3.2 Plankton

Connie Lovejoy[1], Cecilie von Quillfeldt[2], Russell R. Hopcroft[3], Michel Poulin[4], Mary Thaler[1] with contributions from Kristin Arendt[5], Hogni Debes[6], Ástþór Gíslason[7], Ksenia Kosobokova[8]

[1] Université Laval, Canada, [2] Norwegian Polar Institute, Norway, [3] University of Alaska, Fairbanks, U.S., [4] Canadian Museum of Nature, Canada, [5] Greenland Institute of Natural Resource, Greenland, [6] University of the Faroe Islands, Faroe Islands, [7] Marine and Freshwater Research Institute, Iceland, [8] P.P. Shirshov Institute of Oceanology, Russia

Snapshot

- Microbial plankton (Bacteria, Archaea, phytoplankton and heterotrophic protists) and zooplankton are the base of the pelagic Arctic marine food web, feeding large-sized zooplankton, fishes, seabirds and marine mammals. Changes in these species can have cascading effects throughout the ecosystem and can represent the first sign of overall ecosystem shifts. Despite their importance, elements of this taxonomic group are scientifically underappreciated and inadequately known.

- Particularly unknown elements include the diversity of microbes, and plankton distribution over time and space in the Arctic. This impedes better understanding of Arctic marine ecosystem structure and processes, and thus the ability to apply ecosystem based management.

- Warming can have contradictory and surprising effects on plankton. Increased temperature in the Barents Sea and around Svalbard has led to the presence of more southern species of generally less nutritional value to Arctic feeders. However, rising temperatures in the Chukchi Sea are associated with an increase in the presence of large copepods.

- Plankton are strongly affected by climate and differ between open water and ice-cover conditions, current patterns and salinity. Increased open water and less saline surface water could lead to range shifts so that Arctic species are replaced by non-Arctic species, again with unknown consequences for the Arctic marine food web.

- There is a potential risk of harmful/toxic phytoplankton causing public health threats through shellfish consumption, fish and aquatic bird kills, and decreased fitness in marine mammals.

- Systematic monitoring has most frequently occurred around Svalbard and Jan Mayen, the Barents Sea, Iceland, Greenland and the southern Bering Sea.

3.2.1 Introduction

Plankton refers to taxonomically and functionally diverse aquatic organisms that range in size from submicron (<1 µm) to centimetres (cm). For technical terms, see Box 3.1.1. They share a limited ability to control their location against oceanic currents. Phytoplankton are responsible for all primary production in the open ocean and are the base of the pelagic food chain supporting higher trophic levels. Arctic phytoplankton and other protists, which include single-celled micro zooplankton, are the main food for copepods that are the principal food for larger macrozooplankton, and some species of fish and seabirds. Bacterioplankton are essential for degrading organic carbon in the ecosystem, and in the open ocean, including the Arctic, Bacteria and Archaea are responsible for remineralization of nutrients. Heterotrophic and mixotrophic microbial eukaryotes graze on Bacteria and Archaea as well as smaller phytoplankton. All of these single-celled plankton are subject to strong environmental selection. This selectivity is profoundly evident for picophytoplankton (<2 µm), which are exclusively eukaryotic in Arctic waters in contrast to in temperate and tropical regions where picocyanobacteria are ubiquitous (Lovejoy et al. 2007, Li et al. 2009, Balzano et al. 2012). However, picocyanobacteria in the genus Synechococcus are detected by flow cytometry in the Pacific (Bering and Chukchi Seas; Li et al. 2009) and Atlantic gateways, Fram Strait and around Svalbard (Paulsen et al. 2016). Freshwater cyanobacteria phylotypes can also persist in coastal regions, where rivers enter the Arctic (Waleron et al. 2007).

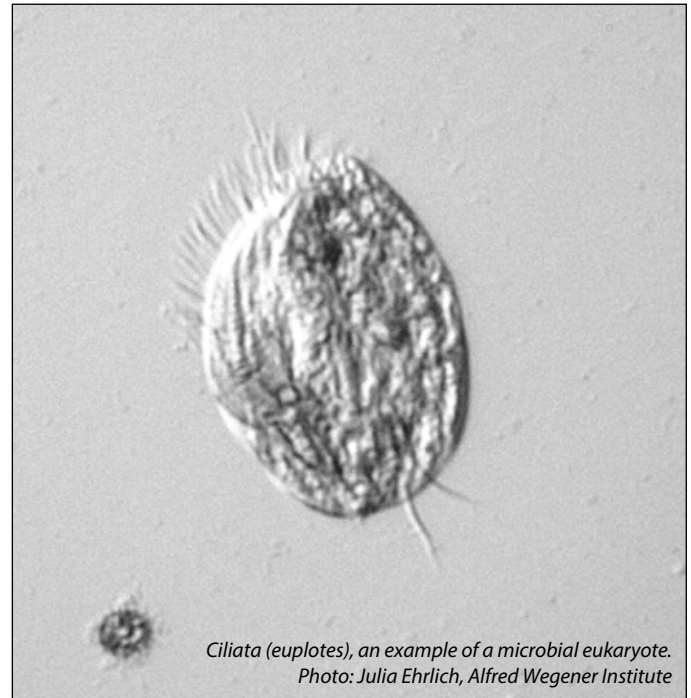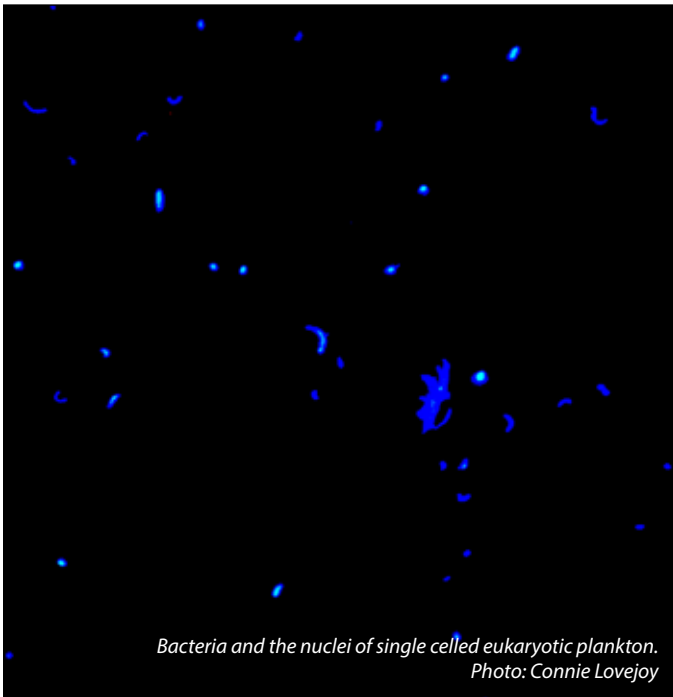In the Arctic as elsewhere, currents, water column stratification and seasonality are recurring processes in any given region and predictable seasonal community patterns can be distinguished, with excursions indicative of change. Microbial communities are sensitive indicators of food web complexity, and the fate of photosynthetic production can be inferred from dominant species or species complexes, where a species complex consists of closely related taxa that may or may not described as species. Some plankton assemblages with their representative species are consumed in the water column, while others have a tendency to sink, either feeding the benthos along shelves or into deep basins, contributing to the biological carbon pump (see Box 3.1.2.1; Morata et al. 2011). Smaller sized (1-20 µm) phytoplankton and their associated heterotrophic assemblages drive pelagic food webs that keep carbon and energy in the upper water column. Grazing activities by metazoan zooplankton moves this carbon up the pelagic food web, and can also enhance organic carbon export to the benthos through rapidly sinking fecal pellets (see Chapter 3.3 and 3.4).

The biodiversity of Bacteria and Archaea has only been appreciated since the advent of the molecular era, as the majority of free-living pelagic microbes resist cultivation. In this sense, the 'historic' records for these organism's date from around 2000 (Huse 2008, Galand et al. 2009). More recently, the distributions of major Bacteria clades have been reviewed in Pedrós-Alió et al. (2015), who found that in the open ocean at the level of classes, Arctic bacterioplankton were similar to that of other open oceans, but with an indication that higher proportions of *beta* and *gamma* proteobacteria compared to *alpha* proteobacteria may be indicative of recent ice cover.

Molecular techniques have also been at the forefront in the discovery of endemic Arctic microbial eukaryotes (Lovejoy et al. 2007, Terrado et al. 2013). Importantly, the most widespread and abundant phytoplankton species in the summer Arctic Ocean is the Arctic picophytoplankton

Micromonas with a pan-Arctic distribution (Lovejoy et al. 2007, Vader et al. 2015). While *Micromonas* is common year round in Svalbard waters (Marquardt et al. 2016), *Phaeocystis pouchetii* can be abundant in summer (Kilias et al. 2014). Overall molecular surveys focusing on specific taxonomic groups have confirmed microscopy records reporting a mix of Arctic and Boreal-Arctic species among phytoplankton (Percopo et al. 2016), as well as heterotrophic protists (Thaler and Lovejoy 2015). Understanding the occurrence patterns of the two types of communities (strictly Arctic versus Boreal-Arctic) promises to be a powerful tool in interpreting the effects of climate change versus seasonality on marine food webs (Luddington et al. 2016).

Most Arctic phytoplankton species have pan-Arctic distributions, which are consistent with long-range transport by Arctic currents (Abelmann 1992, von Quillfeldt 2000, Poulin et al. 2011) that retain populations within the Arctic. Other species enter the Arctic via the Barents Sea and the Bering Strait. In the Pacific, some species may persist in Arctic waters, for example heterotrophic nanoflagellates and Radiolaria (Terrado et al. 2009, Thaler and Lovejoy 2015). In the European Arctic, because of the complex hydrography around Svalbard, for example, there is often a mix of Arctic and North Atlantic species (von Quillfeldt 2000). Recent evidence has found that Boreal-Arctic *Thalassiosira* spp. exit the Arctic though Davis Strait and likely contribute to the North Atlantic spring bloom (Luddington et al. 2016).

Bacteria and the nuclei of single celled eukaryotic plankton.
Photo: Connie Lovejoy

Ciliata (euplotes), an example of a microbial eukaryote.
Photo: Julia Ehrlich, Alfred Wegener Institute

Dinoflagellate Peridiniella catenata.
Photo: Michel Poulin

Calanus glacialis.
Photo: Russ Hopcroft, University of Alaska, Fairbanks

The interconnections between the Arctic and the Atlantic suggest that factors selecting for species in late summer and autumn in the Arctic, could have an influence on the species composition, timing and extent of phytoplankton production well outside of the Arctic. A list of 36 potentially harmful/toxic marine unicellular eukaryote taxa have been recorded in phytoplankton across the Arctic (Poulin et al. 2011). The potential risk of these taxa being responsible for fish and aquatic bird kills and lowered fitness in marine mammals and potential public health threats is unknown at present. However, there have been reported algal toxins presence in marine mammals in the Arctic (Lefebvre et al. 2016).

In contrast to single-celled plankton, metazoan zooplankton are better able to maintain their position within the water column. Metazoan plankton include a wide array of invertebrates, as well as larval stages of fish (ichthyoplankton). The longer life span (months to years) of these organisms allows them to develop more specific life-history strategies, including daily and seasonal vertical migrations that also lead to predictable seasonal cycles, albeit with large inter-annual variability (Falk-Petersen et al. 2009, Berge et al. 2014, Daase et al. 2016). Additionally, most species are adapted to specific depth ranges, yielding characteristic communities that are shared across the Arctic's central basins (Kosobokova et al. 2011), with oceanic communities distinctive from those on the shelves (Grainger 1965, Smoot and Hopcroft 2016).

Arctic zooplankton cover a wide spectrum in terms of species and size range. By far the most well-studied zooplankton in the Arctic are copepods, which have been widely sampled using nets and more recent data from acoustic and optical techniques (e.g., Forest et al. 2012, Trudnowska et al. 2015). Copepods are estimated to account for 80-90% of the zooplankton biomass in the Arctic and are typically very lipid rich. They are directly consumed by many fish and some seabird species, as well as the baleen whales (Ástþórsson and Gislason 1997, Wassmann et al. 2006, Darnis et al. 2012), making them the best available Focal Ecosystem Components (FEC) for zooplankton monitoring. The copepods are dominated by three species of *Calanus* (*C. glacialis*, *C. hyperboreus*, *C. finmarchicus*) whose life cycles involve feeding in surface water during the productive spring and summer, then diapause (~hibernation) at depth during winter (Falk-Petersen et al. 2009). Over 150 other copepod species contribute to the ~350 species reported for Arctic zooplankton communities (Bluhm et al. 2011).

Macrozooplankton are the larger crustaceans, such as hyperiid amphipods and euphausiids, which are also important as prey for marine vertebrates and are further mentioned in the fish, mammal and seabird chapters (Chapters 3.4, 3.5, 3.6). While smaller life-stages of macrozooplankton are routinely sampled using the same nets that are typically used for *Calanus* sampling, the larger individuals require sampling with larger nets (e.g., Auel and Werner 2003, Dalpadado et al. 2016) that have not been routinely deployed in the Arctic due to its ice cover. Newer technologies such as calibrated acoustics (Ressler et al. 2015) promise to close knowledge gaps on euphausiid distribution. Arctic euphausiids are mostly reported in the gateways (Bering Sea and Barents Sea) and in regions where there is enhanced productivity associated with large riverine input, but almost absent from the central basins. Generally,

free-living hyperiid amphipods (e.g., *Themisto* spp.) are more wide-spread and do well in cold water, including the Arctic (Percy 1993), with larger individuals generally being undersampled (Auel and Werner 2003). Sediment trap records are now being exploited to follow hyperiid species changes over time (Kraft et al. 2012) and have confirmed the widespread distribution of this group. Given the sparse data and lack of targeted monitoring, it is impossible to comment on the status and change of these larger macrozooplankton and for these reasons they are not currently treated as FEC by the Circumpolar Biodiversity Monitoring Programme (CBMP) Plankton Expert Network.

