporation into amino acids, etc.). As with carbon, the assimilation or nitrification of nitrogen seems highly dependent on light availability and species distribution, with assimilation at a much higher rate in summer. Experiments have shown that nitrification rates show no difference over a temperature gradient (Horak et al. 2013), so changes in the balance of nitrification/assimilation of NH_4^+ are driven by species abundance and distribution which are in turn a consequence of light and organic carbon availability.

Although bacterial nitrifiers are present during the summer (Hollibaugh et al. 2007), there is a sudden increase in autotrophic algae brought about by increased light availability. Phytoplankton outcompete nitrifiers for NH_4^+ in well-lit ocean layers (Bronk and Ward 2005) which could account for the spike in NH_4^+ assimilation seen in the winter months. When light availability is little to none in winter months, and autotrophic populations are severely reduced, there is little competition for nitrifying bacteria, and nitrification becomes the prominent way in which NH_4^+ is utilised.

Silicon in sea ice is most common in the form of Silicic acid $Si(OH)_4$ and is present in the sea ice through exchange with the surrounding water column (Vancoppenolle et al. 2010). Silicic acid is a vital component of diatom cell walls, and studies have shown that Silicic acid is a major limiting factor in sea-ice autotroph growth (Gosselin et al. 1990). Perhaps the best example is the correlation of $Si(OH)_4$ and chlorophyll concentration in sea ice shown in Cota et al. (1990). Iron is required for phytoplankton growth, photosynthesis and enzyme production (Wang et al. 2014). The concentration of iron present in the ocean is often a limiting factor to primary production, especially in Antarctica (Boyd and Abraham 2001). It has however been shown that sea ice has a much higher concentration of iron (up to two orders of magnitude (Lannuzel et al. 2010) than the surrounding ocean, and so iron is unlikely to have a limiting effect on sea-ice ecosystems.

9.9 Methods Used to Study the Arctic Marine Food Web

Stable isotopes have been used extensively to study the flow of energy and matter between organisms (or food-web function). Earlier studies in this field were based on the natural variability of isotopes and limited to larger organisms that could be physically separated from their environment. For example, the stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals (Hobson et al. 1996). However, recent methodological developments have allowed isotope ratio measurements of microorganisms, and this in turn allows the measurement of entire food webs, from primary producers at the bottom to apex predators at the top (Middelburg 2014; Søreide et al. 2006). Fatty acid (FA) analysis is a well-established tool for studying trophic interactions in marine habitats (Budge et al. 2008; Dalsgaard et al. 2003). It is now being used for comparatively large-scale studies such as that published by Thiemann et al. (2008) who used quantitative fatty acid signature analysis (QFASA) to examine the diets of 1738 individual polar bears (*Ursus maritimus*) sampled across the Canadian Arctic over a 30-year span. The results of their large-scale study indicated a complex relationship between sea-ice conditions, prey population dynamics and polar bear foraging. The method also allows for experimental manipulations (Fraser et al. 1989) and for specific studies of environmental function (Knoblauch et al. 1999).

A significant issue in the Arctic is the bioaccumulation of toxic substances in the food chain. These include polybrominated diphenyl ethers (PBDEs) (Kelly et al. 2008b), hydroxylated and methoxylated polybrominated diphenyl ethers (Kelly et al. 2008a), organochlorines (Skarphedinsdottir et al. 2010), methyl sulfone PCB, 4,4′-DDE metabolites (Letcher et al. 1998) and mercury (Atwell et al. 1998; Gobeil et al. 1999) among many. One fortunate benefit of such bioaccumulation of toxins is that it can actually be used to trace the route of those chemicals through the food chain.

Most targeted food web studies, by necessity, require some form of environmental manipulation, and this can occur at a number of different spatial scales. From laboratory microcosms, people have been able to examine topics such as seasonal carbon and nutrient mineralisation (Rysgaard et al. 1998), nutrient cycling (Freitag et al. 2006), methane production (Damm et al. 2010) and biodegradation studies (Bagi et al. 2014). Mesocosm experiments have been used to study response to elevated CO_2 levels (Niehoff et al. 2013; Pavlov et al. 2014), nutrient manipulation (Larsen et al. 2015), ocean acidification (Riebesell et al. 2013) and differential transfer of marine bacteria to aerosols (Fahlgren et al. 2015). Then there are the exclosures, where specific components are excluded that can be both biological or chemical, and which have been used to study diet-induced changes in the fatty acid composition of Arctic herbivorous copepods (Graeve et al. 1994) or the effects of crude oil on marine phytoplankton (Harrison et al. 1986).

At the still larger scale, there have been foraging behaviour studies, particularly of seabirds, for example, northern fulmars (Hobson and Welch 1992), thick-billed murres (Falk et al. 2002), little auks (Karnovsky et al. 2011), shallow-diving

seabirds and Arctic cod (Matley et al. 2012). In addition, population monitoring has been used for organisms such as marine mammals (Kovacs 2014; Laidre et al. 2008, 2015; Moore and Huntington 2008; Tynan and DeMaster 1997). Ultimately, satellite remote sensing data is also used over very large areas to examine recent trends in sea-ice cover and net primary productivity (NPP) (Brown and Arrigo 2013). So, as food web studies cover an ever wider range of spatial scales (Smith et al. 2005), modelling becomes an essential component in understanding the Arctic marine food web in order to disentangle complex trophic relationships (Legagneux et al. 2012).

Observations of Whole Cells and Pigments Traditionally, protistan diversity in the Arctic has been detected through light microscopy of live samples (Poulin et al. 2011), meaning this seems the ideal method to combine new data with previous observations. Given taxonomically experienced observers, sufficient resolution and magnification on the microscope and the ability to capture uninterpreted records (photographs or videos rather than drawings), light microscopy provides records that are easy to interpret (e.g. Daugbjerg and Moestrup 1993; Vørs 1993; Ikävalko and Gradinger 1997; Lovejoy et al. 2004) in the light of the worldwide taxonomic and natural history literature from the last two centuries (e.g. Larsen and Patterson 1990; Vørs 1992).

The efficiency of microscopy-based sampling can be improved in ecological studies (where species-level identification may not be important) by the use of epifluorescence microscopy, whereby specific cellular compounds such as DNA, chlorophylls a, b and c or phycobiliproteins have fluorescent signals at particular wavelengths. Stains such as DAPI, primulin and lysotracker can be used to show cellular features, e.g. the nucleus, endomembrane system and extracellular scales (Sintes and del Giorgio 2010; Vaulot et al. 2008). Photosynthetic pigments and their cellular distribution in unicellular algae are taxonomically diagnostic (e.g. phycoerythrins in cryptomonad chloroplasts) and can be used to count types of cells very quickly with the aid of image analysis. This technique has been widely used in ecological studies that have established the abundance and importance of bacteria and protists in food webs (Hobbie et al. 1977; Murphy and Haugen 1985).

Samples can be cooled and returned to laboratories for subsequent microscopy (Tong et al. 1997), dilution culturing to estimate abundances (Throndsen 1978; Throndsen and Kristiansen 1991), enrichment culturing to study specific organisms from the culture in higher numbers (e.g. Daugbjerg and Moestrup 1993; Vørs 1993) or isolation of individual species for culture and further study (Andersen and Kawachi 2005). Fine-structural diagnostic features of these organisms can further be studied by electron microscopy, either of filtered environmental samples or of cultures, with numerous rare and novel taxa often described this way (Andersen et al. 1993; Booth and Marchant 1987; Moestrup 1979; Thomsen 1980 *inter alia*).

Where species-level diagnosis is less important than information on abundances of higher-level taxa, the size structure and photosynthetic (fluorescent) characteristics of populations of cells can be studied by flow cytometry (Li and Dickie 2001; Marie et al. 1999; Simon et al. 1994; Vaulot et al. 2008). Pigment signatures can

also be analysed in detail by HPLC (e.g. Andersen et al. 1996), which provides relatively taxon-specific information at varying levels of diversity, dependent on the group, and can be analysed using algorithms such as CHEMTAX (Mackey et al. 1996; Wright et al. 2009), along with the analysis of plankton blooms observed in satellite images (Batten et al. 2003; Gons et al. 2002). Interpretation of HPLC signals can be difficult, as there can be huge diversity within a taxon despite all having a common signature (e.g. haptophytes, Liu et al. 2009), some taxa can share pigment signatures (e.g. diatoms and bolidophytes, Guillou et al. 1999) and other taxa can have multiple signatures, even among ecotypes of a single species (Latasa et al. 2004).

Recently, the powerful tools of molecular biology have been applied to the study of biodiversity in Arctic seas (Radulovici et al. 2010). These new approaches have revealed a surprising diversity including new taxa of bacterioplankton and archaeans (Galand et al. 2009; Kirchman et al. 2009), eukaryotic microbes (Lovejoy and Potvin 2011; Lovejoy et al. 2007) for example gregarine parasites (gregarines are apicomplexans) of amphipods (Prokopowicz et al. 2010). The precise role of these recently discovered assemblages in the pelagic marine food webs and in the cycling of organic matter remains obscure. As well, benthic processes and biodiversity are not yet well resolved for the Arctic seafloor although increased attention has been given in recent years to study the coupling between pelagic production and benthic carbon turnover (Morata et al. 2008; Renaud et al. 2007).

9.10 Biogeography

Whilst on the surface, the Arctic Ocean may seem relatively homogeneous, it is important to remember that there are quite a number of distinct biogeographical zones. This includes the different vertical layers of the Ocean from the air–sea interface down to the benthos. There is then the distinction between coastal regions as compared to the open ocean. For example, Arctic shelves comprise roughly 50 % of the Arctic Ocean and are the regions where sea-ice conditions have changed most dramatically over the last decades (Hassol 2004). There are also the transition and brackish zones such as fjord systems and polynyas. The differences between pack or sea ice and fast ice impose different selection pressures, and there is also the issue of special ecosystems such as hydrothermal vents and commensal communities on or inside marine organisms. Niederberger et al. (2010) carried out a microbial characterisation of a terrestrial methane seep into an Arctic hypersaline, subzero perennial spring. It was found to support a viable microbial community that may use methane as an energy and carbon source to sustain anaerobic oxidation. Then there is the issue of locational stability, with microorganisms being moved around by both air and water currents. Picocyanobacteria are wind transported year round from warmer ocean waters and can establish themselves in the warmer summer climate of the Arctic. This can be demonstrated in Polar ice cores, which contain higher concentrations of chlorophyll and tryptophan at depths corresponding to

local summers that bore similarities to regional fluorescence patterns seen in the picocyanobacteria *Prochlorococcus* and *Synechococcus* (Price and Bay 2012). Next there is the issue of research effort, for example, the fact that proximity of research facilities and comparative ease of logistic access results in specific Arctic locations such as the Amundsen Gulf, Lancaster Sound, Disko, Zackenberg or Svalbard often being more studied than any others. Within each of the separate Arctic zones, there will be also differences in coverage, connectivity and spatial patchiness.

The total number of microbial species is estimated to be between 10^3 and 10^9, and the bacteria are responsible for around half of photosynthesis on Earth (Pedrós-Alió 2006). Marine microorganisms, collectively present at billions of cells per litre, grow at rates of around one doubling per day in surface waters and are consumed at the same rate (Whitman et al. 1998). There could therefore be huge untapped potential in Arctic marine food web biodiversity. It was previously believed that due to small body sizes and huge population sizes, few geographical barriers and mixing of waters due to wind, waves and currents (Collins 2001), marine planktonic microorganisms should not exhibit biogeographical patterns across latitudinal gradients like those seen in many macroscopic animals and plants (Hillebrand 2004). Furthermore, marine planktonic microorganisms should be cosmopolitan, endemic species should be rare and their global diversity low (Fenchel and Finlay 2004; Finlay 2002). However, Pommier et al. (2007) have shown that compositions of marine free-living microbial taxa differ in different locations and this difference may correlate with environmental factors (Giovannoni and Stingl 2005; Martiny et al. 2006) such as salinity gradients (Bouvier and del Giorgio 2002; Crump et al. 2004), depth stratification (Garcia-Martinez and Rodriguez-Valera 2000; Giovannoni et al. 1996; Gordon and Giovannoni 1996; Riemann et al. 1999) and Ocean fronts (Pinhassi and Berman 2003). Arctic biodiversity is therefore much more extensive, ecologically diverse and biogeographically structured than previously thought. Understanding how this diversity is distributed in marine ecosystems, the mechanisms underlying its spatial variation and the significance of the microbiota concerned is growing rapidly (Chown et al. 2015). To date, there have been a variety of specific studies of bacterial biodiversity in Arctic waters. The distribution (Ferrari and Hollibaugh 1999) and phylogenetic composition of bacterioplankton assemblages from the Arctic Ocean (Bano and Hollibaugh 2002) were the first to be addressed, but now we know that hydrography may shape bacterial biogeography of the deep Arctic Ocean (Galand et al. 2010) and that pole-to-pole biogeography of surface and deep marine bacterial communities may exist (Ghiglione et al. 2012).

