

3.1 Sea ice biota

Bodil A. Bluhm¹, Haakon Hop^{1,2}, Igor A. Melnikov³, Michel Poulin⁴, Mikko Vihtakari², R. Eric Collins⁵, Rolf Gradinger¹, Thomas Juul-Pedersen⁶, Cecilie von Quillfeldt²

¹UiT – The Arctic University of Norway, Tromsø, Norway, ²Norwegian Polar Institute, Tromsø, Norway, ³P.P. Shirshov Institute of Oceanology, Moscow, Russia, ⁴Canadian Museum of Nature, Ottawa, Canada, ⁵University of Alaska Fairbanks, U.S., ⁶Greenland Institute of Natural Resources, Nuuk, Greenland

3.1 Sea ice biota	33
3.1.1 Introduction	34
3.1.2 Current monitoring	38
3.1.3 Status and trends of FECs	42
3.1.4 Drivers of observed trends.....	46
3.1.5 Knowledge and monitoring gaps.....	48
3.1.6 Conclusions and key findings.....	50
Appendix 3.1.1: Meiofauna References.....	51
Appendix 3.1.2: Macrofauna References.....	53
References.....	57

Snapshot

- Multi-year sea ice is disappearing and will be replaced by first-year sea ice, which will cause shifts in ice algal communities with cascading effects on the ice-associated ecosystem.
- Seasonal duration of first-year sea ice is expected to become shorter, with more snow on the ice, which may decrease the growth season for ice algae, with unknown consequences for biodiversity.
- Sea ice is an important Arctic habitat that supports a rich diversity of species—many of which we know little about.
- It is possible that sea ice algal community structure has changed in the central Arctic between the 1980s and 2010s. This change probably occurred when sea ice extent and thickness declined, but also when sampling efforts and regions shifted, so it is difficult to attribute change.
- Ice amphipod abundance has declined around Svalbard since the 1980s, coinciding with declining sea ice conditions.
- Changes in sea ice biota are very challenging to detect because sea ice is a dynamic system that has large natural variability, and there has been a lack of consistent sea ice biota monitoring.
- Sea ice biota are affected by temperature and salinity, nutrient and space limitations and the ephemeral nature of the ice habitat, therefore making them very susceptible to climate change.
- Sea ice biota monitoring has occurred most frequently in the central Arctic, Svalbard, Barrow (Alaska) and the Canadian Arctic, with new sites developing in Greenland. Consistent monitoring protocols, equipment and methodology are required.

3.1.1 Introduction

The sea-ice related food web and biodiversity are critical components of the Arctic marine ecosystem. Higher trophic levels are directly or indirectly supported by over 2,000 species of small algae and animals that are associated with sea ice, but are often inconspicuous to the naked eye. These species inhabit a wide range of microhabitats inside the brine channel system, on top of the ice in melt ponds, immediately underneath the ice at the ice-water boundary and including extensive pressure ridges (Figure 3.1.1). The spatial distribution of sea ice biota (hereafter referred to as sympagic or ice biota, cf. Legendre et al. 1992) is shaped by dynamic properties of the sea ice. Spatial scales range from the micrometre dimension of the brine channel network to the metre scale that defines ice thickness and horizontal floe extent, to the hundreds of kilometre scale of ice drift patterns across the entire Arctic Ocean. The origin and age of sea ice are important factors which impact the resulting community composition of sea ice biota, with pronounced differences among biota and living conditions in annual landfast sea ice, offshore annual pack ice and multi-year pack ice (also called drift ice).

The hallmark of climate change is the drastic decline in the sea ice cover over at least the past 40 years since the satellite record has allowed accurate observation and interannual comparisons (e.g., Perovich et al. 2015). The Arctic ice cover has declined during all seasons of the year and, concomitantly, the proportion of multi-year sea ice has decreased while the share of first-year sea ice has increased (Nghiem et al. 2007, Barber et al. 2015). Shifts are expected in ice-associated biota composition, abundance, biomass and the timing of the seasonal development (referred to as phenology) (Gradinger et al. 2010, Leu et al. 2011). Without sufficient monitoring, such changes will be impossible, or

at best difficult to detect until effects are dramatic or until they are detected in other parts of the ecosystem due to the coupled processes between sea ice, water column and benthic biota. Higher trophic levels, including seabirds and marine mammals, can also function as indicators of changes in the lower part of marine food webs because their diets, conditions and survival depend on availability of suitable prey (e.g., Mehlum and Gabrielsen 1993, Bluhm and Gradinger 2008).