Around one-quarter of the metazoan zooplankton species found in the Arctic are truly restricted to the Arctic, with most other species shared with the North Atlantic or North Pacific (Kosobokova et al. 2011), especially in regions of inflow (i.e., the Barents and Chukchi Seas). Near major rivers, brackish-water species may contribute substantially to the zooplankton community (Abramova and Tuschling 2005), while larvae of benthic species become prominent seasonally on the shallow shelves (Questel et al. 2013).

3.2.2 Current monitoring

The motivation and potential funding sources for monitoring plankton varies by taxonomic group. For example, zooplankton species are sometimes monitored as part of fisheries habitat surveys and phytoplankton sometimes monitored in the context of harmful algal bloom threats. While the following summary takes a geographic approach, it is important to note that these different regions mostly have been monitored for different kinds of plankton.

Environmental Monitoring of Svalbard and Jan Mayen (MOSJ) is conducted as part of the Norwegian Government's environmental monitoring. Kongsfjorden is the only fjord in Svalbard where regular monitoring of zooplankton (during summer) has been reported since 1996. Phytoplankton and chlorophyll were added to the annual sampling from 2009. Rijpfjorden on Nordauslandet, north Svalbard, has been opportunistically sampled annually since 2006, but is not included in an established monitoring program (C. von Quillfeldt, pers. comm.). There are however, other cruises at different times of the year to both fjords, such as winter cruises in January conducted by UiT The Arctic University of Norway in collaboration with University Studies in Svalbard (UNIS). The Kongsfjorden marine ecosystem functions under the balance of influx of Atlantic and Arctic waters, and as a consequence the pelagic food web is composed of both boreal and Arctic species. Hop et al. (2002) concluded that Kongsfjorden is particularly suitable as a site for exploring the impacts of possible climate change, with both Atlantic water influx and melting of tidal glaciers being linked to climate variability. With Kongsfjorden receiving variable climatic signals between years, it functions as a climate indicator on a local scale. Subsequent reports suggested that the fjord zooplankton were sensitive indicators of Atlantic inflow during winter (Willis et al. 2008).

Norway is also monitoring phytoplankton and zooplankton species composition elsewhere, for example, in the Barents Sea along predefined transects, once or several times a year with status reports on the different trophic components (McBride 2016).

Systematic monitoring of zooplankton communities off Iceland can be traced back to 1960. Species-resolved analysis for both zooplankton and phytoplankton time series began in 1990 for transects extending from the southern and northern coasts of Iceland (Ástþórsson et al. 2007, Gislason et al. 2014). These transects highlight the different habitats found on opposite sides of the island (Atlantic in south and sub-Arctic in north), as well as the role of advection. More distant waters of the Iceland and Greenland seas have only been sampled periodically.

Monitoring sites are operating in different regions of Greenland including Nuuk (souhwest Greenland), Zackenberg (northeast Greenland) and Disko Bay (west Greenland). Zooplankton and phytoplankton data have been collected at all three locations for more than 10 years, thus comprising the most extensive plankton time series from Greenland. The Nuuk and Zackenberg locations are part of the Greenland Ecosystem Monitoring program (GEM), which collected a multitude of physical, chemical and biological parameters in the marine environment as well as terrestrial, limnic and atmospheric data. Marine monitoring in Disko Bay is planned to be expanded and become part of the GEM program (T. Juul-Pedersen pers. comm.). Together these three sites represent a climate gradient of coastal marine systems in Greenland, i.e., covering high Arctic, Arctic and sub-Arctic sites. The monitoring data collected as part of the GEM program are made publicly available.

There is no formal monitoring of plankton in Canadian waters. Partial monitoring of phytoplankton and zooplankton in Canadian waters has been related to several major research initiatives dating back to 1998 with the North Water Polynya project (NOW) followed by nearly annual campaigns under the Canadian Networks of Centres of Excellence ArcticNet and by the Institute of Ocean Sciences (IOS) Department of Fisheries and Oceans (DFO). Although such oceanographic campaigns occurred nearly annually in the Amundsen Gulf, Baffin Bay and the Canada Basin since 2002, not all planktonic groups have been studied consistently (Hunt et al. 2014). In addition, this work has been at the initiative of individual researchers and data are dispersed. Scattered studies have occurred in other regions. Metadata by Canadian researchers can be found in the Polar Data Catalogue. It is envisioned that a marine monitoring program including the use of molecular data to monitor protists, Bacteria and Archaea will be put in place off Cambridge Bay, once the Canadian High Arctic Research Station opens in 2017 (C. Lovejoy pers. comm.).

The U.S. and Russia have performed decades of zooplankton studies in the southern Bering Sea, the Bering Strait region and northward into the Chukchi Sea. Even though these are not consistent over time and space for monitoring purposes, the southern Bering Sea has been sampled regularly during recent decades (available on the Distributed Biological Observatory). More consistent observations of zooplankton in the Chukchi region began in 2004 under the RUSALCA program (Ershova et al. 2015a) and in 2003 by Pacific Scientific Research Fisheries Centre (TINRO) (Slabinsky and Figurkin 2014). Annual zooplankton observations in the northeastern Chukchi Sea have occurred since 2007 stimulated by oil and gas exploration in the region (Questel et al. 2013), with observations northeast of Barrow ongoing since 2005 (Ashjian et al. 2010). Zooplankton in the American

sector of the Beaufort Sea was well studied from 2010-2014 (Smoot and Hopcroft 2016), but future prospects are unclear. For the zooplankton, all studies consistently show that communities are strongly associated with the water mass properties and origin. In nearly all cases, phytoplankton has only been measured as chlorophyll biomass, while Archaea, Bacteria and heterotrophic protists including microzooplankton have been largely ignored. The U.S. continues within the Pacific Arctic Group to encourage plankton collections as part of its internationally sampled Distributed Biological Observatories in the Bering, Chukchi and Beaufort Sea regions.

Despite its expansive shelf seas, Russia lacks long-term unilateral plankton monitoring activities. As noted above, sampling occurs in conjunction with the U.S. in the Chukchi Sea, in conjunction with Germany in the Laptev Sea and Norway in the Barents Sea. Data sharing with Russian programs remains a significant hurdle to overcome.

The CBMP Plankton Expert Network is not aware of any ongoing long-term monitoring for Bacteria and Archaea anywhere. As sequencing technology continues to improve and become affordable, the CBMP Plankton Expert Network envisions that Bacteria and Archaea will be more systematically monitored in the future. As with Bacteria and Archaea, the CBMP Plankton Expert Network is confident that molecular surveys of microbial eukaryotes can be incorporated into monitoring programs, but know of no routine monitoring at the current time.

Plankton in sample water.
Photo: Caitlin Bailey, The Hidden Ocean 2016,
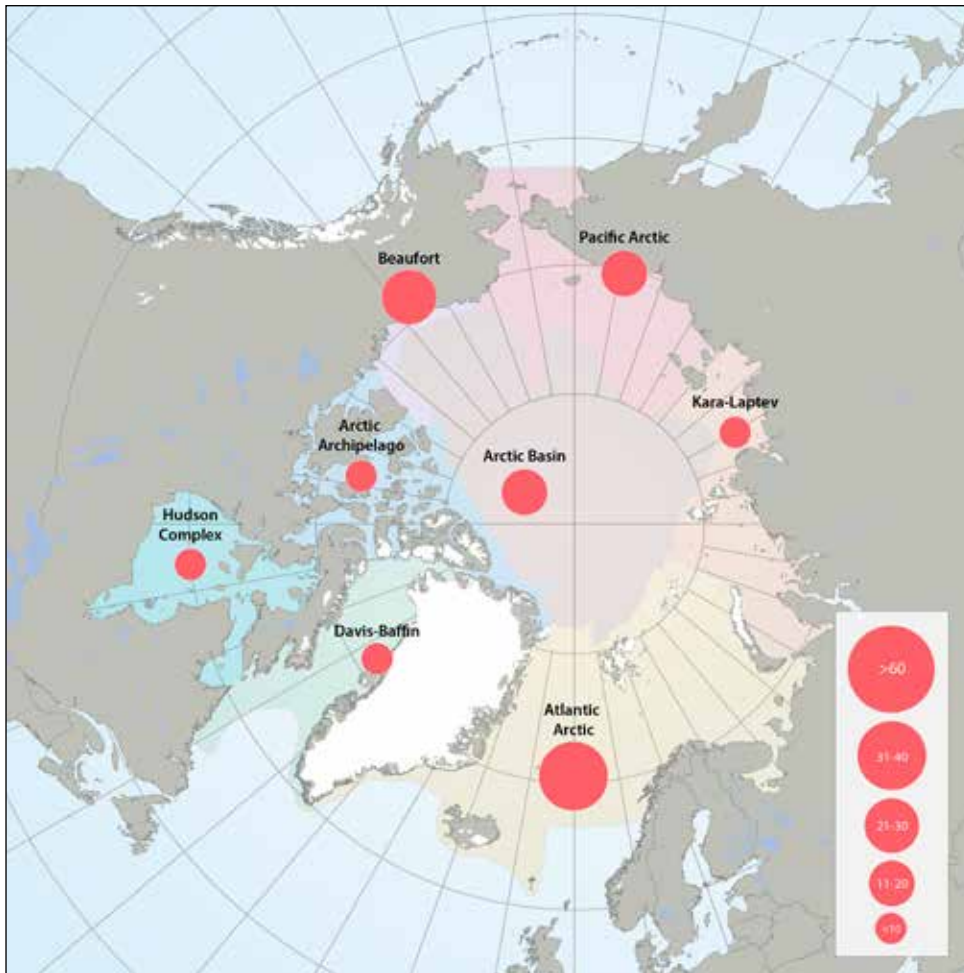Chukchi Borderlands, NOAA

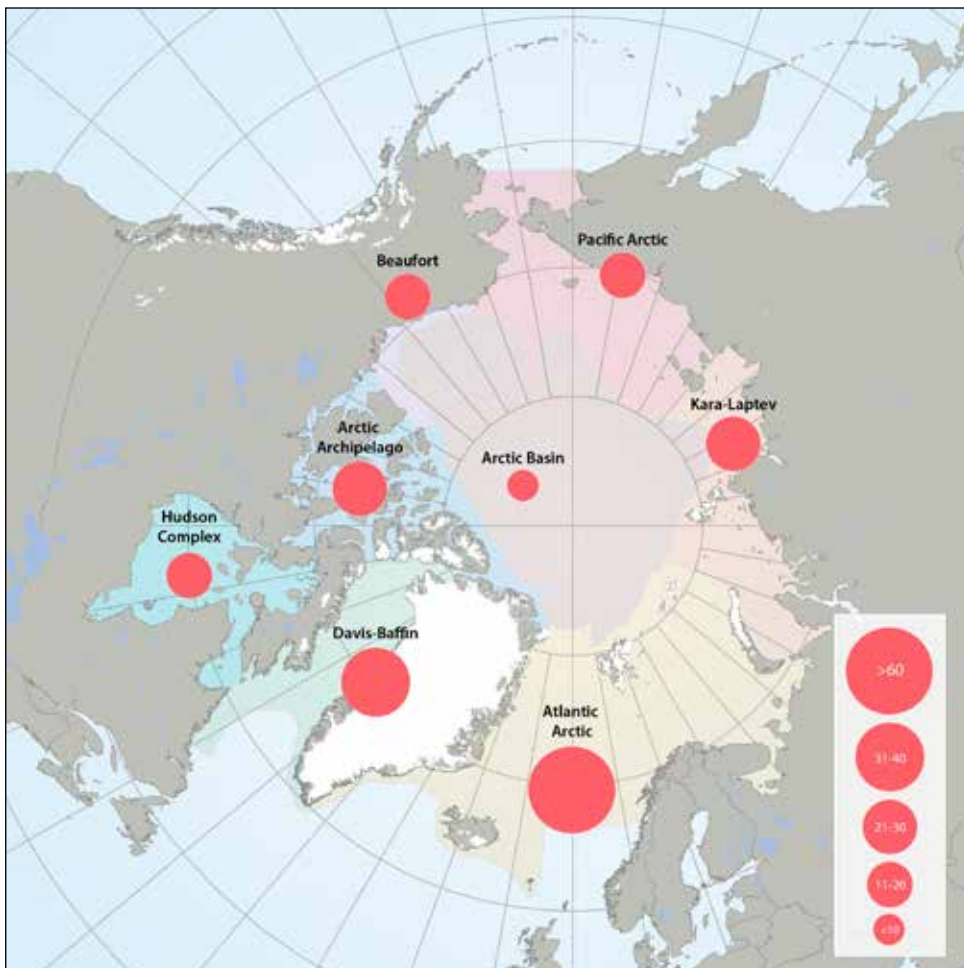Figure 3.2.1a: Map of high throughput sequencing records from the Arctic Marine Areas.

Figure 3.2.1b: Map of records of phytoplankton taxa using microscopy from the Arctic Marine Areas.

3.2.3 Status and trends of FECS

In the *Arctic Biodiversity Assessment* (ABA), plankton were treated under three separate chapters, with zooplankton very briefly mentioned in the Marine Invertebrate chapter (Josefson and Mokievsky 2013), phytoplankton and a few heterotrophic protists in the Plant chapter (Daniëls et al. 2013), and marine heterotrophic protists summarized along with Bacteria and Archaea in the Microbes chapter (Lovejoy 2013). At least for single-celled eukaryotic plankton, the split between heterotrophic and photosynthetic groups masks the true functional diversity and confounds interpretation of how changes in species assemblages could propagate up the food chain. Many single-celled plankton are mixotrophic and can act as both primary producers and grazers, which make trophic classification as phototrophic or heterotrophic deceptive. As different species exhibits different degrees of mixotrophy, there is need to identify species within these groups, without which it will be difficult to model or predict the flow of energy and carbon through the higher food web. Similarly, for zooplankton, knowing the relative abundance of key species is an essential component in predictive models of ecosystem health (Maps et al. 2012). The logistical challenges of accessing ice-covered regions and the slow pace of taxonomic sample processing make understanding seasonal and broad scale patterns challenging. Countries with the longest monitoring programs (e.g., Norway and Iceland) have used bulk wet-weight or displacement volume to estimate zooplankton biomass. However, most investigations in the Svalbard area have calculated biomass from abundance data by applying individual dry-mass values derived from species-specific length-mass relationships or applied published dry mass estimates for species and stages (e.g., Blachowiak-Samolyk et al. 2008). Since the late 1990s, remote sensing of chlorophyll and bulk mesozooplankton biomass from transects has become a standard approach for assessing fisheries productivity (Dalpadado et al. 2014). Such approaches result in a complete loss of the potential for gathering taxonomic information, which is essential for monitoring community changes driven by climate (Richardson 2008).