9.11 DNA Sequencing

A partial, but very powerful solution to the limitations of microscopy is provided by sequencing DNA directly from environmental samples, without first observing or culturing the organisms in the environment (Giovannoni et al. 1990; Pace 1997). For Arctic microbial samples, this specifically removes both the logistical and time limitations associated with light microscopy and eliminates the need to identify organisms by morphology; hence, considerably more organisms can be detected (e.g. Lovejoy et al. 2002, 2006).

Initially, sequencing methods relied on PCR amplification of marker genes from environmental genomic DNA or RNA samples and cloning and sequencing of these PCR products for phylogenetic identification (Giovannoni et al. 1990). By comparing libraries from genomic DNA with ones based on RNA, it is possible to distinguish between DNA samples from cells that are active in the environment, and ones that are from resting stages or dead cells (Stoeck et al. 2007), though the comparison is made complex by the copy number of rDNA molecules contained in the genomes of some taxa (Not et al. 2009). Typically, the marker used to identify protists has been SSU rRNA (small subunit ribosomal RNA), which is highly abundant within cells, evolves slowly enough to provide consistent relationships within distantly related groups and has no evidence of lateral gene transfer. Fragments of this gene may be used for broad phylogenetic identification, although using either the whole gene or both SSU and large subunit ribosomal RNA (LSU rRNA) subunits produces better phylogenetic resolution (Marande et al. 2009; Vaulot et al. 2008). Either universal or specific primers for particular taxa can be used (Bass and Cavalier-Smith 2004), and multiple PCR-primer approaches have considerably improved detection of diversity (Stoeck et al. 2006). Specific "barcoding" markers such as ITS, psbA or RuBisCO have been developed to easily identify diversity at lower levels in particular eukaryotic groups (Frezal and Leblois 2008; Goldstein and DeSalle 2011), including among the protists (e.g. Nassonova et al. 2010).

The clone library approach has revealed significant novel diversity, particularly of very small eukaryotes (Massana and Pedrós-Alió 2008; Vaulot et al. 2008) such as prasinophytes (Guillou et al. 2004) and haptophytes (Liu et al. 2009); and including whole clades that had previously not been recorded, such as the MAST (marine stramenopile) and MALV (marine alveolate) groups (Lopez-Garcia et al. 2001; Moon-van der Staay et al. 2001). Some of the groups found by clone library sequencing methods, such as picozoa (Seenivasan et al. 2013 http://www.ncbi.nlm.nih.gov/pubmed/23555709), were initially deemed unaffiliated with any other eukaryotic taxa (Dawson and Pace 2002; Not et al. 2007), although most of the diversity detected was related to already-known groups (Berney et al. 2004).

However, clone libraries are subject to inherent biases of their own, such as taxon-specific PCR amplification biases, errors in amplification, ligation biases towards short sequences, chimaeric sequences, the expense of Sanger sequencing, the occurrence of rDNA genes in multiple copies within a single cell and the

capacity of DNA to persist as extracellular material (Berney et al. 2004; Foerstner et al. 2006; Stoeck et al. 2010; Vaulot et al. 2008). Libraries also do not show sampling saturation, so even the most intensive library analyses have only recovered a relatively small proportion of the diversity detectable by metagenomic approaches (Not et al. 2009; Stoeck et al. 2010).

Metagenomic sequencing, the direct cloning and sequencing of fragments of environmental DNA (DeLong et al. 2006; Venter et al. 2004) have been developed on the basis of recent advances in high-throughput sequencing technology, based on micro-fabricated high-density picolitre reactors (Margulies et al. 2005). By removing the ligation and transformation steps, it removes some of the larger biases of the clone library approach and considerably more sequencing can be done as hundreds of thousands of sequences are produced in a single sequencing run. The tagging of sequences also allows direct quantification of their abundance (Tedersoo et al. 2010). In prokaryotic microbial communities, metagenomic sequencing has permitted the identification of two orders of magnitude of further novel diversity, particularly of very rare taxa (Sogin et al. 2006) that are impossible to detect by clone-library techniques (Pedrós-Alió 2006). Not et al. (2009) and Stoeck et al. (2010) applied these methods to eukaryotic microbes and discovered that their samples were similarly dominated by very rare sequences. While high-throughput sequencing methods are relatively new, there is increasing application of metagenomic sequencing methods in microbial ecology, allowing the examination of questions regarding diversity, abundance, correlation with abiotic factors (e.g. Comeau et al. 2011) and biogeography.

9.12 Linking Microscopy and Sequence Data

9.12.1 Quantitative Approaches: FISH, FACS and qPCR

Whole-cell microscopical approaches can be linked to environmental sequence data of cultured or uncultured protists through the use of specific oligonucleotide probes targeting taxonomically specific genes such as 18S rRNA (DeLong et al. 1989; Lim et al. 1999). This allows environmental sequences to be tied to their "owners", as seen by microscopy using fluorescent in-situ hybridisation (FISH), and can thus be used to determine both biological identity and abundance (Not et al. 2004), complex morphology (in combination with other stains as examined by Hirst et al. 2011), enabling studies of ecological succession (Larsen et al. 2004), and the ecological functions of unknown protists through stained, live feeding experiments (Massana et al. 2009). Such probes can also be hybridised to gold nanoparticles, for performing simultaneous FISH correlated with immunogold electron microscopy, allowing taxonomically diagnostic morphological details to be observed in previously unknown, uncultured taxa (Gerard et al. 2005; Kolodziej and Stoeck 2007; Stoeck et al. 2003). The same fluorescent oligonucleotide probes

can also be used in flow cytometry (FACS), allowing isolation of individuals (Seenivasan et al. 2013 http://www.ncbi.nlm.nih.gov/pubmed/23555709), quantification of the abundance of particular taxa in a sample, as well as sorting of the sample into pure populations from which large numbers of cells can be obtained (Li 1994; Simon et al. 1994). Quantification and spatiotemporal mapping of protists can also be done using quantitative PCR (qPCR), where oligonucleotide probes are hybridised to PCR-amplified products from environmental samples (Marie et al. 2006; Suzuki et al. 2000; Zhu et al. 2005). This allows a complex picture of distribution and abundance to be built up quickly, even for uncultured organisms of relatively unknown biology, such as the MAST stramenopiles (Rodriguez-Martinez et al. 2009).

9.12.2 Qualitative Approaches: Detecting Species

Sequencing of isolated or cultured protists has linked ecological data based on microscopy and sequence identity, permitting studies on the distribution of particular morphological species or ecotypes (Koch and Ekelund 2005). However, the correspondence between identity determined from isolated organisms, "operational taxonomic units" (OTUs) in environmental sequencing, population genetic structure and morphospecies or morphological ecotypes is highly variable and complex (Schlegel and Meisterfeld 2003), and cases where the alpha-taxonomy of a group is well-known both from sequences and from morphology are rare (Alverson 2008). There is also considerable sequence diversity within many morphospecies (e.g. *Micromonas pusilla*, c.f. Throndsen and Kristiansen 1991; Slapeta et al. 2006), meaning that the degree of correspondence between uncultured environmental sequencing records and natural history records from the last two centuries is unclear (Lopez-Garcia and Moreira 2008). Some progress has been made in distinguishing species from OTUs, using algorithmic methods to distinguish species-level clades (Leliaert et al. 2009) and ribosomal RNA internal transcribed spacer (ITS) sequences (Coleman 2009), which can predict interbreeding in diatoms (Poulickova et al. 2010; Sorhannus et al. 2010) and can potentially be used to detect clades to species level in uncultured stramenopiles (Rodriguez-Martinez et al. 2012).

9.13 Methodological Limitations

The overall picture of ecological diversity of protists is currently changing, due to major improvements in methods for detecting diversity, from light-microscopy-based to sequencing-based approaches. The taxonomy of protists has also recently changed significantly, formerly being based on light microscopy, but more recently reflecting results from molecular phylogenetics (Walker et al. 2011). It is now clear

that ecological studies of Arctic protists have only begun to scratch the surface in understanding population diversity (Archambault et al. 2010; Poulin et al. 2011), despite protists make up a large proportion of the diversity present in Arctic food chains. As the Arctic climate changes rapidly in the next few decades, changes in the communities of protists may have significant effects on food webs generally.

However, while whole-cell methods maintain the link between "real biology" in the field and laboratory-based observations, there are disadvantages and biases inherent in most methods. The length of time required to make taxonomically useful observations using either a light or fluorescence microscope often severely limits the amount of work that can be done on fresh material during time-constrained fieldwork in remote locations such as the Arctic. Culturing-based methods show strong biases, excluding "unculturable" organisms from study. For ecological studies where cells are being counted sometime after initial collection, samples are often preserved in fixatives such as Lugol's iodine, formalin or glutaraldehyde, which can significantly change estimates of diversity and abundance (Epstein 1995; Montagnes et al. 1994). Similar fixatives are also used for electron microscopy of ecological samples and can similarly change estimates of diversity and cell volumes (Vaulot et al. 2008). Sampling, observation time and preservation aspects of microscopy can lead to biases in observations such as missing the early "spike" in prasinophyte green algae during yearly succession in marine communities (Terrado et al. 2008), or very strong biases towards observation of easily-preserved diatoms and dinoflagellates, over unarmoured taxa that become unrecognisable after preservation (Poulin et al. 2011). There are also strong biases in sampling effort, particularly due to the highly variable numbers of taxa observed across the Arctic. For example, the number of taxa observed in Hudson Bay and the Barents Sea tends to be larger than that from Alaska; however, this reported variation is likely to be related to an unintentional bias in the number of field stations present in these regions, the number of microbial researchers often visiting them (Poulin et al. 2011) and the research funding directed to each field station (Archambault et al. 2010). The "taxonomic impediment", linked to the continuous declining numbers of specialist taxonomists with skills in identifying organisms, also affects the documentation of Arctic microbial diversity (Archambault et al. 2010). The unfortunate flip side to that impediment is the fact that many individual taxonomists are able to recognise only certain taxa, often specialising in particular groups and consequently under-reporting other taxa, leading to strong biases in detecting diversity. These factors are compounded by other extrinsic factors such as nomenclatural instability (Lee and Patterson 1998). However, it is worth remembering that despite these biases and limitations, microscopy is the key to both understanding the biological interactions among diverse microbial eukaryotes and linking new data to past records.

9.14 Arctic Microbial Diversity and Endemism

The potential for direct impacts of sea-ice loss begins at the base of the food web, where significant numbers of obligate low-temperature, shade-adapted algal species (Lovejoy et al. 2006, 2007) and radiolarian species endemic to the Arctic Ocean Basin have been found (Lovejoy et al. 2007). The ecological consequences of understanding species-level sequence variation are in detecting diversity from environmental sequence data and assessing whether there is endemism in particular environments (Caron 2009). With this in mind, environmental sequence data can be used to address the ubiquity hypothesis in microbial ecology, which states that "everything is everywhere, but the environment selects" (De Wit and Bouvier 2006). This suggests that latitudinal gradients do not exist in microbial ecology (when ecological factors are accounted for) and, consequently, microbial ecology is fundamentally different from that of macroorganisms (Fenchel and Finlay 2003). This has long been a prevailing paradigm in protistan ecology, though it has generated considerable debate (Caron 2009). The pattern of endemism in protists that emerges from morphological data is mixed (Schlegel and Meisterfeld 2003), with some observations suggesting overwhelming cosmopolitanism of morphospecies (Larsen and Patterson 1990) and that apparent endemism is strongly dependent on extrinsic factors such as the distribution of taxonomically experienced microbial ecologists (Lee and Patterson 2000; Poulin et al. 2011). Other observers have emphasised the hidden diversity in morphospecies (e.g. Mann 1999), and studies of haptophytes, diatoms and green algae in the Antarctic point to strong endemism and geographical isolation with strong latitudinal gradients (Gravalosa et al. 2008; Vyverman et al. 2010). Sampling in polar regions, particularly, is often incomplete and inconsistent, making it difficult to determine whether data supports endemism or cosmopolitanism (Chown and Convey 2007). Diversity and endemism detected by sequence data provide a mixed picture, suggesting some cosmopolitanism (Cermeno et al. 2010; Finlay et al. 2006; Koch and Ekelund 2005) and some endemism (Bass and Cavalier-Smith 2004; Bass et al. 2007), and the assessment may also strongly depend on the relevance of the data to the question. Trivially, the level of sequence identity that is considered an "operational taxonomic unit" determines what diversity is detected, and different taxa may vary at different levels of identity for particular sequences, giving very different overall pictures of diversity between, for example, 95 % and 99 % sequence identity or the V4 and V9 regions of SSU rRNA (Stoeck et al. 2010). Both alpha- and beta-diversity, and endemism, also depend strongly on the genetic marker used (Bass et al. 2007), with rDNA copy number in genomes potentially confounding some results (Not et al. 2009). Considerable morphological diversity presently is known from microscopy of live samples (e.g. Vørs 1993; Ikävalko and Gradinger 1997; Daugbjerg and Moestrup 1993); however, most of the data gathered suggest that a large proportion of this diversity is composed of cosmopolitan species, rather than endemic (e.g. Larsen and Patterson 1990; Vørs 1992; Lee and

Patterson 2000), possibly as a consequence of still relying upon traditional microscopy-based species concepts.