Close association of living organisms with Arctic sea ice has already been reported ~160 years ago by Ehrenberg (1853) and related knowledge has expanded extensively since then by several authors including, for example, Grunow (1884), Nansen (1906), Hsiao (1983), Horner (1985), Melnikov (1997) and others. As a result of international research in largely independent projects, a total of several thousand species of auto-, mixo- and heterotrophs encompassing viruses, bacteria, fungi, microalgae, and other protists and multicellular animals have been recorded (overviews in Poulin et al. 2011, Daniëls et al. 2013, Josefson and Mokievsky 2013, Lovejoy 2013, Bluhm et al. 2017). These include a combination of ice-endemic species, and taxa of pelagic or benthic origin as well as larval (meroplanktonic) stages of benthic fauna. The inventory of ice biota is still incomplete as new species of bacteria, microalgae, fungi and animals continue to be described from the sea ice environment, partly due to the advances of molecular methods during the last decade (Brinkmeyer et al. 2003, Piraino et al. 2008, Collins et al. 2010, Collins 2015). In addition to studies focusing on diversity and phenology in taxonomic composition, the ecology and physiology of selected ice-related organisms have also received increased focus (Arndt and Swadling 2006, Werner 2007, Fuhrmann et al. 2011, Leu et al. 2015). Data on sea ice biota diversity have been collected as part of scientific expeditions over many years, and we present

these here in a pan-Arctic context based on a comprehensive approach of data assimilation and integration. The choice of Focal Ecosystem Components (FECs) considered is based on the *Arctic Marine Biodiversity Monitoring Plan* (Gill et al. 2011; *CBMP Marine Plan*), with some modifications. The CBMP Sea Ice Biota Expert Network has included here: (1) Bacteria and Archaea, assessed by molecular methods; (2) ice algae and other protists, referring to photosynthesizing single-celled eukaryotes, and hetero- and mixotrophic protists, assessed by morphological characters through optical and electron microscopy; (3) ice meiofauna, referring to multicellular organisms larger than $\sim 20 \mu\text{m}$ to $\sim 500 \mu\text{m}$ living inside the ice brine channel network and primarily assessed by morphological characters; and (4) under-ice macrofauna, typically larger than $\sim 500 \mu\text{m}$, here exclusively represented by ice amphipod crustaceans. Sea ice associated fish, specifically polar cod (*Boreogadus saida*; referred to as Arctic cod in North America) and ice cod (*Arctogadus glacialis*; referred to as polar cod in North America), are included in the Fish chapter (Chapter 3.4). Viruses and fungi are excluded in this report, although they may occur in very high abundances in sea ice (Maranger et al. 1994, Hassett et al. 2016a). Virus occurrence exhibits strong seasonal variability, but their hosts (eukaryotes or bacteria) have not yet been identified. Fungi are dominated by Chytridiomycota and Dikarya, and those chytrids parasitizing on diatoms are most abundant during the ice algal spring bloom (Hassett et al. 2016b).

In this report, we consider some aspects of the diversity (here defined as taxon richness and taxonomic composition), abundance, biomass and distribution of these FECs in different ice types, seasons and years, on pan-Arctic distribution scales. In compiling the relevant information, however, it became apparent that such data were not consistently available for all targeted ice biota FECs. Thus, attention is given to the following four topics. First, the CBMP Sea Ice Biota Expert Network presents the *taxonomic composition and species richness* of organism groups for which at least moderate to high taxonomic resolution is available; these include Bacteria and Archaea, ice algae and ice amphipods. Second, the CBMP Sea Ice Biota Expert Network summarizes the *composition and abundance of sympagic meiofauna* at the pan-Arctic scale, but at coarser taxonomic resolution. Third, the CBMP Sea Ice Biota Expert Network gives two examples of the sparse data sets available on seasonal trends in ice biota, here on the abundance of sympagic meiofauna. Finally, *interannual trends* – for which data are even sparser – in community structure of ice algae (and other protists) and densities of ice amphipods are shown, with interpretations reflecting that these are composite data sets rather than monitoring data. Other, more advanced indicators mentioned in Gill et al. (2011), such as ratios between certain taxa, are not included.