The density and type of data on plankton from different regions are highly variable and reflect national interests in some cases and the particular expertise of active researchers at different times in other cases. Here, recent compilations from molecular surveys targeting single-celled plankton are summarized, and then microscopy-based reports of phytoplankton species are followed by a review of the traditional approaches still used for zooplankton

Bacteria and Archaea

Bacteria and Archaea can only be identified using molecular techniques, with most work to date based on the gene coding for the Small Subunit of ribosomal RNA (SSU rRNA gene; 16S rRNA for Bacteria and Archaea). Molecular surveys of Bacteria and Archaea have tended to be more local and project specific and sampling effort maps have not been assembled. Comparison of data sets has also been hampered by the use of different primer pairs targeting different variable regions of the 16S rRNA gene. Nonetheless, the data available indicate that offshore oceanic bacterial groups at the level of phyla and proteobacteria class resemble temperate open-ocean Bacteria, while inshore Bacteria tend to consist of taxa preferring habitats richer in organic substrates (Pedrós-Alió et al. 2015). Time-series data are rare, although one from Amundsen Gulf (Beaufort Sea) suggested significant changes in the relative abundance of key microbial groups before and after the first record summer sea ice minimum in 2007. Over the eight-year study, there was a shift towards more oligotrophic taxa (Comeau et al. 2011). Interestingly, deep-water Arctic communities may be taxonomically similar to Antarctic deep-water communities (Ghiglione et al. 2012), but more extensive sampling is needed.

Microbial eukaryotes identified using molecular techniques

Similar to Bacteria and Archaea, most microbial eukaryotes < 3 µm can only be identified using molecular techniques, and molecular signatures can be used to identify ecotypes and species of nanoflagellates. Molecular identification of many 1-20 µm flagellates has become routine and can also be applied to diatoms and dinoflagellates. However, for these two groups that have well-established morphological taxonomies, microscopy-based verification of species is needed to reconcile molecular data to classic species description to enable comparisons with older literature (Luddington et al. 2012). The 18S rRNA gene, while robust for most groups, has not been able to resolve taxonomic identity within several clades of dinoflagellates and diatoms possibly because of their recent rapid-trait evolution compared to nucleotide changes in the 18S rRNA gene. More reference sequences of known species are needed to reconcile analyses with classical taxonomy. The first microbial eukaryotic 18S rRNA gene surveys date from 2002 (Lovejoy et al. 2006) with the greatest effort in Amundsen Gulf in the Canadian Arctic and where 35 datasets are published and available. Recent efforts around Svalbard have generated 40 datasets (Fig. 3.2.1a). Opportunistic sampling around the North Pole has added additional records of microbial eukaryotes (Bachy et al. 2011). Other records are more sporadic; high through-put sequencing has been used on samples from Baffin Bay, the Canada Basin, the Chukchi Sea, Canadian Arctic Archipelago, Hudson Bay, the Greenland Sea and Laptev Sea (Thaler and Lovejoy 2015; Fig. 3.2.1a). The majority of the raw sequence data are publically available in NCBI GenBank and the Sequence Read Archive (SRA).

For microbial eukaryotes, high through-put sequencing shows a consistent pattern of dominance by dinoflagellates, followed in relative abundance by ciliates and, in the European and Central Arctic Ocean, by marine alveolates (MALVs, see Box 3.1.2). Chlorophytes are consistently abundant, comprising 5-14% of all reads across different regions. By far the majority of the chlorophyte reads correspond to a single Arctic clade of Micromonas, which is 1-2 µm in diameter (Lovejoy et al. 2007, Balzano et al. 2012). Higher relative abundance in terms of reads (sequences) per sample by other groups is rare, for example, reports of higher proportions of haptophytes in the Central Arctic and Atlantic Arctic regions, diatoms in Baffin Bay and Rhizaria in the Pacific Sea and Atlantic Arctic regions (Fig. 3.2.2a).
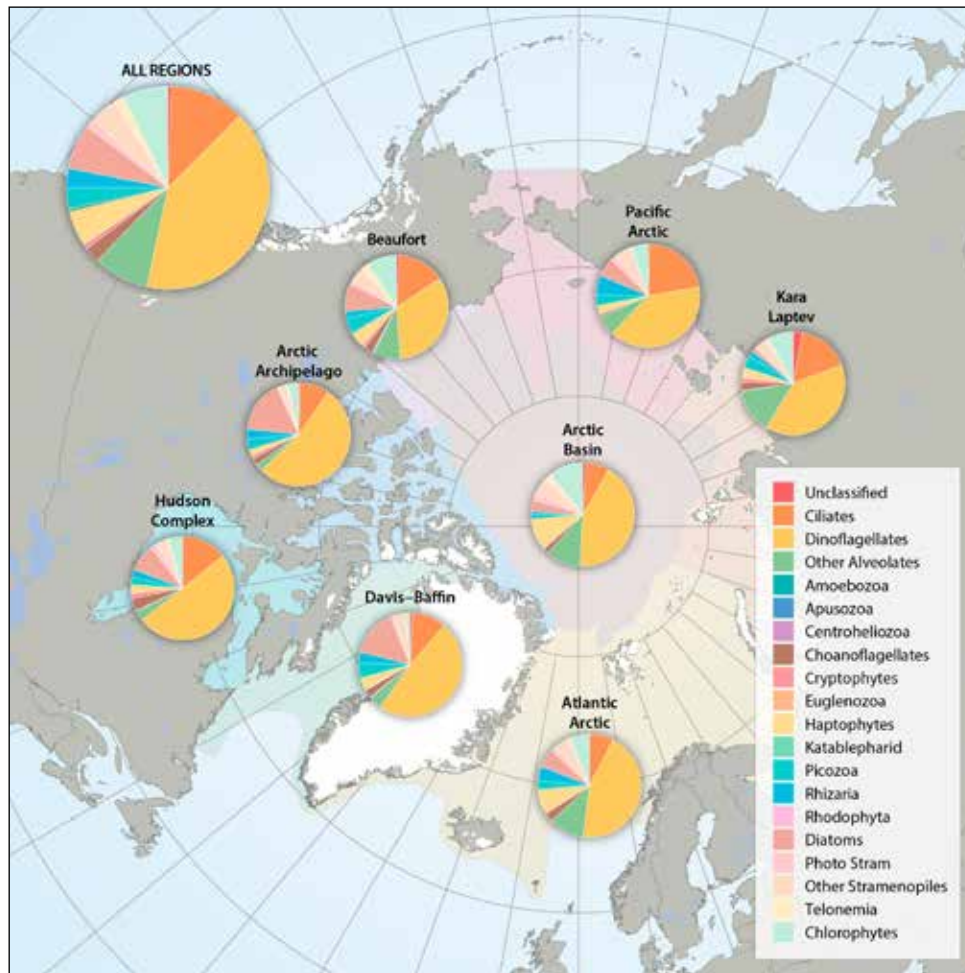
Figure 3.2.2a: Relative abundance of major eukaryote taxonomic groups found by high throughput sequencing of the small-subunit (18S) rRNA gene across Arctic Marine Areas.
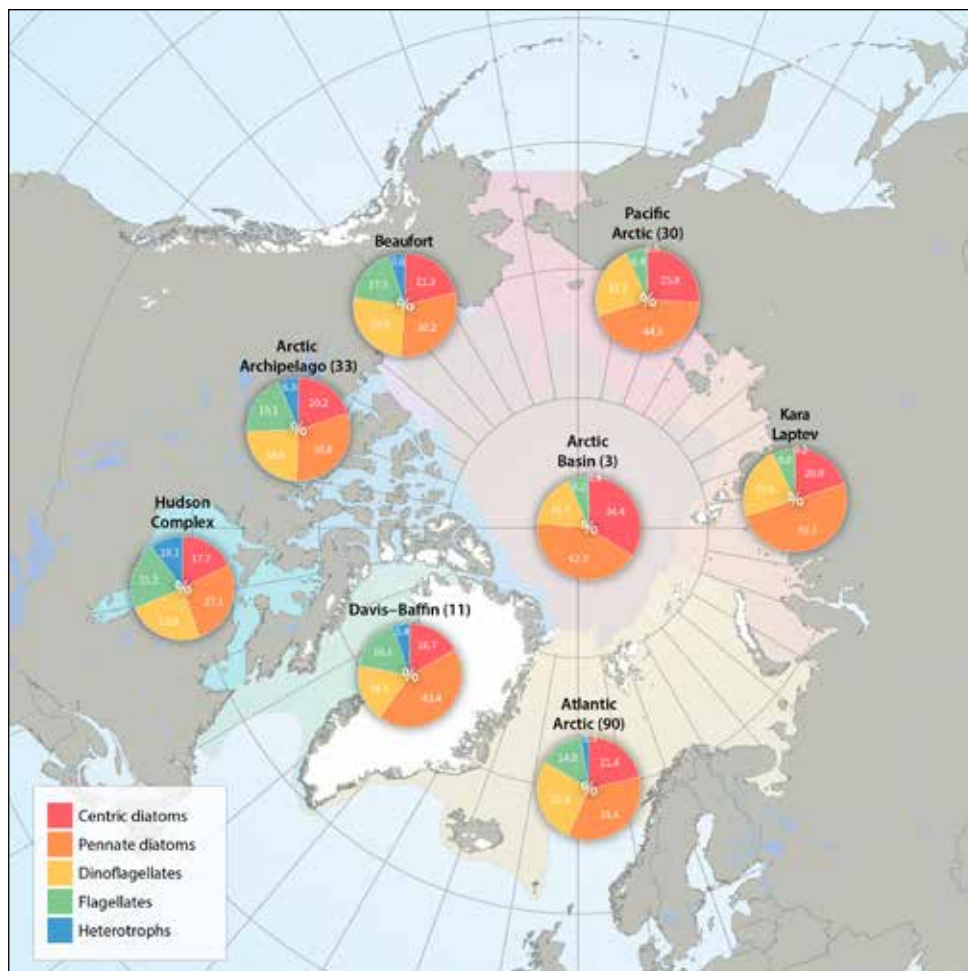

Figure 3.2.2b: Relative abundance of major eukaryote functional groups found by microscopy in the Arctic Marine Areas.

When a single site in the Amundsen Gulf was sampled monthly throughout a winter-spring period, a high degree of temporal structure emerged. Notably there was the gradual increase of haptophytes in the months leading up to the spring bloom, succeeded by an extreme dominance of diatom reads in mid-May and a dominance of chlorophytes in mid-June (Joli et al. 2017; Fig. 3.2.3). This study also highlighted the potential for viral control over the chlorophyte species, especially in winter.

Phytoplankton and larger protists

Traditional taxonomic data for phytoplankton have been recorded over much of the Arctic, but the bulk of knowledge is from Norway and Denmark (Greenland) which have a strong training record in phytoplankton taxonomy. Following up on Poulin et al. (2011) and the *Arctic Biodiversity Assessment*, records for phytoplankton species occurrences, which included other single-celled eukaryotes identified using microscopy, are updated here. The updated information on the phytoplankton sampling effort (Fig. 3.2.1b) and a compilation showing the phytoplankton inventory records for each designated area of the Arctic main regions (Fig. 3.2.2b) are shown. These regions follow the CBMP Arctic Marine Areas (AMAs): Arctic Archipelago, Hudson Complex, Davis Strait-Baffin Bay, Atlantic Arctic, Kara-Laptev, Pacific Arctic, and Arctic Basin. In an updated compilation (January 2016) the number of Arctic phytoplankton species records jumped from 1,874 taxa in 2011 to 2,241. The inventory or reporting effort of phytoplankton and other eukaryotes also reflects sporadic efforts to monitor certain regions in conjunction with other studies, for example the Barents Sea with 28 published papers, the Greenland Sea with 23 and the Svalbard region with 20. Outside of Scandinavian records, there have been 17 studies each for the Davis Strait, Hudson Bay (Canada) and the Laptev Sea (Russia), which are from more readily accessible sites that have been visited repeatedly. Inventories from the U.S. are mostly from the Chukchi and Western Beaufort Seas, corresponding to American territorial waters (Fig. 3.2.1b).

Few time series for microscopy records of phytoplankton are available to date. Most available data sets summarize major algal groups, with some information on the relative abundance of smaller groups. For example, there are records of algae collected from 2002 to 2013 at two stations in Eastern Canadian Arctic and two stations in Western Canadian Arctic. Other short-time series include data from ice-free Kongsfjorden and seasonally ice-covered Rijpfjorden in Svalbard (MOSJ and P. Assmy pers. comm.; Fig. 3.2.5a, b). Both fjords have been extensively sampled, especially during summer, and because of the complex hydrography of the Arctic and Atlantic currents around Svalbard the plankton occurring in fjords can be indicative of major changes in Arctic versus Atlantic currents. Arctic fjords are also indicators of melt, for example, in East Greenland waters the fjord assemblage close to the Greenland Ice Sheet is strongly influenced by the freshwater runoff in mid-summer (Krawczyk et al. 2015a). In general, the phytoplankton succession in the near coastal areas of Greenland is controlled primarily by ocean-fjord-glacier interactions (Krawczyk et al. 2015b).