9.15 Yearly Dynamics

To superimpose another layer of complexity onto understanding the biodiversity of different geographic regions, there is also the issue of yearly dynamics (Giovannoni and Vergin 2012; Seuthe et al. 2011; Terrado et al. 2008). The *winter* Ocean is dark, ice-covered, cold, with fresh water at the surface beneath first-year ice, and warmer water below. While autotrophs from previous seasons persist (Niemi et al. 2011), alveolate heterotrophs dominate in this environment (Terrado et al. 2008, 2009), and more heterotrophs are present for longer in high snow regions (Riedel et al. 2008). In the *winter*–spring *transition*, there is a rapid increase in solar radiation, and although the ocean is still ice-covered, cold (with temp gradient below) and with freshwater at the surface; multiyear ice contains old communities (Terrado et al. 2009). A Prasinophyte spike occurs in late January, while diatoms dominate at least around Svalbard. In spring, there is a rapid increase in solar radiation, retreating ice, upwelling of nutrients and runoff from rivers providing silicates and iron (Andreassen and Wassmann 1998), during which time pennate diatoms dominate in the retreating ice, while haptophytes and centric diatoms start to appear in the now open water. Terrado et al. (2008) have suggested that photosynthetically active radiation drives such changes. Although alveolate diversity still dominates during the spring, prasinophytes bloom early in the season. There occurs a second bloom during which diatoms and cryptophytes subsequently dominate the total activity (Terrado et al. 2011), while ciliates and dinoflagellates come to dominate the diversity (Lovejoy et al. 2002). The Arctic microbial marine food web is dynamic at this point in the yearly cycle with high levels of nutrients and unlimited growth. During spring, and throughout the summer, when light becomes available for photosynthesis, a large biomass of unicellular photosynthetic ice algae develops within the lowermost sections of the ice (Krembs and Deming 2011). In *summer*, very high solar radiation penetrates into the surface layers, and no ice occurs in almost all areas. The microbial loop becomes important at this part of the annual cycle, with characteristically low levels of nutrients and high dissolved organic carbon. July sees the highest biomass for heterotrophs and large autotrophs (Seuthe et al. 2011), and while alveolates still dominate the genomic DNA libraries, there is a radiolatian spike and stramenopile diversity decreases (Terrado et al. 2009). Alveolates also dominate sediments, although they do also appear in surface layers, and stramenopiles dominate between the depths of 20–30 m down from the surface (Luo et al. 2009). In the a*utumn*, solar radiation now rapidly starts to decrease, sea ice forms and upwelling returns. In Kongsfjorden on Svalbard, all biomass starts to decrease by July, although a later bloom during August and September does occur in the far north (Seuthe et al. 2011). As for the *autumn*, alveolates strongly dominate and heterotrophs increase throughout the season(Terrado et al. 2009). Sanders and

Gast (2012) found that in the Canada Basin, around the autumn equinox, mixotrophs dominate a low biomass level. Some algae remain dormant in the ice throughout the winter, bloom when the spring sunshine kick-starts a growth cycle and, eventually, migrate down to the bottom of the ice and enter the water column where they provide a nutritious dietary food source to many marine organisms.

9.16 Environmental Change

Environmental changes are already observed at a pan-Arctic scale and include a decline in the volume and extent of the sea-ice cover (Comiso et al. 2008), an advance in the melt period (Comiso 2006; Markus et al. 2009), and an increase in river discharge to the Arctic Ocean (McClelland et al. 2006; Peterson et al. 2002) due to increasing precipitation and terrestrial ice melt (Peterson et al. 2006). Changes in the microbial community composition can have a direct effect on environmental function. The degree of ice nucleation activity of microbes, either limited ice nucleation activity (as seen by sea-ice bacteria) or high nucleation activity (as seen by *Pseudomonas antarctica* and *Pseudomonas syringae*) will depend on the bacterial diversity and activity in the atmosphere (Junge and Swanson 2008). Human activity in the area is also on the increase. Gerdes et al. (2005) incubated sea ice with crude oil, in order to assess how an oil spill would affect a sea-ice community and saw a shift in community structure to a *Marinobacter*-, *Shewanella*- and *Pseudomonas*-dominated population. The sea-ice community was also shown to degrade [^{14}C] hexadecane at 2–50 % the efficiency of a mesophilic *Marinobacter*.

9.17 Warming Ocean

Global sea surface temperature is approximately 1 °C higher now than 140 years ago and is one of the primary physical impacts of climate change. Sea surface temperature is increasing more rapidly in some areas than others. Projections show the temperature increases will persist throughout this century. Ice-free summers are expected in the Arctic by the end of this century, perhaps even as early as 2040. Already, there is evidence that many marine ecosystems are affected by rising sea temperature. Over the past 25 years, the rate of increase in sea surface temperature has been about 10 times faster than the average rate of increase during the previous century. The microbial communities in the Arctic Ocean are changing due to rising sea temperatures and the dramatic loss of sea ice. In particular, the archaea Marine group I of Thaumarchaeota went from being 60 % of the archaeal community in 2003 to less than 10 % in 2010, and Bacteriodetes populations dropped dramatically greatly affecting bacterial community diversity (Comeau et al. 2011).

9.18 Loss of Sea Ice

Since the mid-twentieth century, the Arctic Ocean has experienced unprecedented sea-ice loss that has accelerated in recent years (Stroeve et al. 2007; Walsh and Chapman 2001). Future sea-ice loss will likely stimulate additional net primary production over the productive Bering Sea shelves, potentially reducing nutrient flux to the downstream western Arctic Ocean (Brown and Arrigo 2013). Increased ice-free conditions may also favour and extend northward the intrusion of Atlantic phytoplankton species (Poulin et al. 2011). On the other hand, sea-ice loss creates additional open-water habitat for phytoplankton, whose growth is traditionally thought to be light-limited under the sea-ice cover (Hill and Cota 2005; Loeng et al. 2005; Smetacek and Nicol 2005). Area-normalised rates of CO_2 fixation in the ice-free zone are generally far higher than in adjacent sea-ice habitats (Arrigo and van Dijken 2003), so sea-ice loss potentially leads to a more productive Arctic Ocean (Brown and Arrigo 2013). A freshening of surface waters may significantly change mineralised eukaryote ecology and distributions; though this may also affect the climate via dimethyl sulphide (DMS) production. Sea-ice loss is also accelerating (Comiso 2006; Comiso et al. 2008; Stroeve et al. 2007) with less multiyear ice, increases in autumn, and winter temp, more wave actions and coastal erosion. The salinity of the Arctic Ocean is also decreasing (McClelland et al. 2006; Peterson et al. 2002, 2006) due to a changing balance between increased river flow from a rainier Eurasia concurrent with decreased inflow originating from a warming and drying North America. We might expect a northwards movement of taxa as polar conditions become more favourable (Hegseth and Sundfjord 2008; Poulin et al. 2011).

9.19 Productivity

Annual mean open water area correlates with primary production (Pabi et al. 2008), and marine phytoplankton accounts for ca. 45 % of the net annual Arctic primary production (Falkowski et al. 2004). Ice algae contribute 57 % of total primary production in Arctic Ocean (Gosselin et al. 1997) and 3–25 % in the Arctic shelf regions (Legendre et al. 1992). Satellite data of phytoplankton concentrations since 1979 suggest decadal-scale fluctuations linked to climate forcing. Data from ocean transparency measurements and chlorophyll suggest global phytoplankton declines by approximately 1 % per year overall, with local fluctuations linked to climate (Boyce et al. 2010). Primary production increases as ice retreats (Frey et al. 2014); encouraged by an earlier melt and later freeze particularly in the Siberian and Svalbard Arctic (Markus et al. 2009).

9.20 Toxin Accumulation

Organochlorine, total mercury (THg), methylmercury (MeHg) and polybrominated diphenyl ether (PBDEs) contaminants accumulate in Arctic marine food chains (Campbell et al. 2005; Kelly et al. 2008a; Norstrom et al. 1998). Borgå et al. (2010) simulated climate change-induced alterations in bioaccumulation of organic contaminants in an Arctic marine food web. Their study demonstrated that organisms with a limited natural habitat range are likely to suffer the most under changing climatic and oceanic conditions. Organisms with a wide natural range are likely to cope better. Climate change is expected to alter environmental distribution of contaminants and their bioaccumulation due to changes in transport, partitioning, carbon pathways and bioaccumulation process rates. The magnitude and direction of these changes and resulting overall bioaccumulation in food webs are currently unknown.

9.21 Atmospheric CO_2 Concentration and Ocean Acidification

Such increasing CO_2 concentration in the atmosphere, leads to increased concentrations in the Oceans, resulting in a decrease in pH. Haptophytes are considered to be the most productive calcifying organisms on the planet (Fiorini et al. 2011) as they play a crucial role in the marine carbon cycle through calcification and photosynthetic carbon production. More specifically, they note that coccolithophores are responsible for about half of the global surface ocean calcification and contribute significantly to the flux of organic matter from the sea surface to deep waters and sediments (Klaas and Archer 2002). Consistent findings have inferred that coccolithophore mass has increased in relation to rising atmospheric pCO_2 over the past two centuries (Halloran et al. 2008; Iglesias-Rodriguez et al. 2008).

9.22 Questions Raised

So as we start to understand more and more about Arctic marine food webs, a number of lines of enquiry stand out. Much of the current interest in the area concerns the functioning of different parts of the communities and their interactions with each other; nonetheless, perhaps most importantly, we are interested in understanding how these interactions and functions might or would change in the face of a changing environment. As the global temperature warms and the climate changes, we are seeing in some places increased terrestrial run off, which will deliver more nutrients to the marine food webs, along with progressively melting

permafrost, which releases both nutrients and potentially new biodiversity into the Arctic Ocean. We know little of the role of sea ice and the effect of its loss. As the sea ice recedes, the patterns of Ocean circulation may change. These circulation patterns deliver nutrients and biodiversity to different regions of the world. We know very little about keystone microbial species and in particular, why are they "keystone" species. With changing selection pressures, we may see colonisation by "new" species, and we have scant understanding of this displacement process. Adding to this are the unknown rates of evolution of species in a changing environment. Gene exchange and dispersal (and indeed gene flow through the microbial community), particularly from the "rare" diversity, have unknown levels of functional redundancy. Rising sea surface temperature is moving us towards ice-free Arctic summers and a changing marine food chain, with progressive Ocean acidification, deoxygenation, bioaccumulation of toxins and oil exploration in the Arctic. Yet we still do not know the full extent of microbial diversity and biogeography, its extent and importance, interactions and feedback loops. The extent of this unknown diversity was vividly illustrated with the recent description of 35 new bacterial phyla (Brown et al. 2015).

9.23 Conclusions

Arctic marine food webs are important because they regulate productivity, biogeochemical cycling and biodiversity, essentially controlling ecosystem function. Polar regions, and more specifically the Arctic, have received a growing interest over the past decades due to the threatening impact of global warming (e.g. Johannessen et al. 1999; Moritz et al. 2002; Serreze et al. 2007; Thomas and Dieckmann 2010). The extreme climate that has prevailed over the Arctic Ocean for several million years has shaped unique marine ecosystems characterised by organisms that are adapted to frigid temperatures, the alternation between polar night and midnight sun, a perennial or seasonal sea-ice cover, limiting nutrients in the stratified surface layer and an extremely pulsed cycle of primary production (Darnis et al. 2012). Sea-ice loss and enhanced productivity have characterised the Arctic Ocean over recent years, and it has been hypothesised that as the ice recedes human impact on these environments will increase in the form of ship traffic, exploration, industrial activities and fisheries. This increase in pollution and further introduction of foreign contaminants will surely have a negative effect on the native species distribution and populations, further exacerbating the problem (Moline et al. 2008). Many questions still remain, and in particular the gaps in our knowledge of the winter microbial food web, so what is urgently needed is a large coordinated, comprehensive "food web" study, the likes of which occurred in the recent International Polar Year.