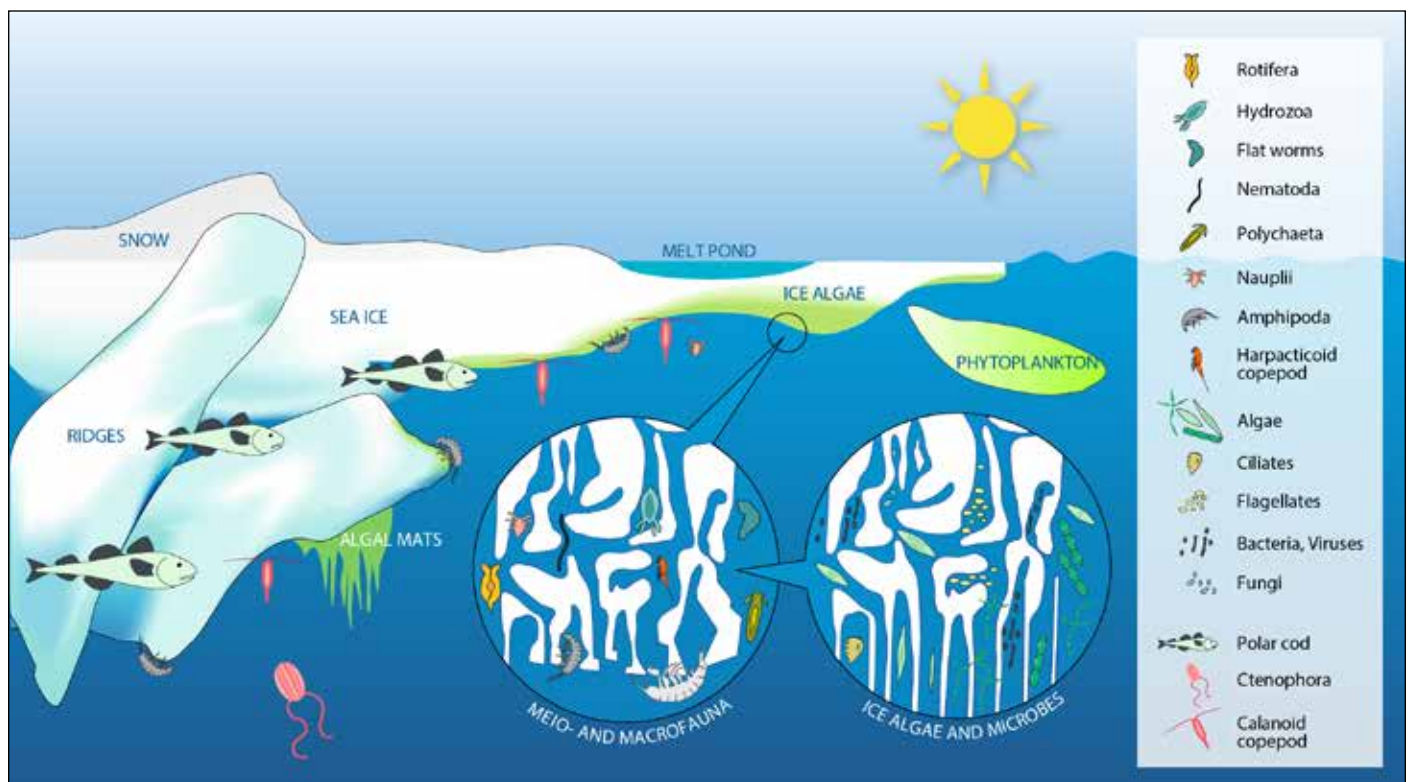


Figure 3.1.1 The Focal Ecosystem Components (FECs) (circles) in sea ice. Sea ice provides a wide range of microhabitats for diverse biota including microbes, single-celled eukaryotes (labelled algae), multicellular meiofauna, larger under-ice fauna (represented by amphipods), as well as polar cod (*Boreogadus saida*). Modified from Bluhm et al. (2017).

Box 3.1.1: Technical terms related to sea ice biota and plankton communities

Algae: phototrophic eukaryotes, especially those associated with surfaces ('ice algae')

Autotrophs: organisms that produce energy-rich organic compounds from inorganic molecules using an external energy source, either sunlight (phototrophy) or additional inorganic molecules (chemotrophy)

Bacteria and Archaea: the largest taxonomic groups of single-celled microbes lacking a nucleus.

Biological Carbon Pump: the mechanism by which carbon dioxide (CO₂) is sequestered to the deep sea. Phototrophs fix CO₂ into biomass and contribute to the biological carbon pump when they sink out of the surface ocean or are consumed by zooplankton that produce fecal pellets that sink out of the surface ocean. The effectiveness of the biological carbon pump is uncertain and relies on a dominance of microalgae.

Copiotrophs: heterotrophs that prefer environments rich in organic matter

Eukaryotes: organisms with a nucleus and other organelles (mitochondria, chloroplasts etc.), including plants, animals, fungi and protists

Flagellates: microbial eukaryotes that have whip-like tails called flagella. Most are either photosynthetic or predators of bacteria

Heterotrophs: organisms that use organic compounds as their energy source, including predators.

Macrofauna: animals visible to the naked eye, generally larger than 500 µm

Marine Alveolates (MALVs): diverse groups of mostly uncultured protists. MALVs mostly occur as parasites or parasitoids of other marine protists and zooplankton

Meiofauna: microscopic animals, between 62 µm and 500 µm in size

Meroplankton: animals that are planktonic for only part of their life cycle (usually larvae)

Microbes: microscopic organisms

Micro- (plankton, phytoplankton, flagellate, algae): microbes between 20 µm and 200 µm in size.