Both Kongsfjorden and Rijpfjorden show inter-annual differences in taxonomic composition, abundance and biomass of phytoplankton during summer, but most taxonomic groups are present every year (Fig. 3.2.5a, b). Dinoflagellates, cryptophytes and other small flagellates from several different classes are among those often contributing to a great portion of the biomass. Diatoms are more common in spring (Hegseth and Tverberg 2013), but have also been recorded at greater depth during summer in Kongsfjorden, then often present as resting stages representing a post-bloom situation (Hasle and Heimdal 1998). According to Kubiszyn et al. (2014), impact from Atlantic inflow variability is not as clear as for the spring bloom in Kongsfjorden, but they concluded that the strength of Atlantic water inflow might also have consequences for the planktonic protist community structure in summer. Furthermore, they found that microplanktonic (ciliates and dinoflagellates) contribution was greatest in the warmest summers. A shift in phytoplankton community composition towards dominance of small-sized phytoplankton under warmer conditions has also been reported in Atlantic water masses west of Spitsbergen (Lalande et al. 2013). Of importance is also whether the inflow of Atlantic water into Kongsfjorden is along the bottom or near the surface (Hegseth and Tverberg 2013). Even though Rijpfjorden is a cold Arctic system during most of the year (January-July), transformed Atlantic water is recorded in the fjord during late autumn. Models suggest that this area north of Svalbard will become particularly affected by temperature increase because of increased advection of heat by the West Spitsbergen Current (Slagstad et al. 2011).

In recent years, the spring bloom in the Barents Sea has been dominated by diatoms, such as *Chaetoceros*, *Skeletonema*, *Thalassiosira* and the prymnesiophyte *Phaeocystis* (Kleiven et al. 2015). During summer, phytoplankton are often distributed in patches consisting largely of small flagellates and dinoflagellates (*Tripos* and *Gymnodinium*). In some years, species of diatoms (mostly *Chaetoceros* spp.) can be dominant during June-August.

Surveys indicate ongoing climate mediated changes, but that there are geographical differences. For example, less sea ice and an increase in atmospheric low pressure systems, which generate stronger winds (and deeper mixing of the upper ocean) as well as a warming and freshening of the surface layer, likely favours smaller species as observed in Canada Basin (Li et al. 2009) and Beaufort Sea of the Canadian Arctic (Ardyna et al. 2011, Tremblay et al. 2012). However, Terrado et al. (2013) found that some small-celled phytoplankton species may be specifically adapted to colder waters, and are likely to be vulnerable to ongoing effects of surface layer warming.

Zooplankton

Zooplankton have been sampled extensively, but not systematically, throughout the Arctic for over a century. True time series of consistently collected samples during the same season at the same locations are relatively rare. For zooplankton, they extend back to the 1960s in Iceland and Norway, but species level data only begin in the 1990s (Gislason and Ástþórsson 1998, Dalpadado et al. 2014), about
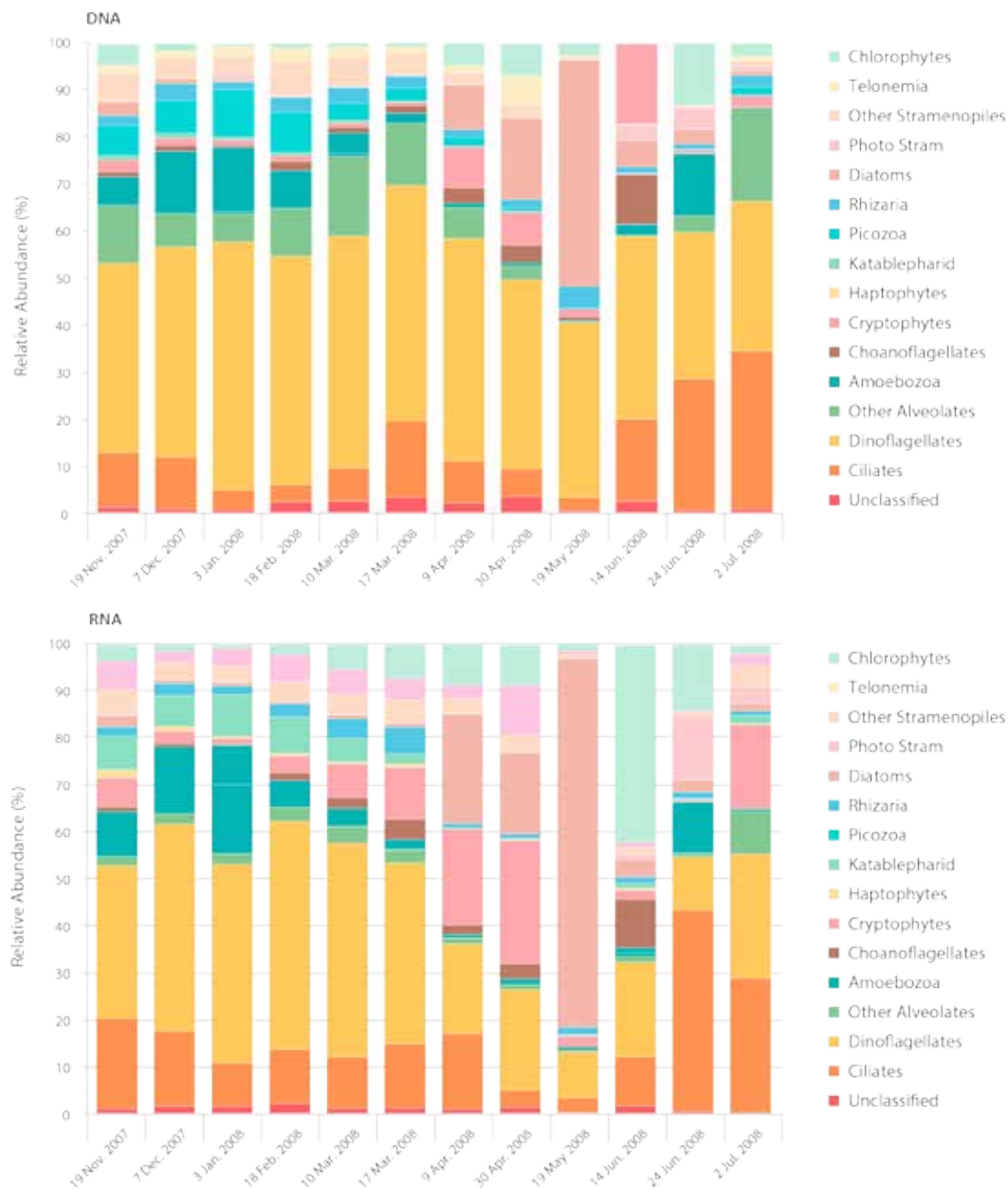
Figure 3.2.3: Relative abundance of major eukaryote taxonomic groups found by high throughput sequencing of the small-subunit (18S) rRNA gene. Time series collected by sampling every 2-6 weeks in Amundsen Gulf of the Beaufort Sea over the winter-spring transition in 2007–2008. Sampling DNA gives information about presence/absence, while sampling RNA gives information about the state of activity of different taxa.

the same time as time series began in Greenland, Canada and the U.S. (see Gill et al. 2011). Despite the relative recency of formal time-series, it is possible to assemble longer-term data for a few regions by pooling historical studies (e.g., Ershova et al. 2015b), although the CBMP Plankton Expert Network expects such time series to be inherently variable and consequently require a larger signal to detect change. Given the diversity and complexity of the Arctic, it is useful to consider separate systems related to their hydrography. As an inflow gateway, the Chukchi Sea has been sporadically sampled over nearly a century, with annual sampling for more than a decade. During this time, the extent and duration of open water has progressively increased. Recently, Ershova et al. (2015b) compiled much of the existing data on metazoan zooplankton to search for temporal trends, along with matching physical data to correlate with environmental forcing. The wide array of sampling gear employed across studies required the authors to focus on the larger copepod species that are captured with less bias across studies. Their analysis revealed that abundance of the four prominent

large-bodied copepods (*Calanus glacialis*, *Eucalanus bungii*. *Metridia pacifica*, and *Neocalanus* spp.) in the Chukchi Sea had increased over the past 80 years. These increases correlated with temperature trends. While three of these species are considered Pacific expatriates, even the Arctic species *Calanus glacialis* had increased in response to regional warming (Fig. 3.2.6).

For Greenland, the abundance of *Microsetella norvegica* is strongly linked to the runoff from the Greenland Ice Sheet influencing the fjord environments in mid-summer (Arendt 2013). The abundance of the neritic copepod *Pseudocalanus* has declined while the abundance of the oceanic copepod *Microcalanus* has increased at Zackenberg. These data suggest that due to reduced sea ice and increased ablation of the Greenland ice sheet, the fjord is subjected to more flushing than in the early 2000s and that this has caused a change in zooplankton species composition (Arendt et al. 2016; Fig. 3.2.7.).

Figure 3.2.4: A time series of cell abundances, as determined by microscopy, of major phytoplankton groups from 2002-2013 for four sites, two in an east-west transect in Amundsen Gulf, Beaufort Sea and two in an east-west transect in northern Baffin Bay.

The zooplankton time series collected at a transect extending from the coast and across the shelf north of Iceland at the southern borders of the Iceland Sea shows that copepods are generally the most numerically abundant group (~40-70%) with the sub-Arctic *Calanus finmarchicus* as the most abundant species among the copepods (~20-60%; Fig. 3.2.8). The time series shows maxima in zooplankton abundance and biomass occurring approximately every five to 10 years (Marine Research Institute 2015). Also striking is the collapse in zooplankton biomass during the cold period in the North Atlantic and to the north of Iceland in the 1960s and it was not until the warm period in the 1990s that biomass levels recovered. These longer-term records indicate that zooplankton biomass variability and species composition to the north of Iceland are positively related to temperature, reflecting the inflow of Atlantic water into the area (Ástþórsson et al. 2007, Gislason et al. 2009, 2014). Ástþórsson and Gislason (1998) showed that the zooplankton biomass is almost two times higher in warm years than in the cold

years. This may reflect the better feeding conditions for the zooplankton due to increased primary production, advection of zooplankton with the Atlantic Water from the south, and faster temperature-dependent growth of the zooplankton in warm years. Data from ships of opportunity fitted with Continuous Plankton Recorders (CPR) would be valuable for documenting such relationships, but these records are rare in the Arctic (Beaugrand 2015).

In Kongsfjorden, Svalbard, the abundance of *Calanus finmarchicus* and *C. glacialis* varied from year to year with periods of more or less equal abundance of the two *Calanus* species interspersed with periods when either the cold-water associated *C. glacialis* or the warm-water associated *C. finmarchicus* dominated (MOSJ, 2015). The larger *C. hyperboreus*, an Arctic deep-water species, is only present in low numbers in Kongsfjorden and contributes little to the total abundance of *Calanus*. Lower water temperatures characterize years with *C. glacialis* dominance whereas

Kongsfjorden

Legend (Kongsfjorden):
- Diatoms
- Chlorophytes
- Choanoflagellates
- Chrysophytes
- Ciliophora
- Cryptophytes
- Dinoflagellates
- Unidentified flagellates
- Prasinophyceae
- Prasinophytes
- Xanthophytes

Rijpfjorden

Legend (Rijpfjorden):
- Diatoms
- Chlorophytes
- Choanoflagellates
- Chrysophytes
- Ciliophora
- Cryptophytes
- Dinoflagellates
- Unidentified flagellates
- Other
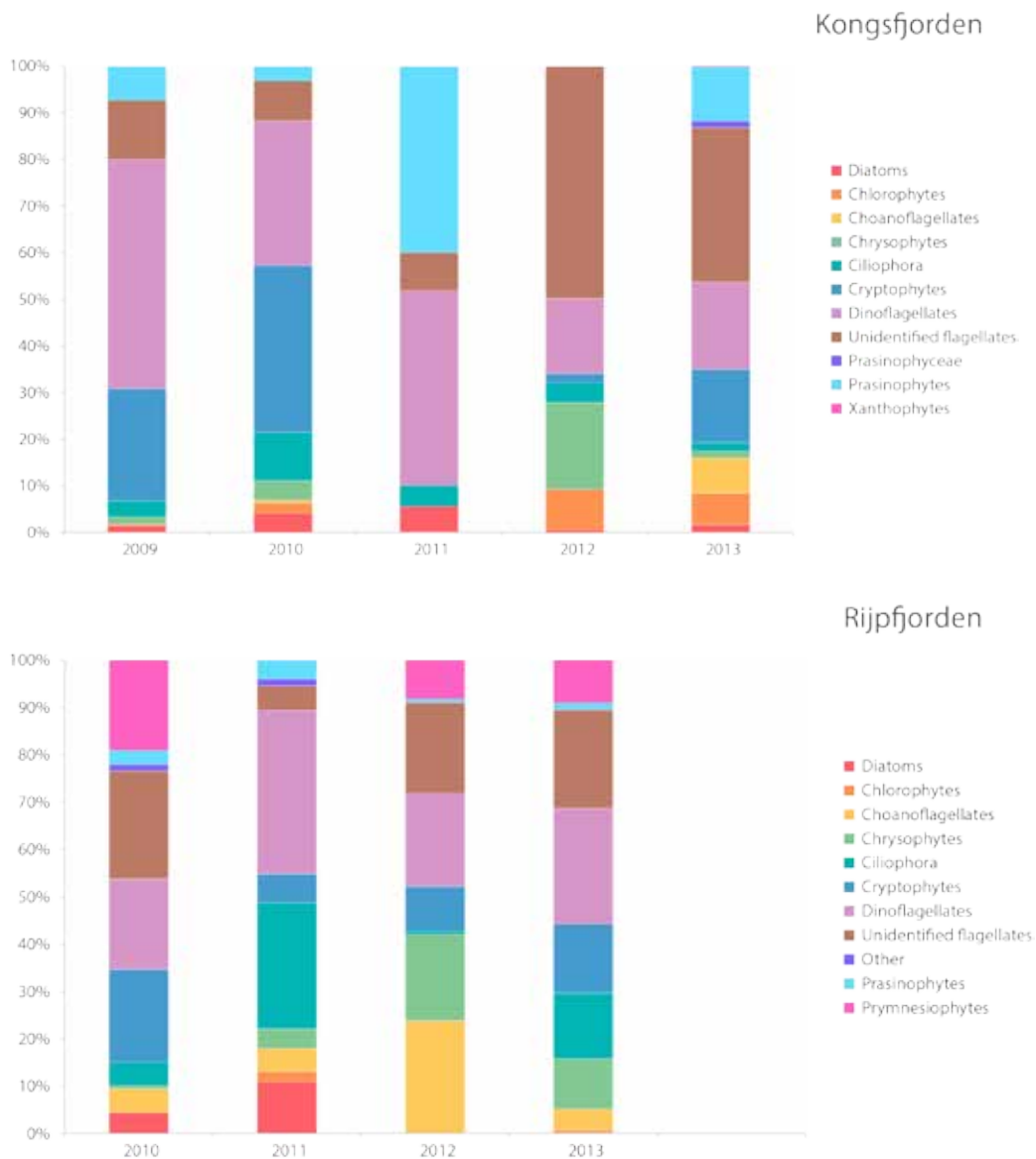- Prasinophytes
- Prymnesiophytes

Figure 3.2.5: Interannual differences in taxonomic composition of phytoplankton during summer in a) Kongsfjorden and b) Rijpfjorden (Source: MOSJ, Norwegian Polar Institute).

dominance of *C. finmarchicus* usually coincides with periods with increasing water temperatures (Fig. 3.2.8a). Research from Rijpfjorden, considered a true Arctic fjord, shows that *C. glacialis* contributes a larger proportion than *C. finmarchicus* inside the fjord, with the latter dominating outside the fjord within the Atlantic water masses. The increase of *C. finmarchicus* in 2007 coincided with a massive influx of warmer water from the shelf areas north of Rijpfjorden, indicating that intrusion of Atlantic water into the fjord sustains its population (Fig. 3.2.8b).