References

Aguirre de Cárcer D, López-Bueno A, Pearce DA, Alcamí A (2015) Biodiversity and distribution of polar freshwater DNA viruses. Sci Adv 1(5):e1400127

Alverson AJ (2008) Molecular systematics and the diatom species. Protist 159:339–353. doi:10.1016/j.protis.2008.04.001

Andersen RA, Kawachi M (2005) Traditional microalgae isolation techniques. In: Andersen RA (ed) Algal culturing techniques. Academic Press, London, pp 83–101

Andersen BM, Steigerwalt AG, O'Connor SP, Hollis DG, Weyant RS, Weaver RE, Brenner DJ (1993) *Neisseria weaveri* sp. nov., formerly CDC group M-5, a gram-negative bacterium associated with dog bite wounds. J Clin Microbiol 31:2456–2466

Andersen P, Hald B, Emsholm H (1996) Toxicity of *Dinophysis acuminata* in Danish coastal waters. In: Oshima Y, Fukuyo Y, Yasumoto T (eds) Harmful and toxic blooms. UNESCO, Paris, pp 281–284

Andreassen IJ, Wassmann P (1998) Vertical flux of phytoplankton and particulate biogenic matter in the marginal ice zone of the Barents Sea in May 1993. Mar Ecol Prog Ser 170:1–14

Angly FE et al (2006) The marine viromes of four oceanic regions. PLoS Biol 4:e368. doi:10.1371/journal.pbio.0040368

Archambault P et al (2010) From sea to sea: Canada's three oceans of biodiversity. PLoS One 5: e12182. doi:10.1371/journal.pone.0012182

Arrigo KR, van Dijken GL (2003) Phytoplankton dynamics within 37 Antarctic coastal polynya systems. J Geophys Res Oceans 108. doi:10.1029/2002jc001739

Arrigo KR, Pabi S, van Dijken GL, Maslowski W (2010) Air-sea flux of CO_2 in the Arctic Ocean, 1998–2003. J Geophys Res Biogeosci 115. doi:10.1029/2009JG001224

Atwell L, Hobson KA, Welch HE (1998) Biomagnification and bioaccumulation of mercury in an Arctic marine food web: insights from stable nitrogen isotope analysis. Can J Fish Aquat Sci 55: 1114–1121. doi:10.1139/f98-001

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257–263. doi:10.3354/meps010257

Bagi A, Pampanin DM, Lanzen A, Bilstad T, Kommedal R (2014) Naphthalene biodegradation in temperate and Arctic marine microcosms. Biodegradation 25:111–125. doi:10.1007/s10532-013-9644-3

Bano N, Hollibaugh JT (2002) Phylogenetic composition of bacterioplankton assemblages from the Arctic Ocean. Appl Environ Microbiol 68:505–518

Bass D, Cavalier-Smith T (2004) Phylum-specific environmental DNA analysis reveals remarkably high global biodiversity of Cercozoa (Protozoa). Int J Syst Evol Microbiol 54:2393–2404. doi:10.1099/ijs.0.63229-0

Bass D, Richards TA, Matthai L, Marsh V, Cavalier-Smith T (2007) DNA evidence for global dispersal and probable endemicity of protozoa. BMC Evol Biol 7:162. doi:10.1186/1471-2148-7-162

Batten SD et al (2003) CPR sampling: the technical background, materials and methods, consistency and comparability. Prog Oceanogr 58:193–215. doi:10.1016/j.pocean.2003.08.004

Becquevort S, Dumont I, Tison JL, Lannuzel D, Sauvée ML, Chou L, Schoemann V (2009) Biogeochemistry and microbial community composition in sea ice and underlying seawater off East Antarctica during early spring. Polar Biol 32:879–895. doi:10.1007/s00300-009-0589-2

Béjà O et al (2000) Bacterial rhodopsin: evidence for a new type of phototrophy in the sea. Science 289:1902–1906

Berney C, Fahrni J, Pawlowski J (2004) How many novel eukaryotic 'kingdoms'? Pitfalls and limitations of environmental DNA surveys. BMC Biol 2:13. doi:10.1186/1741-7007-2-13

Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. Ecol Appl 18:S77–S96. doi:10.1890/06-0562.1

Booth BC, Marchant HJ (1987) Parmales, a new order of marine chrysophytes, with descriptions of three new genera and seven new species. J Phycol 23:245–260. doi:10.1111/j.1529-8817.1987.tb04132.x

Borgå K, Saloranta TM, Ruus A (2010) Simulating climate change-induced alterations in bioaccumulation of organic contaminants in an Arctic marine food web. Environ Toxicol Chem 29:1349–1357. doi:10.1002/etc.159

Borriss M, Helmke E, Hanschke R, Schweder T (2003) Isolation and characterization of marine psychrophilic phage-host systems from Arctic sea ice. Extremophiles 7:377–384. doi:10.1007/s00792-003-0334-7

Bouvier TC, del Giorgio PA (2002) Compositional changes in free-living bacterial communities along a salinity gradient in two temperate estuaries. Limnol Oceanogr 47:453–470. doi:10.4319/lo.2002.47.2.0453

Bowman JS, Deming JW (2010) Elevated bacterial abundance and exopolymers in saline frost flowers and implications for atmospheric chemistry and microbial dispersal. Geophys Res Lett 37. doi:10.1029/2010GL043020

Bowman JP, McCammon SA, Brown MV, Nichols DS, McMeekin TA (1997) Diversity and association of psychrophilic bacteria in Antarctic sea ice. Appl Environ Microbiol 63:3068–3078

Bowman JS, Rasmussen S, Blom N, Deming JW, Rysgaard S, Sicheritz-Ponten T (2012) Microbial community structure of Arctic multiyear sea ice and surface seawater by 454 sequencing of the 16S RNA gene. ISME J 6:11–20. doi:10.1038/ismej.2011.76

Boyce DG, Lewis MR (2010) Worm B. Global phytoplankton decline over the past century Nature 466:591–596, http://www.nature.com/nature/journal/v466/n7306/abs/nature09268.html#supplementary-information

Boyd PW, Abraham ER (2001) Iron-mediated changes in phytoplankton photosynthetic competence during SOIREE. Deep Sea Res II Top Stud Oceanogr 48:2529–2550. doi:10.1016/S0967-0645(01)00007-8

Brinkmeyer R, Knittel K, Jürgens J, Weyland H, Amann R, Helmke E (2003) Diversity and structure of bacterial communities in Arctic versus Antarctic pack ice. Appl Environ Microbiol 69:6610–6619. doi:10.1128/AEM.69.11.6610-6619.2003

Bronk DA, Ward BB (2005) Inorganic and organic nitrogen cycling in the Southern California Bight. Deep Sea Res I Oceanogr Res Pap 52:2285–2300. doi:10.1016/j.dsr.2005.08.002

Brown ZW, Arrigo KR (2013) Sea ice impacts on spring bloom dynamics and net primary production in the Eastern Bering Sea. J Geophys Res Oceans 118:43–62. doi:10.1029/2012JC008034

Brown CT et al (2015) Unusual biology across a group comprising more than 15% of domain Bacteria. Nature 523:208–211. doi:10.1038/nature14486, http://www.nature.com/nature/journal/v523/n7559/abs/nature14486.html#supplementary-information

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divoky GJ (2008) Tracing carbon flow in an Arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157: 117–129. doi:10.1007/s00442-008-1053-7

Campbell LM, Norstrom RJ, Hobson KA, Muir DCG, Backus S, Fisk AT (2005) Mercury and other trace elements in a pelagic Arctic marine food web (Northwater Polynya, Baffin Bay). Sci Total Environ 351–352:247–263. doi:10.1016/j.scitotenv.2005.02.043

Caron DA (2009) Past president's address: Protistan biogeography: why all the fuss? J Eukaryot Microbiol 56:105–112. doi:10.1111/j.1550-7408.2008.00381.x

Cermeno P, de Vargas C, Abrantes F, Falkowski PG (2010) Phytoplankton biogeography and community stability in the ocean. PLoS One 5:e10037. doi:10.1371/journal.pone.0010037

Cho JC, Giovannoni SJ (2004) Cultivation and growth characteristics of a diverse group of oligotrophic marine Gammaproteobacteria. Appl Environ Microbiol 70:432–440

Chown SL, Convey P (2007) Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. Philos Trans R Soc B Biol Sci 362:2307–2331. doi:10.1098/rstb.2006.1949

Chown SL, Clarke A, Fraser CI, Cary SC, Moon KL, McGeoch MA (2015) The changing form of Antarctic biodiversity. Nature 522:431–438. doi:10.1038/nature14505
Coleman AW (2009) Is there a molecular key to the level of "biological species" in eukaryotes? A DNA guide. Mol Phylogenet Evol 50:197–203. doi:10.1016/j.ympev.2008.10.008
Collins A (2001) Ocean circulation. In: University O (ed) Ocean circulation. Butterworth-Heinemann, Boston, MA, pp 208–209
Collins RE, Rocap G, Deming JW (2010) Persistence of bacterial and archaeal communities in sea ice through an Arctic winter. Environ Microbiol 12:1828–1841. doi:10.1111/j.1462-2920.2010.02179.x
Comeau AM, Li WKW, Tremblay J-É, Carmack EC, Lovejoy C (2011) Arctic Ocean microbial community structure before and after the 2007 record sea ice minimum. PLoS One 6:e27492. doi:10.1371/journal.pone.0027492
Comiso JC (2006) Arctic warming signals from satellite observations. Weather 61:70–76. doi:10.1256/wea.222.05
Comiso JC, Parkinson CL, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophys Res Lett 35. doi:10.1029/2007GL031972
Connon SA, Giovannoni SJ (2002) High-throughput methods for culturing microorganisms in very-low-nutrient media yield diverse new marine isolates. Appl Environ Microbiol 68:3878–3885
Cota GF, Kottmeier ST, Robinson DH, Smith WO Jr, Sullivan CW (1990) Bacterioplankton in the marginal ice zone of the Weddell Sea: biomass, production and metabolic activities during austral autumn. Deep Sea Res A Oceanogr Res Pap 37:1145–1167. doi:10.1016/0198-0149(90)90056-2
Crump BC, Hopkinson CS, Sogin ML, Hobbie JE (2004) Microbial biogeography along an estuarine salinity gradient: combined influences of bacterial growth and residence time. Appl Environ Microbiol 70:1494–1505. doi:10.1128/AEM.70.3.1494-1505.2004
Curtis TP, Sloan WT, Scannell JW (2002) Estimating prokaryotic diversity and its limits. Proc Natl Acad Sci USA 99:10494–10499
Dalsgaard J, St John M, Kattner G, Muller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340
Damm E, Helmke E, Thoms S, Schauer U, Nöthig E, Bakker K, Kiene RP (2010) Methane production in aerobic oligotrophic surface water in the central Arctic Ocean. Biogeosciences 7:1099–1108. doi:10.5194/bg-7-1099-2010
Darnis G, Robert D, Pomerleau C, Link H, Archambault P, Nelson RJ, Geoffroy M, Tremblay J-É, Lovejoy C, Ferguson SH, Hunt BPV, Fortier L (2012) Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. Clim Change 115(1):179–205
Daugbjerg N, Moestrup Ø (1993) Four new species of Pyramimonas (Prasinophyceae) from Arctic Canada including a light and electron microscopic description of *Pyramimonas quadrifolia* sp. nov. Eur J Phycol 28:3–16. doi:10.1080/09670269300650021
Dawson SC, Pace NR (2002) Novel kingdom-level eukaryotic diversity in anoxic environments. Proc Natl Acad Sci USA 99:8324–8329. doi:10.1073/pnas.062169599
De Wit R, Bouvier T (2006) 'Everything is everywhere, but, the environment selects'; what did Baas Becking and Beijerinck really say? Environ Microbiol 8:755–758. doi:10.1111/j.1462-2920.2006.01017.x
DeLong EF, Wickham GS, Pace NR (1989) Phylogenetic stains: ribosomal RNA-based probes for the identification of single cells. Science 243:1360–1363
DeLong EF et al (2006) Community genomics among stratified microbial assemblages in the ocean's interior. Science 311:496–503. doi:10.1126/science.1120250
Deming JW (2002) Psychrophiles and polar regions. Curr Opin Microbiol 5:301–309
Devos N, Ingouff M, Loppes R, Matagne RF (1998) Rubisco adaptation to low temperatures: a comparative study in psychrophilic and mesophilic unicellular algae. J Phycol 34:655–660. doi:10.1046/j.1529-8817.1998.340655.x

Eicken H (1992) Salinity profiles of Antarctic sea ice: field data and model results. J Geophys Res Oceans 97:15545–15557. doi:10.1029/92JC01588

Epstein SS (1995) Simultaneous enumeration of protozoa and micrometazoa from marine sandy sediments. Aquat Microb Ecol 9(3):219–227

Fahlgren C et al (2015) Seawater mesocosm experiments in the Arctic uncover differential transfer of marine bacteria to aerosols. Environ Microbiol Rep 7:460–470. doi:10.1111/1758-2229.12273

Falk K, Benvenuti S, Dall Antonia L, Kampp K (2002) Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an inter-colony comparison. Mar Ecol Prog Ser 231:293–302

Falkowski P, Koblfzek M, Gorbunov M, Kolber Z (2004) Development and application of variable chlorophyll fluorescence techniques in marine ecosystems. In: Papageorgiou G, Govindjee (eds) Chlorophyll a fluorescence, vol 19, Advances in photosynthesis and respiration. Springer, Dordrecht, pp 757–778. doi:10.1007/978-1-4020-3218-9_30

Fenchel T (1982) Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as bacterial consumers. Mar Ecol Prog Ser 9:35–42

Fenchel T (1988) Marine plankton food chains. Annu Rev Ecol Syst 19:19–38. doi:10.1146/annurev.es.19.110188.000315

Fenchel T, Finlay BJ (2003) Is microbial diversity fundamentally different from biodiversity of larger animals and plants? Eur J Protistol 39:486–490. doi:10.1078/0932-4739-00025

Fenchel T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. BioScience 54(8):777–784

Ferrari VC, Hollibaugh JT (1999) Distribution of microbial assemblages in the Central Arctic Ocean Basin studied by PCR/DGGE: analysis of a large data set. Hydrobiologia 401:55–68. doi:10.1023/A:1003773907789

Filée J, Tétart F, Suttle CA, Krisch HM (2005) Marine T4-type bacteriophages, a ubiquitous component of the dark matter of the biosphere. Proc Natl Acad Sci USA 102:12471–12476. doi:10.1073/pnas.0503404102

Finlay BJ (2002) Global dispersal of free-living microbial eukaryote species. Science 296:1061–1063. doi:10.1126/science.1070710

Finlay BJ, Esteban GF, Brown S, Fenchel T, Hoef-Emden K (2006) Multiple cosmopolitan ecotypes within a microbial eukaryote morphospecies. Protist 157:377–390. doi:10.1016/j.protis.2006.05.012

Fiorini S, Middelburg JJ, Gattuso J-P (2011) Testing the effects of elevated pCo_2 on Coccolithophores (Prymnesiophyceae): comparison between haploid and diploid life stages. J Phycol 47:1281–1291. doi:10.1111/j.1529-8817.2011.01080.x

Foerstner KU, von Mering C, Bork P (2006) Comparative analysis of environmental sequences: potential and challenges. Philos Trans R Soc B Biol Sci 361:519–523. doi:10.1098/rstb.2005.1809

Fraser AJ, Sargent JR, Gamble JC, Seaton DD (1989) Formation and transfer of fatty acids in an enclosed marine food chain comprising phytoplankton, zooplankton and herring (*Clupea harengus* L.) larvae. Mar Chem 27:1–18. doi:10.1016/0304-4203(89)90024-8

Freitag TE, Chang L, Prosser JI (2006) Changes in the community structure and activity of betaproteobacterial ammonia-oxidizing sediment bacteria along a freshwater-marine gradient. Environ Microbiol 8:684–696. doi:10.1111/j.1462-2920.2005.00947.x

Frey KE, Comiso JC, Cooper LW, Gradinger RR, Grebmeier JM, Saitoh S-I, Tremblay J-E (2014) Arctic Ocean primary productivity. National Oceanic and Atmospheric Administration, Washington, DC, http://www.arctic.noaa.gov/reportcard/ocean_primary_productivity.html

Frezal L, Leblois R (2008) Four years of DNA barcoding: current advances and prospects. Infect Genet Evol 8:727–736. doi:10.1016/j.meegid.2008.05.005

Fuhrman JA (1999) Marine viruses and their biogeochemical and ecological effects. Nature 399:541–548

Fuhrman JA, Steele JA, Hewson I, Schwalbach MS, Brown MV, Green JL, Brown JH (2008) A latitudinal diversity gradient in planktonic marine bacteria. Proc Natl Acad Sci USA 105:7774–7778. doi:10.1073/pnas.0803070105

Galand PE, Casamayor EO, Kirchman DL, Lovejoy C (2009) Ecology of the rare microbial biosphere of the Arctic Ocean. Proc Natl Acad Sci USA 106:22427–22432. doi:10.1073/pnas.0908284106

Galand PE, Potvin M, Casamayor EO, Lovejoy C (2010) Hydrography shapes bacterial biogeography of the deep Arctic Ocean. ISME J 4:564–576. doi:10.1038/ismej.2009.134

Garcia-Martinez J, Rodriguez-Valera F (2000) Microdiversity of uncultured marine prokaryotes: the SAR11 cluster and the marine Archaea of Group I. Mol Ecol 9:935–948

Gerard E, Guyot F, Philippot P, Lopez-Garcia P (2005) Fluorescence in situ hybridisation coupled to ultra small immunogold detection to identify prokaryotic cells using transmission and scanning electron microscopy. J Microbiol Methods 63:20–28. doi:10.1016/j.mimet.2005.02.018

Gerdes B, Brinkmeyer R, Dieckmann G, Helmke E (2005) Influence of crude oil on changes of bacterial communities in Arctic sea-ice. FEMS Microbiol Ecol 53:129–139. doi:10.1016/j.femsec.2004.11.010

Ghiglione J-F et al (2012) Pole-to-pole biogeography of surface and deep marine bacterial communities. Proc Natl Acad Sci USA 109:17633–17638. doi:10.1073/pnas.1208160109

Giovannoni SJ, Stingl U (2005) Molecular diversity and ecology of microbial plankton. Nature 437:343–348. doi:10.1038/nature04158

Giovannoni SJ, Vergin KL (2012) Seasonality in ocean microbial communities. Science 335:671–676. doi:10.1126/science.1198078

Giovannoni SJ, Britschgi TB, Moyer CL, Field KG (1990) Genetic diversity in Sargasso Sea bacterioplankton. Nature 345:60–63. doi:10.1038/345060a0

Giovannoni SJ, Rappe MS, Vergin KL, Adair NL (1996) 16S rRNA genes reveal stratified open ocean bacterioplankton populations related to the Green Non-Sulfur bacteria. Proc Natl Acad Sci USA 93:7979–7984

Gobeil C, Macdonald RW, Smith JN (1999) Mercury profiles in sediments of the Arctic Ocean Basins. Environ Sci Technol 33:4194–4198. doi:10.1021/es990471p

Golden KM, Ackley SF, Lytle VI (1998) The percolation phase transition in sea ice. Science 282:2238–2241

Goldstein PZ, DeSalle R (2011) Integrating DNA barcode data and taxonomic practice: determination, discovery, and description. BioEssays 33:135–147. doi:10.1002/bies.201000036

Gons HJ, Ebert J, Hoogveld HL, van den Hove L, Pel R, Takkenberg W, Woldringh CJ (2002) Observations on cyanobacterial population collapse in eutrophic lake water. Antonie Van Leeuwenhoek 81:319–326

González JM, Moran MA (1997) Numerical dominance of a group of marine bacteria in the alpha-subclass of the class Proteobacteria in coastal seawater. Appl Environ Microbiol 63:4237–4242

Gordon DA, Giovannoni SJ (1996) Detection of stratified microbial populations related to Chlorobium and Fibrobacter species in the Atlantic and Pacific oceans. Appl Environ Microbiol 62:1171–1177

Gosselin M, Legendre L, Therriault J-C, Demers S (1990) Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic). J Phycol 26:220–232. doi:10.1111/j.0022-3646.1990.00220.x

Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep Sea Res II Top Stud Oceanogr 44:1623–1644. doi:10.1016/S0967-0645(97)00054-4

Gradinger R (2008) Sea ice. Institute of Marine Sciences, University of Alaska, Fairbanks, AK, http://www.arcodiv.org/news/NPRB_report2_final.pdf

Gradinger R (2009) Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep Sea Res II Top Stud Oceanogr 56:1201–1212. doi:10.1016/j.dsr2.2008.10.016

Gradinger R, Bluhm B (2004) In-situ observations on the distribution and behavior of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the High Arctic Canada Basin. Polar Biol 27:595–603. doi:10.1007/s00300-004-0630-4

Graeve M, Kattner G, Hagen W (1994) Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: experimental evidence of trophic markers. J Exp Mar Biol Ecol 182:97–110. doi:10.1016/0022-0981(94)90213-5

Gravalosa JM, Flores J-A, Sierro FJ, Gersonde R (2008) Sea surface distribution of coccolithophores in the eastern Pacific sector of the Southern Ocean (Bellingshausen and Amundsen Seas) during the late austral summer of 2001. Mar Micropaleontol 69:16–25. doi:10.1016/j.marmicro.2007.11.006

Grieg FS, Smith C, Azam F (1996) Abundance and production of bacteria and viruses in the Bering and Chukchi Seas. Mar Ecol Prog Ser 131:287–300

Guillou L, Chrétiennot-Dinet M-J, Medlin LK, Claustre H, Goër SL-d, Vaulot D (1999) Bolidomonas: a new genus with two species belonging to a new algal class, the Bolidophyceae (Heterokonta). J Phycol 35:368–381. doi:10.1046/j.1529-8817.1999.3520368.x

Guillou L et al (2004) Diversity of picoplanktonic prasinophytes assessed by direct nuclear SSU rDNA sequencing of environmental samples and novel isolates retrieved from oceanic and coastal marine ecosystems. Protist 155:193–214. doi:10.1078/143446104774199592

Halloran PR, Hall IR, Colmenero-Hidalgo E, Rickaby REM (2008) Evidence for a multi-species coccolith volume change over the past two centuries: understanding a potential ocean acidification response. Biogeosciences 5:1651–1655. doi:10.5194/bg-5-1651-2008

Hambly E, Suttle CA (2005) The viriosphere, diversity, and genetic exchange within phage communities. Curr Opin Microbiol 8:444–450. doi:10.1016/j.mib.2005.06.005

Harrison PJ, Cochlan WP, Acreman JC, Parsons TR, Thompson PA, Dovey HM, Xiaolin C (1986) The effects of crude oil and Corexit 9527 on marine phytoplankton in an experimental enclosure. Mar Environ Res 18:93–109. doi:10.1016/0141-1136(86)90002-4

Hassol SJ (2004) Impacts of a warming Arctic. Arctic Climate Impact Assessment, Canada

Hegseth EN, Sundfjord A (2008) Intrusion and blooming of Atlantic phytoplankton species in the high Arctic. J Mar Syst 74:108–119. doi:10.1016/j.jmarsys.2007.11.011

Helmke E, Weyland H (2004) Psychrophilic versus psychrotolerant bacteria–occurrence and significance in polar and temperate marine habitats. Cell Mol Biol 50:553–561

Hill V, Cota G (2005) Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002. Deep Sea Res II Top Stud Oceanogr 52:3344–3354. doi:10.1016/j.dsr2.2005.10.001

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. Am Nat 163:192–211. doi:10.1086/381004

Hirst MB, Kita KN, Dawson SC (2011) Uncultivated microbial eukaryotic diversity: a method to link SSU rRNA gene sequences with morphology. PLoS One 6:e28158. doi:10.1371/journal.pone.0028158

Hobbie JE, Daley RJ, Jasper S (1977) Use of nuclepore filters for counting bacteria by fluorescence microscopy. Appl Environ Microbiol 33:1225–1228

Hobson KA, Welch HE (1992) Observations of foraging northern fulmars (*Fulmarus glacialis*) in the Canadian High Arctic. Arctic 45(2):150–153

Hobson KA, Schell DM, Renouf D, Noseworthy E (1996) Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can J Fish Aquat Sci 53:528–533. doi:10.1139/f95-209

Hollibaugh JT, Lovejoy C, Murray AE (2007) Microbiology in polar oceans. Oceanography 20:140–145

Horak REA, Whitney H, Shull DH, Mordy CW, Devol AH (2013) The role of sediments on the Bering Sea shelf N cycle: insights from measurements of benthic denitrification and benthic DIN fluxes. Deep Sea Res II Top Stud Oceanogr 94:95–105. doi:10.1016/j.dsr2.2013.03.014