The Arctic *C. glacialis* has decreased further south in the Barents Sea, while *C. finmarchicus* is more stable, but fluctuates from year to year (van der Meeren et al. 2014). Furthermore, a gradual decrease in the quantity of zooplankton has been observed recently in the Norwegian part of the Barents Sea. Typical cold-water species, such as the amphipod *Themisto libellula*, has decreased, whereas the more Atlantic *T. abyssorum* has increased in both the Barents Sea and Fram Strait (Advisory Forum on Monitoring and Institute of Marine Research 2015). In addition, southerly euphausiid species such as *Meganyctiphanes norvegica* and *Nematoscelis megalops* are occurring in the Barents Sea (Eriksen et al. 2016).

3.2.4 Drivers of observed trends

By far the most relevant driver influencing plankton in the Arctic is changes in the climate system, which has a major influence on currents in the Arctic, with impacts on the plankton community. Climate also affects the duration of open water versus seasonal sea ice and the extent of seasonal ice cover. Deeper wind-driven mixing during an extended open water season could favour smaller species of phytoplankton due to lower average light levels in the resulting deeper mixed layer. Increased freshwater in the surface could also shift species composition to species with wider salinity tolerances, replacing the marine Arctic species. The seasonal extent of ice cover is relevant to the timing and duration of the spring bloom and the species of phytoplankton that may be favoured, with small flagellates able to begin growth earlier in the year, because of their ability to use lower light levels compared to diatoms. Early blooms of flagellates such as *Phaeocystis* would tend to draw surface nutrients down leaving little for diatoms that are better adapted to higher light levels near the summer solstice. Similarly, as the major remineralizers in this ecosystem, bacteria also experience some seasonal fluctuations.
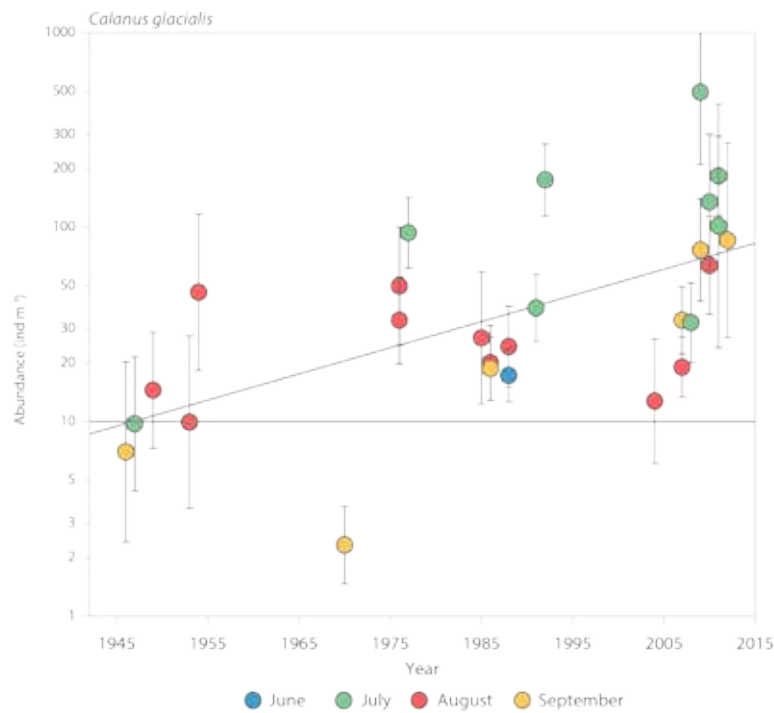
Figure 3.2.6: Abundance of the copepod Calanus glacialis *in the Chukchi Sea, 1945-2012 (after Ershova et al. 2015b).*

The **duration and extent of ice cover** impact the larger zooplankton that have life cycles closely tied with spring maximum phytoplankton production, when they rapidly grow and accumulate lipids for the long winter. Depending on the species and quantity of lipid reserves, they may have an annual life cycle or reproduce after two or three years. Zooplankton communities living in deep water likely still experience some seasonality due to higher fluxes of surface production into the deep ocean shortly after spring maximum. Although climate change can result in increased water temperatures in the upper water column (10-20 m) of the polar mixed layer, the deeper layers show little seasonal or long-term variability. Consequently, changes in the timing, magnitude, and total annual productivity of the phytoplankton and microzooplankton, which include ciliates and dinoflagellates that compete with zooplankton as grazers but are also sources of food, are thought to have the greatest potential impact on metazoan zooplankton.

A scenario of increased annual production from a longer and more spatially extensive ice-free summer could be expected to enhance zooplankton productivity. Concurrently, shifts in the seasonal timing (phenology) of species life-history traits can be anticipated. Such enhanced secondary productivity has been shown to operate in the North Water Polynya (Ringuette et al. 2002) and more recently suggested as the cause of long-term increases in zooplankton in the Chukchi Sea (Ershova et al. 2015b). More open water, with an extended duration, may favour stronger wind events that increase upwelling in autumn and therefore add nutrients to surface water that act to precondition the extent of the following spring bloom. However, in other regions of the Arctic, such as the Canada Basin and large parts of the Beaufort Sea, no net increase in productivity is expected because early ice melt would increase stratification and prevent nutrient input into the euphotic zone (Monier et al. 2015). A region-specific, lower annual production could have a consequent effect on zooplankton productivity.

3.2.5 Knowledge and monitoring gaps

Approach to monitoring temporal and spatial changes

Traditional Knowledge (TK)

Because of the small mostly invisible nature of plankton, there is likely only indirect Traditional Knowledge (TK) on plankton across the Arctic. TK that might be related would include narratives of brown water consistent with high biomass blooms of diatoms, *Phaeocystis* or pelagophytes, feeding frenzy by cod or other vertebrates, indicative of zooplankton or larval concentrations. Local reports of "red feed", dense aggregations of copepods, off the coast of Norway could provide a long-term record of *Calanus finmarchicus* populations (Wiborg 1976). Reports of episodes or seasonal occurrence of strong sea smell would also be consistent with high dimethylsulfoniopropionate (DMSP) concentrations indicative of phytoplankton blooms. There are also records of jellyfish piled upon beaches. Such knowledge needs to be recorded.

Traditional net hauls and microscopy

Biological collections to create basic planktonic species inventories for Arctic waters can be traced back to some of the earliest science expeditions over a century ago. For example, quantitative zooplankton data in the Pacific Arctic began in the 1930s (e.g., Johnson 1934, Stepanova 1937a, b) and noted the significant influence of Pacific fauna in the Chukchi Sea. The use of what are now considered coarse meshes (i.e., 50-100 μm, for phytoplankton and 0.5-1 mm for zooplankton) severely biased our historical impression of community composition. For phytoplankton, only larger species or groups with robust cell walls, such as thecate dinoflagellates and diatoms, would have remained intact
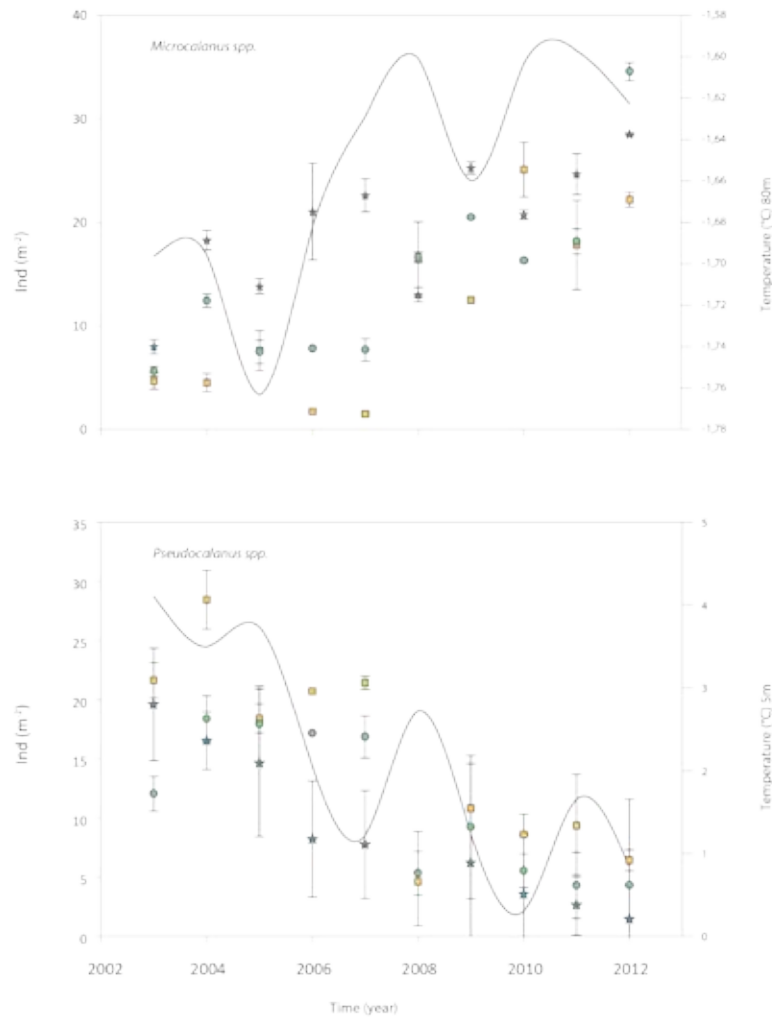
Figure 3.2.7: Temperature and copepod abundance in Zackenberg, northeastern Greenland. Temperature is measured at 80 m for Microcalanus *and 5 m for* Pseudocalanus *(Arendt et al. 2016).*

after the rough handling and use of harsh preservatives at that time. Lack of standardized collection tools, especially mesh size for zooplankton and nets versus whole water samples for phytoplankton, collection depths, and inconsistent sampling locations (see maps in Gill et al. 2011) has greatly hampered attempts to assemble and interpret data. Changes in taxonomy, particularly the splitting or merging of species, have further complicated analysis. Consequently, although zooplankton have been extensively sampled over many regions of the Arctic, basic maps of species distribution and abundance are not readily available and are only now emerging for the some of the larger and most prominent crustaceans.

The inflow gateways have always contained large numbers of expatriated species from the Atlantic or Pacific that are considered to be non-viable in the Arctic (Nelson et al. 2009, Wassmann et al. 2015). While there is some indication that the prominence, penetration and duration of expatriate zooplankton species are increasing (Weydmann et al. 2014, Ershova et al. 2015b, Kristiansen et al. 2016), it is still thought that the sub-zero temperatures that occur during winter will make it difficult for non-Arctic species to gain a permanent year-round presence. The situation for microbes and phytoplankton is unknown. Late-summer and mid-winter sampling programs at coastal communities would be useful to test these assumptions. Metagenomic approaches may provide practical means of assessing shifting biodiversity as well as the presence of invaders.

Future directions

The CBMP Plankton Expert Network will continue to search out existing data (see below), while encouraging Arctic nations to extend existing time series and fill in regions were data is sparse. Standard microscopy has been used to monitor larger phytoplankton (Canada, Norway, Svalbard, and Greenland), and remains the method of choice in most zooplankton studies. Microscopy is the practical choice for larger planktonic groups, as the equipment needed is readily available and not technically complex. However, comparability of data from different laboratories requires taxonomic expertise, which is becoming rare. An alternative or complement to microscopy identification is the use of marker genes to identify species, although this approach requires infrastructure and access to sequencing facilities. Comparative molecular studies on a pan-Arctic scale would also benefit from the harmonization of classification systems. The utility of molecular approaches depends on curated reference databases, which are now becoming increasingly populated. In principle, zooplankton species can be identified provided suitable markers are found, and at finer levels different populations of the same species have been mapped (Nelson et al. 2009, Questel et al. 2016).