Horner R, Schrader GC (1982) Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. Arctic 35(4): 457–571

Iglesias-Rodriguez MD et al (2008) Phytoplankton calcification in a high-CO_2 world. Science 320: 336–340

Ikävalko J, Gradinger R (1997) Flagellates and heliozoans in the Greenland Sea ice studied alive using light microscopy. Polar Biol 17:473–481. doi:10.1007/s003000050145

Janech MG, Krell A, Mock T, Kang J-S, Raymond JA (2006) Ice-binding proteins from sea ice diatoms (Bacillariophyceae). J Phycol 42:410–416. doi:10.1111/j.1529-8817.2006.00208.x

Johannessen OM, Shalina EV, Miles MW (1999) Satellite evidence for an Arctic sea ice cover in transformation. Science 286:1937–1939

Junge K, Swanson BD (2008) High-resolution ice nucleation spectra of sea-ice bacteria: implications for cloud formation and life in frozen environments. Biogeosciences 5:865–873. doi:10.5194/bg-5-865-2008

Junge K, Imhoff F, Staley T, Deming JW (2002) Phylogenetic diversity of numerically important Arctic sea-ice bacteria cultured at subzero temperature. Microb Ecol 43:315–328. doi:10.1007/s00248-001-1026-4

Junge K, Eicken H, Deming JW (2004) Bacterial activity at -2 to -20 degrees C in Arctic wintertime sea ice. Appl Environ Microbiol 70:550–557

Kapoor A et al (2008) A highly divergent picornavirus in a marine mammal. J Virol 82:311–320. doi:10.1128/jvi.01240-07

Karnovsky NJ et al (2011) Inter-colony comparison of diving behavior of an Arctic top predator: implications for warming in the Greenland Sea. Mar Ecol Prog Ser 440:229–240

Kedra M et al (2015) Status and trends in the structure of Arctic benthic food webs. Polar Res 34 (incl suppl)

Kelly BC, Ikonomou MG, Blair JD, Gobas FA (2008a) Bioaccumulation behaviour of polybrominated diphenyl ethers (PBDEs) in a Canadian Arctic marine food web. Sci Total Environ 401:60–72. doi:10.1016/j.scitotenv.2008.03.045

Kelly BC, Ikonomou MG, Blair JD, Gobas FAPC (2008b) Hydroxylated and methoxylated polybrominated diphenyl ethers in a Canadian Arctic marine food web. Environ Sci Technol 42:7069–7077. doi:10.1021/es801275d

Kirchman DL, Moran XAG, Ducklow H (2009) Microbial growth in the polar oceans - role of temperature and potential impact of climate change. Nat Rev Microbiol 7:451–459. doi:10.1038/nrmicro2115

Klaas C, Archer DE (2002) Association of sinking organic matter with various types of mineral ballast in the deep sea: implications for the rain ratio. Glob Biogeochem Cycles 16(4):1116. doi:10.1029/2001GB001765

Knoblauch C, Jorgensen BB, Harder J (1999) Community size and metabolic rates of psychrophilic sulfate-reducing bacteria in Arctic marine sediments. Appl Environ Microbiol 65: 4230–4233

Koch TA, Ekelund F (2005) Strains of the heterotrophic flagellate *Bodo designis* from different environments vary considerably with respect to salinity preference and SSU rRNA gene composition. Protist 156:97–112. doi:10.1016/j.protis.2004.12.001

Kolodziej K, Stoeck T (2007) Cellular identification of a novel uncultured marine stramenopile (MAST-12 Clade) small-subunit rRNA gene sequence from a Norwegian estuary by use of fluorescence in situ hybridization-scanning electron microscopy. Appl Environ Microbiol 73: 2718–2726. doi:10.1128/aem.02158-06

Kovacs KM (2014) Circumpolar ringed seal (*Pusa hispida*) monitoring: CAFF's ringed seal monitoring network. Norsk Polarinstitutt, Tromsø http://brage.bibsys.no/xmlui/handle/11250/191472

Krembs C, Deming J (2011) Sea ice: a refuge for life in polar seas? National Oceanic and Atmospheric Administration. Accessed 31 Jul 2015

Laidre KL, Stirling I, Lowry LF, Wiig Ø, Heide-Jørgensen MP, Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol Appl 18: S97–S125. doi:10.1890/06-0546.1

Laidre KL et al (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conserv Biol 29:724–737. doi:10.1111/cobi.12474

Lannuzel D et al. (2010) Distribution of dissolved iron in Antarctic sea ice: spatial, seasonal, and inter-annual variability. J Geophys Res Biogeosci 115. doi:10.1029/2009JG001031

Larsen J, Patterson DJ (1990) Some flagellates (Protista) from tropical marine sediments. J Nat Hist 24:801–937. doi:10.1080/00222939000770571

Larsen A et al (2004) Spring phytoplankton bloom dynamics in Norwegian coastal waters: microbial community succession and diversity. Limnol Oceanogr 49:180–190. doi:10.4319/lo.2004.49.1.0180

Larsen A, Egge JK, Nejstgaard JC, Di Capua I, Thyrhaug R, Bratbak G, Thingstad TF (2015) Contrasting response to nutrient manipulation in Arctic mesocosms are reproduced by a minimum microbial food web model. Limnol Oceanogr 60:360–374. doi:10.1002/lno.10025

Latasa M, Scharek R, Gall FL, Guillou L (2004) Pigment suites and taxonomic groups in Prasinophyceae. J Phycol 40:1149–1155. doi:10.1111/j.1529-8817.2004.03136.x

Lee WJ, Patterson DJ (1998) Diversity and geographic distribution of free-living heterotrophic flagellates - analysis by primer. Protist 149:229–244. doi:10.1016/s1434-4610(98)70031-8

Lee WJ, Patterson DJ (2000) Heterotrophic flagellates (Protista) from marine sediments of Botany Bay. Aust J Nat Hist 34:483–562. doi:10.1080/002229300299435

Legagneux P et al (2012) Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. Ecology 93:1707–1716

Legendre M, Teugels GG, Cauty C, Jalabert B (1992) A comparative study on morphology, growth rate and reproduction of *Clarias gariepinus* (Burchell, 1822), *Heterobranchus longifilis* Valenciennes, 1840, and their reciprocal hybrids (Pisces, Clariidae). J Fish Biol 40:59–79. doi:10.1111/j.1095-8649.1992.tb02554.x

Leliaert F, Verbruggen H, Wysor B, De Clerck O (2009) DNA taxonomy in morphologically plastic taxa: algorithmic species delimitation in the Boodlea complex (Chlorophyta: Cladophorales). Mol Phylogenet Evol 53:122–133. doi:10.1016/j.ympev.2009.06.004

Lennon JT, Khatana SA, Marston MF, Martiny JB (2007) Is there a cost of virus resistance in marine cyanobacteria? ISME J 1:300–312. doi:10.1038/ismej.2007.37

Letcher RJ, Norstrom RJ, Muir DCG (1998) Biotransformation versus bioaccumulation: sources of methyl sulfone PCB and 4,4′-DDE metabolites in the polar bear food chain. Environ Sci Technol 32:1656–1661. doi:10.1021/es970886f

Li WKW (1994) Primary production of prochlorophytes, cyanobacteria, and eucaryotic ultraphytoplankton: measurements from flow cytometric sorting. Limnol Oceanogr 39:169–175. doi:10.4319/lo.1994.39.1.0169

Li WK, Dickie PM (2001) Monitoring phytoplankton, bacterioplankton, and virioplankton in a coastal inlet (Bedford Basin) by flow cytometry. Cytometry 44:236–246

Lim EL, Dennett MR, Caron DA (1999) The ecology of *Paraphysomonas imperforata* based on studies employing oligonucleotide probe identification in coastal water samples and enrichment cultures. Limnol Oceanogr 44:37–51. doi:10.4319/lo.1999.44.1.0037

Liu H et al (2009) Extreme diversity in noncalcifying haptophytes explains a major pigment paradox in open oceans. Proc Natl Acad Sci USA 106:12803–12808. doi:10.1073/pnas.0905841106

Lizotte MP, Priscu JC (1998) Pigment analysis of the distribution, succession, and fate of phytoplankton in the Mcmurdo Dry Valley Lakes of Antarctica. In: Ecosystem dynamics in a polar desert: the Mcmurdo Dry Valleys, Antarctica. American Geophysical Union, Washington, DC, pp 229–239. doi:10.1029/AR072p0229

Loeng H et al (2005) Marine systems. In: Arris L, Heal B, Symon C (eds) Arctic climate impact assessment. Cambridge University Press, Cambridge, pp 453–538

Lopez-Garcia P, Moreira D (2008) Tracking microbial biodiversity through molecular and genomic ecology. Res Microbiol 159:67–73. doi:10.1016/j.resmic.2007.11.019
Lopez-Garcia P, Rodriguez-Valera F, Pedrós-Alió C, Moreira D (2001) Unexpected diversity of small eukaryotes in deep-sea Antarctic plankton. Nature 409:603–607. doi:10.1038/35054537
Lovejoy C, Potvin M (2011) Microbial eukaryotic distribution in a dynamic Beaufort Sea and the Arctic Ocean. J Plankton Res 33:431–444. doi:10.1093/plankt/fbq124
Lovejoy C, Legendre L, Martineau M-J, Bâcle J, von Quillfeldt CH (2002) Distribution of phytoplankton and other protists in the North Water. Deep Sea Res II Top Stud Oceanogr 49:5027–5047. doi:10.1016/S0967-0645(02)00176-5
Lovejoy C, Price NM, Legendre L (2004) Role of nutrient supply and loss in controlling protist species dominance and microbial food-webs during spring blooms. Aquat Microb Ecol 34: 79–92
Lovejoy C, Massana R, Pedrós-Alió C (2006) Diversity and distribution of marine microbial eukaryotes in the Arctic Ocean and adjacent seas. Appl Environ Microbiol 72:3085–3095. doi:10.1128/aem.72.5.3085-3095.2006
Lovejoy C et al (2007) Distribution, phylogeny, and growth of cold-adapted Picoprasinophytes in Arctic seas. J Phycol 43:78–89. doi:10.1111/j.1529-8817.2006.00310.x
Luo W, Li H, Cai M, He J (2009) Diversity of microbial eukaryotes in Kongsfjorden. Svalbard Hydrobiologia 636:233–248. doi:10.1007/s10750-009-9953-z
Mackey DJ, Higgins HW, Wright SW (1996) CHEMTAX - a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. Mar Ecol Prog Ser 144:265–283. doi:10.3354/meps144265
Mann DG (1999) The species concept in diatoms. Phycologia 38:437–495
Marande W, López-García P, Moreira D (2009) Eukaryotic diversity and phylogeny using small- and large-subunit ribosomal RNA genes from environmental samples. Environ Microbiol 11: 3179–3188. doi:10.1111/j.1462-2920.2009.02023.x
Margulies M et al (2005) Genome sequencing in microfabricated high-density picolitre reactors. Nature 437:376–380. doi:10.1038/nature03959
Marie D, Brussaard CPD, Thyrhaug R, Bratbak G, Vaulot D (1999) Enumeration of marine viruses in culture and natural samples by flow cytometry. Appl Environ Microbiol 65:45–52
Marie D, Zhu F, Balagué V, Ras J, Vaulot D (2006) Eukaryotic picoplankton communities of the Mediterranean Sea in summer assessed by molecular approaches (DGGE, TTGE, QPCR). FEMS Microbiol Ecol 55:403–415. doi:10.1111/j.1574-6941.2005.00058.x
Markus T, Stroeve JC, Miller J (2009) Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. J Geophys Res Oceans 114. doi:10.1029/2009JC005436
Martiny JB et al (2006) Microbial biogeography: putting microorganisms on the map. Nat Rev Microbiol 4:102–112. doi:10.1038/nrmicro1341
Massana R, Pedrós-Alió C (2008) Unveiling new microbial eukaryotes in the surface ocean. Curr Opin Microbiol 11:213–218. doi:10.1016/j.mib.2008.04.004
Massana R et al (2004) Phylogenetic and ecological analysis of novel marine stramenopiles. Appl Environ Microbiol 70:3528–3534. doi:10.1128/AEM.70.6.3528-3534.2004
Massana R, del Campo J, Dinter C, Sommaruga R (2007) Crash of a population of the marine heterotrophic flagellate *Cafeteria roenbergensis* by viral infection. Environ Microbiol 9: 2660–2669. doi:10.1111/j.1462-2920.2007.01378.x
Massana R, Unrein F, Rodriguez-Martinez R, Forn I, Lefort T, Pinhassi J, Not F (2009) Grazing rates and functional diversity of uncultured heterotrophic flagellates. ISME J 3:588–596
Matley JK, Crawford RE, Dick TA (2012) Summer foraging behaviour of shallow-diving seabirds and distribution of their prey, Arctic cod (*Boreogadus saida*), in the Canadian Arctic. Polar Res 31(incl suppl)
McClelland JW, Déry SJ, Peterson BJ, Holmes RM, Wood EF (2006) A pan-Arctic evaluation of changes in river discharge during the latter half of the 20th century. Geophys Res Lett 33. doi:10.1029/2006GL025753

Metz JG et al (2001) Production of polyunsaturated fatty acids by polyketide synthases in both prokaryotes and eukaryotes. Science 293:290–293. doi:10.1126/science.1059593
Middelburg JJ (2014) Stable isotopes dissect aquatic food webs from the top to the bottom. Biogeosciences 11:2357–2371. doi:10.5194/bg-11-2357-2014
Mock T, Junge K (2007) Psychrophilic diatoms: mechanisms for survival in freeze-thaw cycles. In: Seckbach J (ed) Algae and cyanobacteria in extreme environments. Springer, New York
Moestrup Ø (1979) Identification by electron microscopy of marine nanoplankton from New Zealand, including the description of four new species. NZ J Bot 17:61–95. doi:10.1080/0028825X.1979.10425161
Moline MA et al (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. Ann NY Acad Sci 1134:267–319. doi:10.1196/annals.1439.010
Montagnes DJS, Berges JA, Harrison PJ, Taylor FJR (1994) Estimating carbon, nitrogen, protein, and chlorophyll a from volume in marine phytoplankton. Limnol Oceanogr 39:1044–1060. doi:10.4319/lo.1994.39.5.1044
Moon-van der Staay SY, De Wachter R, Vaulot D (2001) Oceanic 18S rDNA sequences from picoplankton reveal unsuspected eukaryotic diversity. Nature 409:607–610. doi:10.1038/35054541
Moore SE, Huntington HP (2008) Arctic marine mammals and climate change: impacts and resilience. Ecol Appl 18:S157–S165. doi:10.1890/06-0571.1
Morata N, Renaud PE, Brugel S, Hobson KA, Johnson BJ (2008) Spatial and seasonal variations in the pelagic–benthic coupling of the southeastern Beaufort Sea revealed by sedimentary biomarkers. Mar Ecol Prog Ser 371:47–63
Moritz RE, Bitz CM, Steig EJ (2002) Dynamics of recent climate change in the Arctic. Science 297:1497–1502
Murphy LS, Haugen EM (1985) The distribution and abundance of phototrophic ultraplankton in the North Atlantic. Limnol Oceanogr 30:47–58. doi:10.4319/lo.1985.30.1.0047
Mykytczuk NC, Foote SJ, Omelon CR, Southam G, Greer CW, Whyte LG (2013) Bacterial growth at -15 degrees C; molecular insights from the permafrost bacterium *Planococcus halocryophilus* Or1. ISME J 7:1211–1226. doi:10.1038/ismej.2013.8
Nassonova E, Smirnov A, Fahrni J, Pawlowski J (2010) Barcoding amoebae: comparison of SSU, ITS and COI genes as tools for molecular identification of naked lobose amoebae. Protist 161:102–115. doi:10.1016/j.protis.2009.07.003
Nichols DS, Olley J, Garda H, Brenner RR, McMeekin TA (2000) Effect of temperature and salinity stress on growth and lipid composition of *Shewanella gelidimarina*. Appl Environ Microbiol 66:2422–2429
Niederberger TD et al (2010) Microbial characterization of a subzero, hypersaline methane seep in the Canadian High Arctic. ISME J 4:1326–1339. doi:10.1038/ismej.2010.57
Niehoff B, Schmithüsen T, Knüppel N, Daase M, Czerny J, Boxhammer T (2013) Mesozooplankton community development at elevated CO2 concentrations: results from a mesocosm experiment in an Arctic fjord. Biogeosciences 10:1391–1406. doi:10.5194/bg-10-1391-2013
Nielsen S, Sand-Jensen K, Borum J, Geertz-Hansen O (2002) Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. Estuaries 25:1025–1032. doi:10.1007/BF02691349
Niemi A, Michel C, Hille K, Poulin M (2011) Protist assemblages in winter sea ice: setting the stage for the spring ice algal bloom. Polar Biol 34:1803–1817. doi:10.1007/s00300-011-1059-1
Norkko A, Thrush SF, Cummings VJ, Gibbs MM, Andrew NL, Norkko J, Schwarz AM (2007) Trophic structure of coastal Antarctic food webs associated with changes in sea ice and food supply. Ecology 88:2810–2820
Norstrom RJ et al (1998) Chlorinated hydrocarbon contaminants in polar bears from eastern Russia, North America, Greenland, and Svalbard: biomonitoring of Arctic pollution. Arch Environ Contam Toxicol 35:354–367

Not F, Latasa M, Marie D, Cariou T, Vaulot D, Simon N (2004) A single species, *Micromonas pusilla* (Prasinophyceae), dominates the eukaryotic picoplankton in the Western English Channel. Appl Environ Microbiol 70:4064–4072. doi:10.1128/aem.70.7.4064-4072.2004

Not F et al (2007) Picobiliphytes: a marine picoplanktonic algal group with unknown affinities to other eukaryotes. Science 315:253–255. doi:10.1126/science.1136264

Not F, del Campo J, Balague V, de Vargas C, Massana R (2009) New insights into the diversity of marine picoeukaryotes. PLoS One 4:e7143. doi:10.1371/journal.pone.0007143

NSIDC (2015) All about sea ice. Accessed 31 Jul 2015

Pabi S, van Dijken GL, Arrigo KR (2008) Primary production in the Arctic Ocean, 1998–2006. J Geophys Res Oceans 113. doi:10.1029/2007JC004578

Pace NR (1997) A molecular view of microbial diversity and the biosphere. Science 276:734–740

Pavlov AK, Silyakova A, Granskog MA, Bellerby RGJ, Engel A, Schulz KG, Brussaard CPD (2014) Marine CDOM accumulation during a coastal Arctic mesocosm experiment: no response to elevated pCO_2 levels. J Geophys Res Biogeosci 119:1216–1230. doi:10.1002/2013JG002587

Pearce DA, Wilson WH (2003) Viruses in Antarctic ecosystems. Antarct Sci 15:319–331

Pedrós-Alió C (2006) Marine microbial diversity: can it be determined? Trends Microbiol 14: 257–263. doi:10.1016/j.tim.2006.04.007

Peterson BJ et al (2002) Increasing river discharge to the Arctic. Ocean Sci 298:2171–2173. doi:10.1126/science.1077445

Peterson BJ, McClelland J, Curry R, Holmes RM, Walsh JE, Aagaard K (2006) Trajectory shifts in the Arctic and Subarctic freshwater cycle. Science 313:1061–1066

Petrich C, Eicken H (2009) Growth, structure and properties of sea ice. In: Dieckman GS, Thomas DN (eds) Sea ice. Wiley-Blackwell, Oxford, pp 23–77

Piepenburg D et al (2011) Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. Mar Biodivers 41:51–70. doi:10.1007/s12526-010-0059-7

Pinhassi J, Berman T (2003) Differential growth response of colony-forming alpha- and gamma-proteobacteria in dilution culture and nutrient addition experiments from Lake Kinneret (Israel), the eastern Mediterranean Sea, and the Gulf of Eilat. Appl Environ Microbiol 69: 199–211

Pomeroy LR, Weibe WJ (2001) Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquat Microb Ecol 23:187–204

Pommier T et al (2007) Global patterns of diversity and community structure in marine bacterioplankton. Mol Ecol 16:867–880. doi:10.1111/j.1365-294X.2006.03189.x

Poulickova A, Vesela J, Neustupa J, Skaloud P (2010) Pseudocryptic diversity versus cosmopolitanism in diatoms: a case study on *Navicula cryptocephala* Kutz. (Bacillariophyceae) and morphologically similar taxa. Protist 161:353–369. doi:10.1016/j.protis.2009.12.003

Poulin M, Daugbjerg N, Gradinger R, Ilyash L, Ratkova T, von Quillfeldt C (2011) The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: a first-attempt assessment. Mar Biodivers 41:13–28. doi:10.1007/s12526-010-0058-8

Price PB, Bay RC (2012) Marine bacteria in deep Arctic and Antarctic ice cores: a proxy for evolution in oceans over 300 million generations. Biogeosciences 9:3799–3815. doi:10.5194/bg-9-3799-2012

Prokopowicz A, Rueckert S, Leander B, Michaud J, Fortier L (2010) Parasitic infection of the hyperiid amphipod *Themisto libellula* in the Canadian Beaufort Sea (Arctic Ocean), with a description of *Ganymedes themistos* sp. n. (Apicomplexa, Eugregarinorida). Polar Biol 33: 1339–1350. doi:10.1007/s00300-010-0821-0

Purdy KJ, Nedwell DB, Embley TM (2003) Analysis of the sulfate-reducing bacterial and methanogenic archaeal populations in contrasting Antarctic sediments. Appl Environ Microbiol 69:3181–3191

Radulovici AE, Archambault P, Dufresne F (2010) DNA barcodes for marine biodiversity: moving fast forward? Diversity 2:450–472

Rappe MS, Connon SA, Vergin KL, Giovannoni SJ (2002) Cultivation of the ubiquitous SAR11 marine bacterioplankton clade. Nature 418:630–633. doi:10.1038/nature00917

Ravenschlag K, Sahm K, Pernthaler J, Amann R (1999) High bacterial diversity in permanently cold marine sediments. Appl Environ Microbiol 65:3982–3989

Raymond JA, Janech MG, Fritsen CH (2009) Novel ice-binding proteins from a psychrophilic Antarctic alga (chlamydomonadaceae, chlorophyceae). J Phycol 45:130–136. doi:10.1111/j.1529-8817.2008.00623.x

Renaud PE, Morata N, Ambrose WG Jr, Bowie JJ, Chiuchiolo A (2007) Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. J Exp Mar Biol Ecol 349:248–260. doi:10.1016/j.jembe.2007.05.021

Rex RM, Tiffany RAS, Matthew TC, David LK (2007) Diversity, abundance, and biomass production of bacterial groups in the western Arctic Ocean. Aquat Microb Ecol 47:45–55

Riebesell U, Gattuso JP, Thingstad TF, Middelburg JJ (2013) Preface — Arctic Ocean acidification: pelagic ecosystem and biogeochemical responses during a mesocosm study. Biogeosciences 10:5619–5626. doi:10.5194/bg-10-5619-2013

Riedel A, Michel C, Gosselin M, LeBlanc B (2008) Winter–spring dynamics in sea-ice carbon cycling in the coastal Arctic Ocean. J Mar Syst 74:918–932. doi:10.1016/j.jmarsys.2008.01.003

Riemann LF, Steward G, Fandino LB, Campbell L, Landry MR, Azam F (1999) Bacterial community composition during two consecutive NE Monsoon periods in the Arabian Sea studied by denaturing gradient gel electrophoresis (DGGE) of rRNA genes. Deep Sea Res II Top Stud Oceanogr 46:1791–1811. doi:10.1016/S0967-0645(99)00044-2

Rodriguez-Martinez R, Labrenz M, del Campo J, Forn I, Jurgens K, Massana R (2009) Distribution of the uncultured protist MAST-4 in the Indian Ocean, Drake Passage and Mediterranean Sea assessed by real-time quantitative PCR. Environ Microbiol 11:397–408. doi:10.1111/j.1462-2920.2008.01779.x

Rodriguez-Martinez R, Rocap G, Logares R, Romac S, Massana R (2012) Low evolutionary diversification in a widespread and abundant uncultured protist (MAST-4). Mol Biol Evol 29:1393–1406. doi:10.1093/molbev/msr303

Russell NJ (1997) Psychrophilic bacteria–molecular adaptations of membrane lipids. Comp Biochem Physiol A Physiol 118:489–493

Rysgaard SR, Thamdrup B, Risgaard-Petersen N, Fossing H, Berg P, Christensen PB, Dalsgaard T (1998) Seasonal carbon and nutrient mineralization in a high-Arctic coastal marine sediment, Young Sound, Northeast Greenland. Mar Ecol Prog Ser 175:261–276

Sanders RW, Gast RJ (2012) Bacterivory by phototrophic picoplankton and nanoplankton in Arctic waters. FEMS Microbiol Ecol 82:242–253. doi:10.1111/j.1574-6941.2011.01253.x

Sanders RW, Caron DA, Berninger U-G (1992) Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: an inter-ecosystem comparison. Mar Ecol Prog Ser 86:1–14