Figure 3.2.8: Time series of relative proportions of Arctic and Atlantic Calanus *species in Kongsfjorden (top) and Rijpfjorden (bottom) (Source: MOSJ, Norwegian Polar Institute).*

The recent advent of high through-put multiplex sequencing, where many samples can be analysed simultaneously, will facilitate monitoring of the smallest species. Although uptake of these methods into long-term monitoring protocols has been slow, standardized protocols are being developed (C. Lovejoy pers. comm.). The CBMP Plankton Expert Network recommends the use of both traditional visual identification and, particularly for the unicellular groups, molecular approaches to determine biodiversity. The persistent water mass layering of Arctic seas and the close coupling between microbial communities and water masses (Monier et al. 2013) suggest that monitoring could be based at key easily accessed sites and depths. For instance, for phytoplankton, the CBMP Expert Network suggests sampling in focal regions with a history of monitoring using Niskin-like bottles targeting samples collected from the surface and at the subsurface chlorophyll maximum depths. By knowing the basic oceanography of those areas, results can be extrapolated over larger areas. Over the last 10 years the CBMP Plankton Expert Network has worked towards identifying key plankton species that are indicative of the state of the ecosystem and have relevance to other biological FECs. The CBMP Plankton Expert Network will continue to develop species distribution indices, using the approach exemplified in Luddington et al. (2016), with defined Arctic and Boreal-Arctic species complexes.

Currently there is little (or no) monitoring of the vast majority of single-celled species, with most information available on the occurrence of zooplankton, especially larger calanoid copepods. Some (incomplete) time series exist for phytoplankton (cell abundance and biomass) in the Beaufort Sea and Baffin Bay from roughly 1999 to present and from the Barents Sea from 2005 and Svalbard, but inferring change from such sporadic samplings is difficult. These limited time series suggest trends, but it is not clear whether zooplankton species are following or leading the same climate-mediated trends detected in fish and mammal species distributions. In addition, our analysis of the relatively scant species data available for single-celled plankton, especially phytoplankton and heterotrophic protists, indicate that they too are influenced by climate-driven change and species data would contribute to the understanding of ecosystem status. It can be argued that changes at the base of the food web would be the first sentinel signals of overall ecosystem shifts.

Significant amounts of old data still need to be recovered, especially for zooplankton. Historical data are invaluable in extending the window of observation backward at a faster pace, and at lower cost than what we gain by moving forward. For older data, the major limitation is locating the station-resolved data, either in researcher's unpublished notes or the grey literature. While many older projects are published, the tendency to average data when preparing publications, and ignoring rarer taxa, makes the data that can be recovered of limited value for modern reanalysis. The significant changes that have occurred in taxonomy of zooplankton over the last century, and interest in examining shifts in phenology, further suggest that existing historical collections should be re-examined to resolve their species and life-stage composition. The greatest challenge in existing contemporary data sets remains a commitment of funds to keep these time-series operating.

While it is possible to look for synchronicity in trends across datasets, it is difficult to pool them into a quantitative analysis if they differ in collecting or processing protocols. Efforts should continue to standardize methods across researchers, with more opportunities for different research groups to interact. However, if dominant species changes are reported that are dramatically different from historical records, this would be a good indication of regime changes or crossing a tipping point (Wassmann and Lenton 2012). While summer through late-summer provides little information on the dominant spring bloom species, it is a period when species composition can be less variable—at least in the Beaufort Sea (Comeau et al. 2011). However, given the importance of the timing and extent of ice melt to stratification and light penetration there is a need to better understand early season bloom dynamics that may set the stage for the remainder of the growing season. Broader seasonal sampling is needed to establish baselines and detect possible trends in species composition. Summer
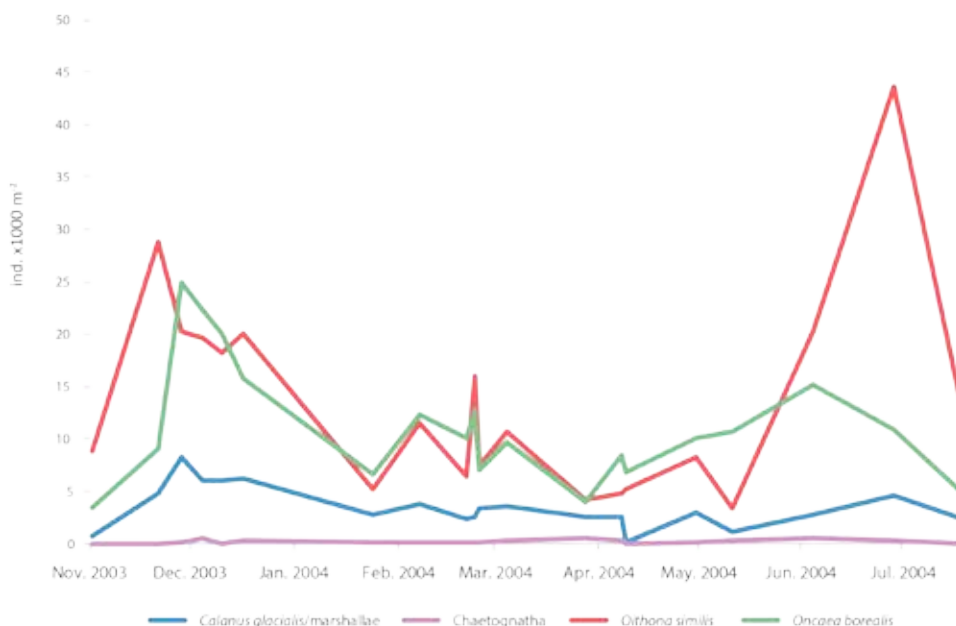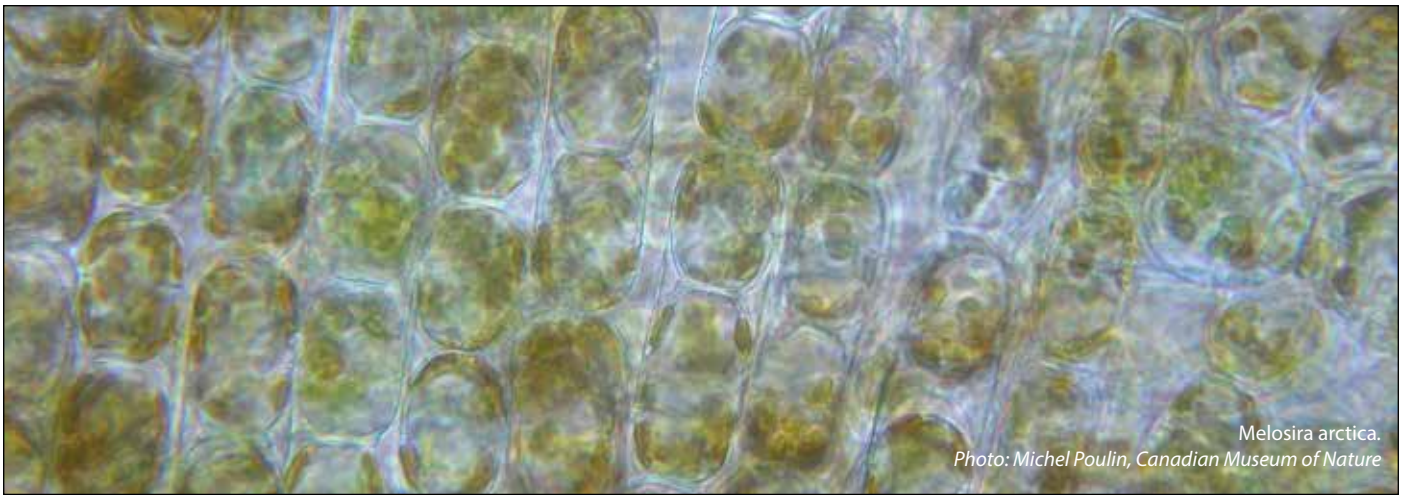

Figure 3.2.9: Seasonal time series of the major zooplankton in Franklin Bay, Canada.

Melosira arctica.
Photo: Michel Poulin, Canadian Museum of Nature

sampling is more acceptable for zooplankton monitoring, given the large existing data records, but some late-summer and autumn sampling would be useful for exploring phenological changes in life-stages.

In closing, most planktonic studies are concentrated around summer and early autumn. While drifting ice stations have provided year-round observations over the basins (e.g., Kosobokova 1982, Ashjian et al. 2003), except for Svalbard and the Barents Sea, the shelves are comparably understudied during winter. Recent observations from Franklin Bay in the Canadian Beaufort Sea (Fig. 3.2.9) (Darnis and Fortier 2014) and Svalbard fjords (Berge et al. 2015, Grigor et al. 2015) suggest that winter is a more active period than previously believed. Thus, more attention and monitoring should be carried out in winter. Working from research stations with easy access to the sea could facilitate year-round studies of some species provided field-ready infrastructure becomes available.

Access to data

Smaller, single-celled eukaryotes have been studied using molecular techniques with data mostly targeting variable regions of the 18S rRNA gene. The majority of this work has been carried out in Canadian waters, but with the cost of sequencing and development of easy to use bioinformatics pipeline, many more regions are being sampled at least once. However, except for ArcticNet regions sampled since 2005 in the Beaufort Sea and northern Baffin Bay, the Canada Basin since 2012 and more recently around Svalbard (Norway) (Vader et al. 2015, Marquardt et al. 2016), most studies report only one or few isolated samples. The majority of the raw data are available in archives such as GenBank Sequence Read Archive (SRA), and for most journals that publish such studies, it is required that data should they be publicly available. In terms of stations sampled, the greatest sampling effort of high through-put sequencing in Arctic marine water columns have been in the Beaufort Sea/ Amundsen Gulf region and around Svalbard. High through-put sequencing has also been used on samples from the Chukchi Sea, Canadian Arctic Archipelago, Baffin Bay, Hudson Bay, the Greenland Sea and Laptev Sea. For net-based sampling of phytoplankton and zooplankton, there is still no universal repository for data, either globally or for the Arctic specifically. Clearer policies on data release and incentives for release of older data appear warranted.

3.2.6 Conclusions and key findings

The functional and taxonomic diversity of microbes in the Arctic is vast and a scientifically underappreciated source of biodiversity.

Phytoplankton are a species-rich domain of the Arctic marine environment, containing half of the diversity reported for the world oceans. Heterotrophic and mixotrophic species are similarly diverse, with many species likely restricted to Arctic waters.

Plankton are the base of the Arctic marine food web, and knowledge of species distributions over space and time is inadequate despite the fact that changes at the base of the food web will be the first sentinel sign of overall ecosystem shifts. More information is essential for our understanding of ecosystem structure and processes and, thus, relevant for ecosystem-based management of ocean areas.

Changes in the hydrography will have a profound effect on the species living in the Arctic due to their intimate relationship with physical oceanography and specific water masses.

The lack of taxonomic information from bulk zooplankton and chlorophyll sampling during recent decades impedes our ability to assess ecosystem changes in the Arctic. Species-specific information is essential for monitoring community changes driven by climate.

With Arctic governments increasingly interested in the Arctic region, both geopolitically and as an indicator of climate change, there are initiatives to build and run research stations year-round. A key consideration for site selection should be access to the sea and inclusion of full-spectrum plankton monitoring.

References

Abelmann, A. 1992. Diatom assemblages in Arctic sea ice - indicator for ice drift pathways. Deep-Sea Research Part A, 39(2): 525-538.

Abramova, E. and Tuschling, K. 2005. A 12-year study of the seasonal and interannual dynamics of mesozooplankton in the Laptev Sea: Significance of salinity regime and life cycle patterns. Global Planetary Change, 48(1-3): 141-164.

Advisory Forum on Monitoring and Institute of Marine Research. 2015. State of the Environment Norway. Norwegian Environment Agency, Ministry of Climate and Environment, Oslo, Norway. Online.

Ardyna, M., Gosselin, M., Michel, C., Poulin, M. and Tremblay, J.-E. 2011. Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic: contrasting oligotrophic and eutrophic regions. Marine Ecology Progress Series, 442: 37-57.

Arendt, K.E., Agersted, M.D., Sejr, M.K. and Juul-Pedersen, T. 2016. Glacial meltwater influences on plankton community structure and the importance of top-down control (of primary production) in a NE Greenland fjord. Estuary Coast Shelf Science, 183(A): 123-135.

Arendt, K.E., Juul-Pedersen, T., Mortensen, J., Blicher, M.E. and Rysgaard, S. 2013. A 5-year study of seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord reveals dominance of *Microsetella norvegica* (Crustacea, Copepoda). Journal of Plankton Research, 35(1): 105-120.

Ashjian, C.J., Braund, S.R., Campbell, R.G., George, J.C., Kruse, J., Maslowski, W., Moore, S.E., Nicolson, C.R., Okkonen, S.R., Sherr, B.F., Sherr, E.B. and Spitz, Y. 2010. Climate variability, oceanography, bowhead whale distribution, and Iñupiat subsistence whaling near Barrow, AK. Arctic, 63(2): 179-194.

Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M. and Keuren, D.V. 2003. Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. Deep-Sea Research I, 50(10-11): 1235-1261.

Ástþórsson, O.S. and Gislason, A. 1997. On the food of capelin in the subarctic waters north of Iceland. Sarsia, 82(2): 81-86.

Ástþórsson, O.S., Gislason, A. and Jonsson, S. 2007. Climate variability and the Icelandic marine ecosystem. Deep-Sea Research II, 54(23-26): 2456–2477.

Auel, H. and Werner, I. 2003. Feeding, respiration and life history of the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. Journal of Experimental Marine Biology and Ecology, 296(2): 183-197.

Balzano, S., Gourvil, P., Siano, R., Chanoine, M., Marie, D., Lessard, S., Sarno, D. and Vaulot, D. 2012. Diversity of cultured photosynthetic flagellates in the northeast Pacific and Arctic Oceans in summer. Biogeosciences, 9: 4553-4571.

Bachy, C., Lopez-Garcia, P., Vereshchaka, A. and Moreira, D. 2011. Diversity and vertical distribution of microbial eukaryotes in the snow, sea ice and seawater near the North Pole at the end of the polar night. Frontiers in Microbiology, 2: 106.