Säwström C, Granéli W, Laybourn-Parry J, Anesio AM (2007) High viral infection rates in Antarctic and Arctic bacterioplankton. Environ Microbiol 9:250–255. doi:10.1111/j.1462-2920.2006.01135.x

Schlegel M, Meisterfeld R (2003) The species problem in protozoa revisited. Eur J Protistol 39:349–355. doi:10.1078/0932-4739-00003

Schmid MC et al (2007) Anaerobic ammonium-oxidizing bacteria in marine environments: widespread occurrence but low diversity. Environ Microbiol 9:1476–1484. doi:10.1111/j.1462-2920.2007.01266.x

Schnack-Schiel SB (2003) The macrobiology of sea ice. In: Thomas DN, Dieckmann GS (eds) Sea ice: an introduction to its physics, chemistry, biology and geology. Wiley-Blackwell, Oxford, pp 211–239

Serreze MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533–1536

Seuthe L, Töpper B, Reigstad M, Thyrhaug R, Vaquer-Sunyer R (2011) Microbial communities and processes in ice-covered Arctic waters of the northwestern Fram Strait (75 to 80°N) during the vernal pre-bloom phase. Aquat Microb Ecol 64:253–266

Sheldon RW (1972) Size separation of marine seston by membrane and glass-fiber filters. Limnol Oceanogr 17:494–498. doi:10.4319/lo.1972.17.3.0494

Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar Ecol Prog Ser 352:187–197

Short SM, Suttle CA (2002) Sequence analysis of marine virus communities reveals that groups of related algal viruses are widely distributed in nature. Appl Environ Microbiol 68:1290–1296. doi:10.1128/AEM.68.3.1290-1296.2002

Short CM, Suttle CA (2005) Nearly identical bacteriophage structural gene sequences are widely distributed in both marine and freshwater environments. Appl Environ Microbiol 71:480–486. doi:10.1128/aem.71.1.480-486.2005

Simon N, Barlow RG, Marie D, Partensky F, Vaulot D (1994) Characterization of oceanic photosynthetic picoeukaryotes by flow cytometry. J Phycol 30:922–935. doi:10.1111/j.0022-3646.1994.00922.x

Sintes E, del Giorgio PA (2010) Community heterogeneity and single-cell digestive activity of estuarine heterotrophic nanoflagellates assessed using lysotracker and flow cytometry. Environ Microbiol 12:1913–1925. doi:10.1111/j.1462-2920.2010.02196.x

Skarphedinsdottir H, Gunnarsson K, Gudmundsson GA, Nfon E (2010) Bioaccumulation and biomagnification of organochlorines in a marine food web at a pristine site in Iceland. Arch Environ Contamin Toxicol 58:800–809. doi:10.1007/s00244-009-9376-x

Skidmore M, Jungblut A, Urschel K, Junge (2012) Cryospheric environments in Polar regions (glaciers and ice sheets, sea ice and ice shelves). In: Whyte L, Miller RV (eds) Polar microbiology: life in a deep freeze. ASM Press, Washington, DC, pp 218–239

Slapeta J, Lopez-Garcia P, Moreira D (2006) Global dispersal and ancient cryptic species in the smallest marine eukaryotes. Mol Biol Evol 23:23–29. doi:10.1093/molbev/msj001

Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. Nature 437:362–368

Smith VH, Foster BL, Grover JP, Holt RD, Leibold MA, Denoyelles F Jr (2005) Phytoplankton species richness scales consistently from laboratory microcosms to the world's oceans. Proc Natl Acad Sci USA 102:4393–4396. doi:10.1073/pnas.0500094102

Sogin ML et al (2006) Microbial diversity in the deep sea and the underexplored "rare biosphere". Proc Natl Acad Sci USA 103:12115–12120. doi:10.1073/pnas.0605127103

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a - two-source food web model. Prog Oceanogr 71:59–87. doi:10.1016/j.pocean.2006.06.001

Sorhannus U, Ortiz JD, Wolf M, Fox MG (2010) Microevolution and speciation in *Thalassiosira weissflogii* (Bacillariophyta). Protist 161:237–249. doi:10.1016/j.protis.2009.10.003

Srinivas TN et al (2009) Bacterial diversity and bioprospecting for cold-active lipases, amylases and proteases, from culturable bacteria of kongsfjorden and Ny-alesund, Svalbard, Arctic. Curr Microbiol 59:537–547. doi:10.1007/s00284-009-9473-0

Stabeno P, Napp J, Mordy C, Whitledge T (2010) Factors influencing physical structure and lower trophic levels of the eastern Bering Sea shelf in 2005: sea ice, tides and winds. Prog Oceanogr 85:180–196

Stewart FJ, Fritsen CH (2004) Bacteria-algae relationships in Antarctic sea ice. Antarct Sci 16:143–156

Stewart R, Possingham H (2005) Efficiency, costs and trade-offs in marine reserve system design. Environ Model Assess 10:203–213. doi:10.1007/s10666-005-9001-y

Stirling I (1997) The importance of polynyas, ice edges, and leads to marine mammals and birds. J Mar Syst 10:9–21. doi:10.1016/S0924-7963(96)00054-1

Stoeck T, Taylor GT, Epstein SS (2003) Novel eukaryotes from the permanently anoxic Cariaco Basin (Caribbean Sea). Appl Environ Microbiol 69:5656–5663

Stoeck T, Hayward B, Taylor GT, Varela R, Epstein SS (2006) A multiple PCR-primer approach to access the microeukaryotic diversity in environmental samples. Protist 157:31–43. doi:10.1016/j.protis.2005.10.004

Stoeck T, Zuendorf A, Breiner HW, Behnke A (2007) A molecular approach to identify active microbes in environmental eukaryote clone libraries. Microb Ecol 53:328–339. doi:10.1007/s00248-006-9166-1

Stoeck T, Bass D, Nebel M, Christen R, Jones MDM, Breiner H-W, Richards TA (2010) Multiple marker parallel tag environmental DNA sequencing reveals a highly complex eukaryotic community in marine anoxic water. Mol Ecol 19:21–31. doi:10.1111/j.1365-294X.2009.04480.x

Stoecker DK, Gustafson DE, Black MMD, Baier CT (1998) Population dynamics of microalgae in the upper land-fast sea ice at a snow-free location. J Phycol 34:60–69. doi:10.1046/j.1529-8817.1998.340060.x

Stringer WJ, Groves JE (1991) Location and areal extent of Polynyas in the Bering and Chukchi Seas. Arctic 44(5):1–171

Stroeve J, Holland MM, Meier W, Scambos T, Serreze M (2007) Arctic sea ice decline: faster than forecast. Geophys Res Lett 34. doi:10.1029/2007GL029703

Suttle CA (2005) Viruses in the sea. Nature 437:356–361

Suttle CA (2007) Marine viruses — major players in the global ecosystem. Nat Rev Microbiol 5:801–812

Suzuki MT, Taylor LT, DeLong EF (2000) Quantitative analysis of small-subunit rRNA genes in mixed microbial populations via 5′-nuclease assays. Appl Environ Microbiol 66:4605–4614

Tedersoo L et al (2010) 454 Pyrosequencing and Sanger sequencing of tropical mycorrhizal fungi provide similar results but reveal substantial methodological biases. New Phytol 188:291–301. doi:10.1111/j.1469-8137.2010.03373.x

Terrado R, Lovejoy C, Massana R, Vincent WF (2008) Microbial food web responses to light and nutrients beneath the coastal Arctic Ocean sea ice during the winter–spring transition. J Mar Syst 74:964–977. doi:10.1016/j.jmarsys.2007.11.001

Terrado R, Vincent WF, Lovejoy C (2009) Mesopelagic protists: diversity and succession in a coastal Arctic ecosystem. Aquat Microb Ecol 56:25–39

Terrado R, Medrinal E, Dasilva C, Thaler M, Vincent W, Lovejoy C (2011) Protist community composition during spring in an Arctic flaw lead polynya. Polar Biol 34:1901–1914. doi:10.1007/s00300-011-1039-5

Thiemann GW, Iverson SJ, Stirling I (2008) Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. Ecol Monogr 78:591–613. doi:10.1890/07-1050.1

Thomas DN, Dieckmann GS (2002) Antarctic Sea ice--a habitat for extremophiles. Science 295:641–644. doi:10.1126/science.1063391

Thomas DN, Dieckmann GS (2010) Sea ice. Wiley-Blackwell, Oxford, 621 pp

Thomas DN, Kattner G, Engbrodt R, Giannelli V, Kennedy H, Haas C, Dieckmann GS (2001) Dissolved organic matter in Antarctic sea ice. Ann Glaciol 33:297–303. doi:10.3189/172756401781818338

Thomsen HA (1980) Two species of *Trigonaspis* gen. nov. (Prymnesiophyceae) from West Greenland. Phycologia 19:218–229. doi:10.2216/i0031-8884-19-3-218.1

Throndsen J (1978) Productivity and abundance of ultra- and nanoplankton in Oslofjorden. Sarsia 63:273–284. doi:10.1080/00364827.1978.10411349

Throndsen J, Kristiansen S (1991) *Micromonas pusilla* (Prasinophyceae) as part of pico-and nanoplankton communities of the Barents Sea. Polar Res 10(1) (Special Issue: Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Part 1)

Tong S, Vørs N, Patterson DJ (1997) Heterotrophic flagellates, centrohelid heliozoa and filose amoebae from marine and freshwater sites in the Antarctic. Polar Biol 18:91–106. doi:10.1007/s003000050163

Tynan CT, DeMaster DP (1997) Observations and predictions of Arctic climatic change: potential effects on marine mammals. Arctic 50(4):289–399

Van den Hoek C, Mann DG, Jahns HM (1996) Algae: an introduction to phycology. Cambridge University Press, Cambridge

Vancoppenolle M, Goosse H, de Montety A, Fichefet T, Tremblay B, Tison J-L (2010) Modeling brine and nutrient dynamics in Antarctic sea ice: the case of dissolved silica. J Geophys Res Oceans 115. doi:10.1029/2009JC005369

Vaulot D, Eikrem W, Viprey M, Moreau H (2008) The diversity of small eukaryotic phytoplankton ($\leq$3 μm) in marine ecosystems. FEMS Microbiol Rev 32:795–820. doi:10.1111/j.1574-6976.2008.00121.x

Venter JC et al (2004) Environmental genome shotgun sequencing of the Sargasso Sea. Science 304:66–74. doi:10.1126/science.1093857

Vørs N (1992) Heterotrophic amoebae, flagellates and heliozoa from the Tvärminne area, Gulf of Finland, in 1988–1990. Ophelia 36:1–109. doi:10.1080/00785326.1992.10429930

Vørs N (1993) Marine heterotrophic amoebae, flagellates and heliozoa from Belize (Central America) and Tenerife (Canary Islands), with descriptions of new species, *Luffisphaera bulbochaete* N. Sp., *L. longihastis* N. Sp., *L. turriformis* N. Sp. and *Paulinella intermedia* N. sp. J Eukaryot Microbiol 40:272–287. doi:10.1111/j.1550-7408.1993.tb04917.x

Vyverman W et al (2010) Evidence for widespread endemism among Antarctic micro-organisms. Polar Sci 4:103–113. doi:10.1016/j.polar.2010.03.006

Walker G, Dorrell RG, Schlacht A, Dacks JB (2011) Eukaryotic systematics: a user's guide for cell biologists and parasitologists. Parasitology 138:1638–1663. doi:10.1017/s0031182010001708

Walsh JE, Chapman WL (2001) 20th-century sea-ice variations from observational data. Ann Glaciol 33:444–448. doi:10.3189/172756401781818671

Wang Q et al. (2014) Cloning, expression, purification, and characterization of glutaredoxin from Antarctic sea-ice bacterium *Pseudoalteromonas* sp. AN178. BioMed Res Int 2014:246871. doi:10.1155/2014/246871

Wells LE, Deming JW (2006) Modelled and measured dynamics of viruses in Arctic winter sea-ice brines. Environ Microbiol 8:1115–1121. doi:10.1111/j.1462-2920.2006.00984.x

Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes: the unseen majority. Proc Natl Acad Sci USA 95:6578–6583

Wright S, Ishikawa A, Marchant H, Davidson A, van den Enden R, Nash G (2009) Composition and significance of picophytoplankton in Antarctic waters. Polar Biol 32:797–808. doi:10.1007/s00300-009-0582-9

Zhu F, Massana R, Not F, Marie D, Vaulot D (2005) Mapping of picoeucaryotes in marine ecosystems with quantitative PCR of the 18S rRNA gene. FEMS Microbiol Ecol 52:79–92. doi:10.1016/j.femsec.2004.10.006