Berge, J., Cottier, F., Varpe, Ø., Renaud, P.E., Kwasniewski, S., Griffiths, C., Søreide, J.E., Johnsen, G., Aubert, A., Bjærke, O., Hovinen, J., Jung-Madsen, S., Tveit, M. and Majaneva, S. 2014. Arctic complexity: a case study on diel vertical migration of zooplankton. Journal of Plankton Research, 36(5): 1279–1297.

Berge, J., Daase, M., Renaud, P.E., Ambrose Jr., W.G., Darnis, G., Last, K.S., Leu, E., Cohen, J. H., Johnsen, G., Moline, M.A., Cottier, F., Varpe, Ø., Shunatova, N., Bałazy, P., Morata, N., Massabuau, J.-C., Falk-Petersen, S., Kosobokova, K., Hoppe, C.J.M., Węsławski, J.M,. Kukliński, P., Legeżyńska, J., Nikishina, D., Cusa, M., Kędra, M., Włodarska-Kowalczuk, M., Vogedes, D., Camus, L., Tran, D., Michaud, E., Gabrielsen, T.M., Granovitch, A., Gonchar, A., Krapp, R. and Callesen, T.A. 2015 Unexpected levels of biological activity during the polar night offer new perspectives on a warming Arctic. Current Biology, 25(19), 2555-2561.

Beaugrand, G. 2015. Theoretical basis for prediction climate-induced abrupt shifts in the oceans. Philisophical Transactions of the Royal Society B, 370(1659): 20130264.

Blachowiak-Samolyk, K., Søreide, J.E., Kwasniewski, S., Sundfjord, A., Hop, H., Falk-Petersen, S. and Hegseth, E.N. 2008. Hydrodynamic control of mesozooplankton abundance and biomass in northern Svalbard waters (79-81°N). Deep-Sea Research Part II, 55: 2210-2224.

Bluhm, B.A., Gebruk, A.V., Gradinger, R., Hopcroft, R.R., Huettmann, F., Kosobokova, K.N., Sirenko, S.I. and Weslawski, J.M. 2011. Arctic marine biodiversity – an update of species richness and examples of biodiversity change. Oceanography, 24(3): 198-214.

Comeau, A.M., Li, W.K.W., Tremblay, J.E., Carmack, E.C. and Lovejoy, C. 2011. Arctic microbial community structure before and after the 2007 record sea ice minimum. PLoS ONE, 6(11): e27492.

Dalpadado, P., Arrigo, K.R., Hjøllo, S.S., Rey, F., Ingvaldsen, R.B., Sperfeld, E., Dijken, G.L.V., Stige, L.C., Olsen, A. and Ottersen, G. 2014. Productivity in the Barents Sea - Response to recent climate variability. PLoS ONE, 9(5): e95273.

Dalpadado, P., Hop, H., Rønning, J., Pavlov, V., Sperfeld, E., Buchholz, F., Rey, A. and Wold, A. 2016. Distribution and abundance of euphausiids and pelagic amphipods in Kongsfjorden, Isfjorden and Rijpfjorden (Svalbard) and changes in their relative importance as key prey in a warming marine ecosystem. Polar Biology, 39(10): 1765-1784.

Daase, M., Hop, H. and Falk-Petersen, S. 2016. Small-scale diel vertical migration of zooplankton in the High Arctic. Polar Biology, 39(7): 1213-1223.

Daniëls, F.J.A., Gillespie, L.J. and Poulin, M. 2013. Plants. In: H. Meltofte (ed.). 2013. Arctic Biodiversity Assessment, Status and trends in Arctic Biodiversity. Conservation of Arctic Flora and Fauna, Akureyri, Iceland, pp 311-353.

Darnis, G. and Fortier, L. 2014. Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean). Journal of Plankton Research, 36(4): 1092-1108.

Darnis, G., Robert, D., Pomerleau, C., Link, H., Archambault, P., Nelson, R., Geoffroy, M., Tremblay, J.-E., Lovejoy, C., Ferguson, S., Hunt, B. and Fortier, L. 2012. Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. Climatic Change, 115(1): 179-205.

Eriksen, E., Skjoldal, H.R., Dolgov, A.V., Orlova, E.L. and Prozorkevich, D.V. 2016. The Barents Sea euphausiids: methodological aspects of monitoring and estimation of abundance and biomass. ICES Journal of Marine Science, 73(6): 1533-1544.

Ershova, E.A., Hopcroft, R.R. and Kosobokova, K.N. 2015a. Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004-2012. Polar Biology, 38(9): 1461-1481.

Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., Matsuno, K., Nelson, R.J., Yamaguchi, A. and Eisner, L.B. 2015b. Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945-2012. Oceanography, 28(3): 100-115.

Falk-Petersen, S., Mayzaud, P., Kattner, G. and Sargent, J.R. 2009. Lipids and life strategy of Arctic *Calanus*. Marine Biology Research, 5(1): 18-39.

Forest A., Stemmann, L., Picheral, M., Budorf, L., Robert, D., Fortier, L. and Babin, M. 2012. Size distribution of particles and zooplankton across the shelf-basin system in southeast Beaufort Sea: combined results from an Underwater Vision Profiler and vertical net tows. Biogeosciences, 9(4): 1301-1320.

Galand, P.E., Casamayor, E.O., Kirchman, D.L., Potvin, M. and Lovejoy, C. 2009. Unique archaeal assemblages in the Arctic Ocean unveiled by massively parallel tag sequencing. The ISME Journal, 3(7): 860-869.

Ghiglione, J.F., Galand, P.E., Pommier, T., Pedrós-Alió, C., Maas, E.W., Bakker, K., Bertilson, S., Kirchmanj, D.L., Lovejoy, C., Yager, P.L. and Murray, A.E. 2012. Pole-to-pole biogeography of surface and deep marine bacterial communities. PNAS, 109(43): 17633-17638.

Gill, M.J., Crane, K., Hindrum, R., Arneberg, P., Bysveen, I., Denisenko, N.V., Gofman, V., Grant-Friedman, A., Guðmundsson, G., Hopcroft, R.R., Iken, K., Labansen, A., Liubina, O.S., Melnikov, I.A., Moore, S.E., Reist, J.D., Sirenko, B.I., Stow, J., Ugarte, F., Vongraven, D. and Watkins, J. 2011. Arctic Marine Biodiversity Monitoring Plan. CAFF Monitoring Series Report No. 3, Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland.

Gislason, A. and Ástþórsson, O.S. 1998. Seasonal variations in biomass, abundance and composition of zooplankton in the subarctic waters north of Iceland. Polar Biology, 20(2): 85-94.

Gislason, A., Petursdóttir, H., Ástþórsson, O.S., Guðmundsson, K. and Valdimarsson, H. 2009. Interannual variability in abundance and community structure of zooplankton south and north of Iceland in relation to environmental conditions in spring 1990–2007. Journal of Plankton Research, 31(5): 541–551.

Gislason, A., Petursdóttir, H. and Guðmundsson, K. 2014. Long-term changes in abundance of Calanus finmarchicus south and north of Iceland in relation to environmental conditions and regional diversity in spring 1990-2013. ICES Journal of Marine Science, 71(9): 2539–2549.

Grainger, E.H. 1965. Zooplankton from the Arctic Ocean and adjacent Canadian waters. Journal of the Fisheries Research Board of Canada, 22(2): 543-564.

Grigor, J.J., Marais, A.E., Falk-Petersen, S. and Varpe, O. 2015. Polar night ecology of a pelagic predator, the chaetognath Parasagitta elegans. Polar Biology, 38(1): 87-98.

Hasle, G.R. and Heimdal, B.R. 1998. The net phytoplankton in Kongsfjorden Svalbard July 1988 with general remarks on species composition of Arctic phytoplankton. Polar Research, 17: 31-52.

Hegseth, E.N. and Tverberg, V. 2013. Effect of Atlantic water inflow on timing of the phytoplankton spring bloom in a high Arctic fjord (Kongsfjorden Svalbard). Journal of Marine Systems, 113-114: 94-105.

Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwasniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Wlodarska-Kowalezuk, M., Lydersen, C., Weslawski, J.M., Cochrane, S., Gabrielsen, G.W., Leakey, R.J.G., Lønne, O.J., Zajaczkowski, M., Falk-Petersen, S., Kendall, M., Wängberg, S.Å., Bischof, K., Voronkov, A.Y., Kovaltchouk, N.A., Wiktor, J., Poltermann, M., di Prisco, G., Papucci, C. and Gerland, S. 2002. The marine ecosystem of Kongsfjorden Svalbard. Polar Research, 21(1): 167-208.

Hunt, B.P.V., Nelson, R.J., Williams, B., McLaughlin, F.A., Young, K.V., Brown, K.A., Vagle, S. and Carmack, E.C. 2014. Zooplankton community structure and dynamics in the Arctic Canada Basin during a period of intense environmental change (2004–2009). Journal of Geophysical Reseach Oceans, 119(4): 2518–2538.

Huse, S.M., Dethlefsen, L., Huber, J.A., Welch, D.M., Relman, D.A. and Sogin, M.L. 2008. Exploring microbial diversity and taxonomy using SSU rRNA hypervariable tag sequencing. PLoS Genetics, 4(11): e1000255.

Johnson, M.W. 1934. The production and distribution of zooplankton in the surface waters of the Bering Sea and Bering Strait, Part II. In: Report of the oceanographic cruise U.S. Coast Guard Cutter Chelan, Bering Sea and Bering Strait, 1934. United States Coast Guard, pp 1-380.

Joli, N., Monier, A., Logares, R. and Lovejoy, C. 2017. Seasonal patterns in Arctic prasinophytes and inferred ecology of Bathycoccus unveiled in an Arctic winter metagenome. The ISME Journal.

Josefson, A.B. and Mokievsky, V. 2013. Marine invertebrates. In: H. Meltofte (ed.). 2013. Arctic Biodiversity Assessment, Status and trends in Arctic Biodiversity. Conservation of Arctic Flora and Fauna, Akureyri, Iceland, pp 277-309.

Kilias, E.S., Peeken, I. and Metfies, K. 2014. Insight into protest diversity in Arctic sea ice and melt-pond aggregate obtained by pyrosequencing. Polar Research, 33: 23466.

Kleiven, M.R., Naustvoll, L.J., Larsen, S.H. and Larionow, V. 2015. Phytoplankton. Barents Sea Environmental Status.

BarentsPortal, Barents Sea Environmental Status, A Norwegian-Russian Collaboration.

Kosobokova, K.N. 1982. Composition and distribution of the biomass of zooplankton in the central Arctic Basin. Oceanology, 22: 744-750.

Kosobokova, K.N., Hirche, H.-J. and Hopcroft, R.R. 2011. Patterns of zooplankton diversity through the depths of the Arctic's central basins. Marine Biodiversity, 41(1): 29–50.

Kraft, A., Bauerfeind, E., Nothig, E.-M. and Bathmann, U.V. 2012. Size structure and life cycle patterns of dominant pelagic amphipods collected as swimmers in sediment traps in the eastern Fram Strait. Journal of Marine Systems, 95; 1-15.

Krawczyk, D., Arendt, K., Juul-Pedersen, T., Sejr, M.K., Blicher, M.E. and Jakobsen, H.H. 2015a. Spatial and temporal distribution of planktonic protists in the East Greenland fjord and offshore waters. Marine Ecology Progress Series, 538: 99-116.

Krawczyk, D.W., Witkowski, A., Juul-Pedersen, T., Arendt, K.E., Mortensen, J. and Rysgaard, S. 2015b. Microplankton succession in a SW Greenland tidewater glacial fjord influenced by coastal inflows and run-off from the Greenland Ice Sheet. Polar Biology, 38(9): 1515-1533.

Kristiansen, I., Gaard, E., Hátún, H., Jonasdóttir, S. and Ferreira, A.S.A. 2016. Persistent shift of Calanus spp. in the southwestern Norwegian Sea since 2003, linked to ocean climate. ICES Journal of Marine Science, 73(5): 1319-1329.

Kubiszyn, A.M., Piwosz, K., Wiktor Jr., J.M. and Wiktor, J.M. 2014. The effect of inter-annual Atlantic water inflow variability on the planktonic protist community structure in the West Spitsbergen waters during the summer. Journal of Plankton Research, 36(5): 1190-1203.

Lalande, C., Bauerfeind, E., Nöthig, E.-A. and Beszczynska-Möller, A. 2013. Impact of a warm anomaly on export fluxes of biogenic matter in the eastern Fram Strait. Progress in Oceanography, 109: 70-77.

Lefebvre, K.A., Quakenbush, L., Frame, E., Huntington, K.B., Sheffield, G., Stimmelmayr, R., Bryan, A., Kendrick, P., Ziel, H., Goldstein, T., Snyde, J.A., Gelatt, T., Gulland, F., Dickerson, B. and Gill, V. 2016. Prevalence of algal toxins in Alaskan marine mammals foraging in a changing arctic and subarctic environment. Harmful Algae, 55: 13–24.

Li, W.K.W., McLaughlin, F.A., Lovejoy, C. and Carmack, E.C. 2009. Smallest algae thrive as the Arctic Ocean freshens. Science, 326(5952): 539-539.

Lovejoy, C. 2013. Microorganisms. In: H. Meltofte (ed.). 2013. Arctic Biodiversity Assessment, Status and trends in Arctic Biodiversity. Conservation of Arctic Flora and Fauna, Akureyri, Iceland, pp 372-382.

Lovejoy, C., Massana, R. and Pedrós-Alió, C. 2006. Diversity and distribution of marine microbial eukaryotes in the Arctic Ocean and adjacent seas. Applied and Environmental Microbiology, 72(5): 3085-3095.

Lovejoy, C., Vincent, W.F., Bonilla, S., Roy, S., Martineau, M.J., Terrado, R., Potvin, M., Massana, R. and Pedrós-Alió, C. 2007. Distribution, phylogeny, and growth of cold-adapted picoprasinophytes in arctic seas. Journal of Phycology, 43(1): 78-89.

Luddington, I.A., Kaczmarska, I. and Lovejoy, C. 2012. Distance and character-based evaluation of the V4 region of the 18S rRNA gene for the identification of diatoms (Bacillariophyceae). PLoS ONE, 7(9): e45664.

Luddington, I.A., Lovejoy, C. and Kaczmarska, I. 2016. Species-rich meta-communities of the diatom order Thalassiosirales in the Arctic and northern Atlantic Ocean. Journal of Plankton Research, 38(4): 781-797.

McBride, M.M., Hansen, J.R., Korneev, O., Titov, O. (Eds.) Stiansen, J.E., Tchernova, J., Filin, A., Ovsyannikov A. (Co-eds.) 2016. Joint Norwegian - Russian environmental status 2013. Report on the Barents Sea Ecosystem. Part II - Complete report. IMR/PINRO Joint Report Series, 2016 (2), 359pp. ISSN 1502-8828.

Maps, F., Pershing, A.J. and Record, N.R. 2012. A generalized approach for simulating growth and development in diverse marine copepod species. ICES Journal of Marine Science, 69(3):

370-379.

Marine Research Institute. 2015. Environmental conditions in Icelandic waters 2014. Hafrannsóknastofnun Fjölrit, 181. Marine Research Institute, Reykjavík. [in Icelandic with English summary].

Marquardt, M., Vader, A., Stubner, E.I., Reigstad, M. and Gabrielsen, T.M. 2016. Strong seasonality of marine microbial eukaryotes in a High-Arctic Fjord (Isfjorden, in West Spitsbergen, Norway). Applied and Environmental Microbiology, 82(6): 1868-1880.

McBride, M.M., Hansen, J.R., Korneev, O., Titov, O., Stiansen, J.E., Tchernova, J., Filin, A., Ovsyannikov A. (Eds.). 2016. Joint Norwegian - Russian environmental status 2013. Report on the Barents Sea Ecosystem. Part II - Complete report. IMR/PINRO Joint Report Series, 2016 (2),Bergen, Norway, pp 359. Online.

Monier, A., Comte, J., Babin, M., Forest, A., Matsuoka, A. and Lovejoy, C. 2015. Oceanographic structure drives the assembly processes of microbial eukaryotic communities. The ISME Journal, 9(4): 990-1002.

Monier, A., Terrado, R., Thaler, M., Comeau, A., Medrinal, E. and Lovejoy, C. 2013. Upper Arctic Ocean water masses harbor distinct communities of heterotrophic flagellates. Biogeosciences, 10(6): 4273-4286.

Morata, N., Poulin, M. and Renaud, P. 2011. A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor. Polar Biology, 34(1): 101-112.

MOSJ- Environmental monitoring of Svalbard and Jan Mayen. 2015. Zooplankton species composition in Kongsfjorden (Calanus spp.). Environmental monitoring of Svalbard and Jan Mayen (MOSJ). Norwegian Polar Institute. Online.

Nelson, R.J., Carmack, E.C., McLaughlin, F.A. and Cooper, G.A. 2009. Penetration of Pacific zooplankton into the western Arctic Ocean tracked with molecular population genetics. Marine Ecology Progress Series, 381: 129-138.

Paulsen, M.L., Doré, H., Garczarek, L., Seuthe, L., Müller, O., Sandaa, R-A., Bratbak, G. and Larsen, A. 2016. Synechococcus in the Atlantic Gateway to the Arctic Ocean. Frontiers in Marine Science, 3 (191).

Pedrós-Alió, C., Potvin, M. and Lovejoy, C. 2015. Diversity of planktonic microorganisms in the Arctic Ocean. Progress in Oceanography, 139: 233-243.

Percopo, I., Ruggiero, M.V., Balzano, S., Gourvil, P., Lundholm, N., Siano, R., Tammilehto, A., Vaulot, D. and Sarno, D. 2016. Pseudo-nitzschia arctica sp. nov., a new cold-water cryptic Pseudo-nitzschia species within the P. pseudodelicatissima complex. Journal of Phycology, 52(2): 184–199.

Percy, J.A. 1993. Reproduction and growth of the Arctic hyperiid Amphipod Themisto libellua Mandt. Polar Biology, 13(2): 131-139.

Poulin, M., Daugbjerg, N., Gradinger, R., Ilyash, L., Ratkova, T. and von Quillfeldt, C. 2011. The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: a first-attempt assessment. Marine Biodiversity, 41(1): 13-28.

Questel, J.M., Clarke, C. and Hopcroft, R.R. 2013. Seasonal and interannual variation in the planktonic communities of the north-eastern Chukchi Sea during the summer and early fall. Continental Shelf Research, 67: 23-41.

Questel J.M., Hopcroft, R.R., Blanco-Bercial, L. and Bucklin, A. 2016. Phylogeography and connectivity of the Pseudocalanus (Copepoda: Calanoida) species complex in the eastern North Pacific and the Pacific Arctic Region. Journal of Plankton Research, 38(3): 610-623.

Ressler, P.H., Dalpadado, P., Macaulay, G.J., Handegard, N. and Skem-Mauritzen, M. 2015. Acoustic surveys of euphausiids and models of baleen whale distribution in the Barents Sea. Marine Ecology Progress Series, 527: 13-29.

Richardson, A.J. 2008. In hot water: zooplankton and climate change. ICES Journal of Marine Science, 65(3): 279-295.

Ringuette, M., Fortier, L., Fortier, M., Runge, J.A., Belancer, S., Laroucher, P., Weslawski, J.-M. and Kwasniewski, S. 2002. Advanced recruitment and accelerated population development in Arctic calanoid copepods of the North Water.

Deep-Sea Research Part II, 49(22-23): 5081-5099.

Slabinsky, A. and Figurkin, A.L. 2014. Structure of planktonic community in the southern part of the Chukchi Sea in summer period. Notifications TINRO, 178 [in Russian].

Slagstad, D., Ellingsen, I.H. and Wassmann, P. 2011. Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. Progress in Oceanography, 90(1-4): 117–131.

Smoot, C.S. and Hopcroft, R.R. 2016. Cross-shelf gradients of epipelagic zooplankton communities of the Beaufort Sea and the influence of localized hydrographic features. Journal of Plankton Research, 39(1): 65-78.

Stepanova, V.S. 1937a. Biological indicators of currents in the northern Bering and southern Chukchi Seas. Issled Morei SSSR, 25: 175-216 [in Russian].

Stepanova, V.S. 1937b. Distribution of Bering Sea water in the Chukchi Sea (from data of the analysis of zooplankton from a cruise on the icebreaker Krasin in 1935). Trudy Arkt Nauch-Issled Inst., 82: 113-143.

Terrado, R., Scarcella, K., Thaler, M., Vincent, W.F. and Lovejoy, C. 2013. Small phytoplankton in Arctic seas: vulnerability to climate change. Biodiversity, 14(1): 2-18.

Terrado, R., Vincent, W.F. and Lovejoy, C. 2009. Mesopelagic protists: diversity and succession in a coastal Arctic ecosystem. Aquatic Microbial Ecology, 56(1): 25-39.

Thaler, M. and Lovejoy, C. 2015. Biogeography of heterotrophic flagellate populations indicates the presence of generalist and specialist taxa in the Arctic Ocean. Applied and Environmental Microbiology, 81(6): 2137-2148.

Tremblay, J.-É., Robert, D., Varela, D., Lovejoy, C., Darnis, G., Nelson, R.J. and Sastri, A. 2012. Current state and trends in Canadian Arctic marine ecosystems: I Primary production. Climatic Change, 115(1): 161-178.

Trudnowska, E., Sagan, S., Kwasniewski, S., Darecki, M. and Blachowiak-Samolyk, K. 2015. Fine-scale zooplankton vertical distribution in relation to hydrographic and optical characteristics of the surface waters on the Arctic shelf. Journal of Plankton Research 37(1): 120-133.

Vader, A., Marquardt, M., Meshram, A.R. and Gabrielsen, T.M. 2015. Key Arctic phototrophs are widespread in the polar night. Polar Biology, 38(1): 13-21.

van der Meeren, G.I, Skotte, G., Ottersen, G., Franzen, S., Jørgensen, N.M., Frie, A.K.H., Selvik, I. and Svensen, H.I. 2014. Forvaltningsplan Barentshavet – rapport fra Overvåkingsgruppen 2014. Fisken og havet, Special Issue: 1b-2014.115.

von Quillfeldt, C.H. 2000. Common diatom species in arctic spring blooms: their distribution and abundance. Botanica Marina 43(6): 499-516.

Waleron, M., Waleron, K., Vincent, W.F. and Wilmotte, A. 2007. Allochthonous inputs of riverine picocyanobacteria to coastal waters in the Arctic Ocean. FEMS Microbiology Ecology, 59(2): 356-365.

Wassmann, P. and Lenton, T.M. 2012. Arctic tipping points in an earth system perspective. AMBIO, 41(1): 1-9.

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Wing Gabrielsen, G., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D. and Pavlova, O. 2006. Food webs and carbon flux in the Barents Sea. Progress in Oceanography, 71(2-4): 232-287.

Wassmann, P., Kosobokova, K.N., Slagstad, D., Drinkwater, K.F., Hopcroft, R.R., Moore, S.E., Ellingsen, I., Nelson, R.J., Carmack, E., Popova, E., Berge, J. 2015. The contiguous domains of Arctic Ocean advection: Trails of life and death. Progress in Oceanography, 139: 42-65

Weydmann, A., Carstensen, J., Goszczko, I., Dmoch, K., Olszewska, A. and Kwasniewski, S. 2014. Shift towards the dominance of boreal species in the Arctic: inter-annual and spatial zooplankton variability in the West Spitsbergen Current. Marine Ecology Progress Series, 501: 41-52.

Wiborg, K.F. 1976. Fishery and commercial exploitation of Calanus

finmarchicus in Norway. ICES Journal of Marine Science, 36(3): 251-258.

Willis, K.J., Cottier, F.R. and S. Kwasniewski. 2008. Impact of warm water advection on the winter zooplankton community in an Arctic fjord. Polar Biology, 31(4): 475-481.
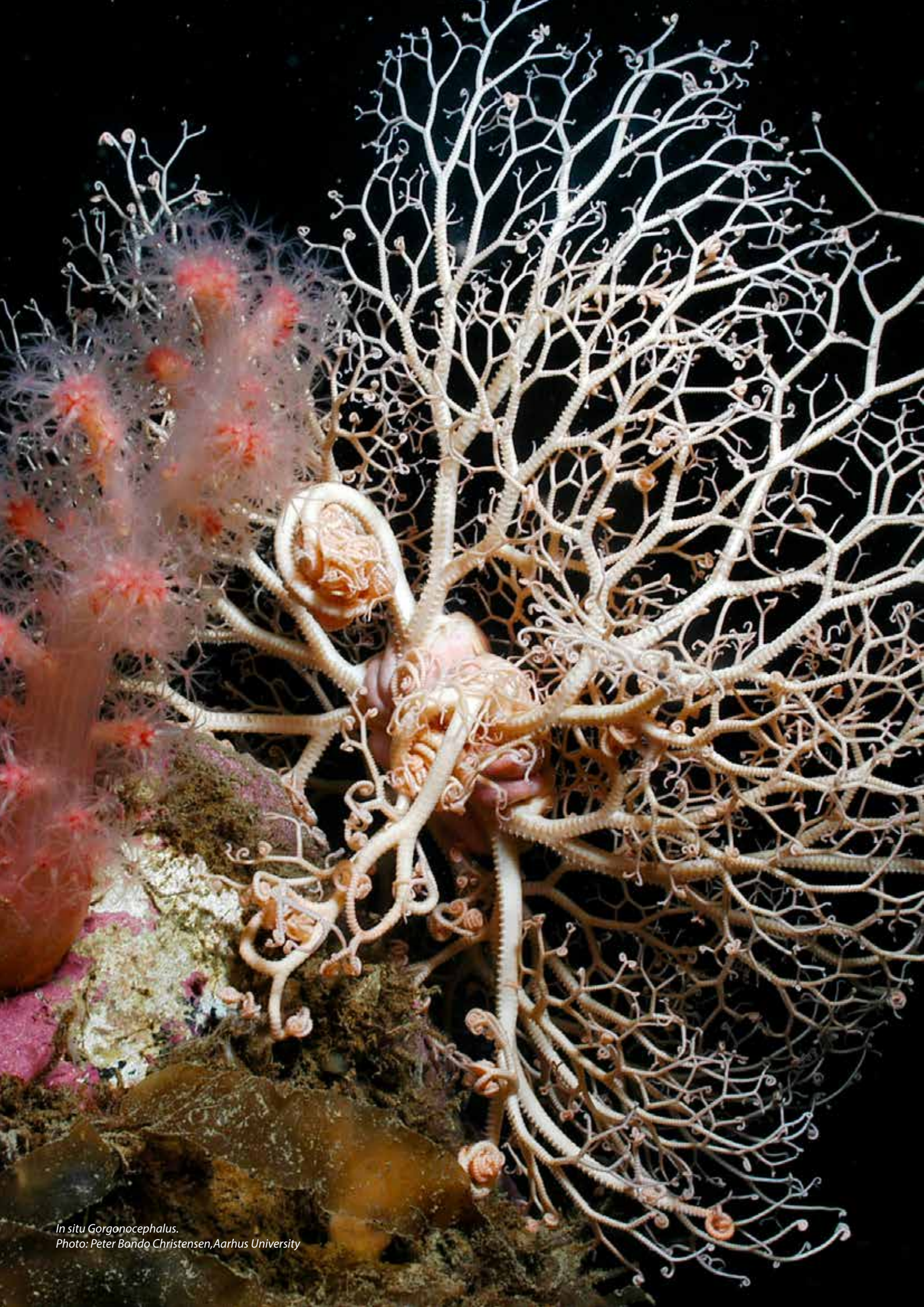
In situ Gorgonocephalus.
Photo: Peter Bondo Christensen, Aarhus University