Mixotrophs: microbes that are both autotrophic and heterotrophic, including some Bacteria and Archaea, and eukaryotic microbes that can both photosynthesize and consume organic matter or other microbes

Nano- (plankton, phytoplankton, flagellate): microbes between 2 µm and 20 µm in size

Oligotrophs: microbes that prefer environments with low nutrient concentrations

Phytoplankton: phototrophic microbes that live in the water column

Photosynthesis: the process of producing energy-rich organic compounds from inorganic molecules using sunlight as an energy source

Phototrophs: organisms that photosynthesize

Pico- (plankton, phytoplankton, flagellate): organisms between 0.2 µm and 2 µm in size

Plankton: free-floating organisms that cannot swim against currents

Protists: single-celled microbial eukaryotes

Sympagic: ice-associated biota

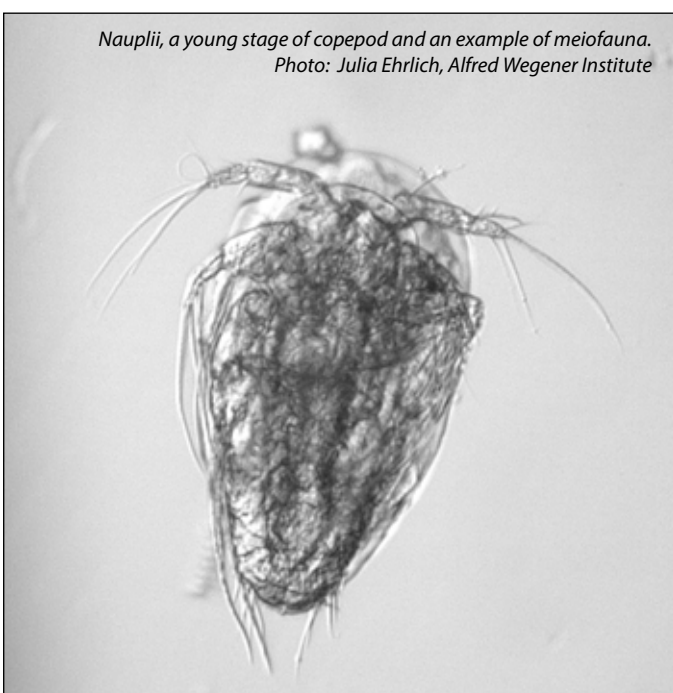
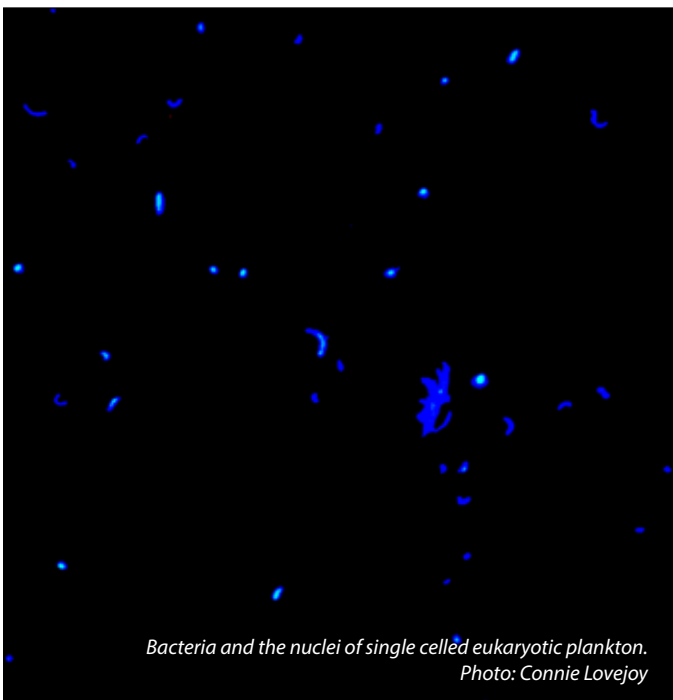
Ice sampling in the Canadian Beaufort Sea.
Photo: Michel Poulin, Canadian Museum of Nature



Bottom of ice core with algae.
Photo: Michel Poulin, Canadian Museum of Nature

Table 3.1.1. Current estimates of species richness and peak abundances of the four FECs reviewed in this chapter. OTU – operational taxonomic unit (approximately at the “genus” level in this analysis). Relative to the Arctic Marine Biodiversity Monitoring Plan (Gill et al. 2011), Bacteria and Archaea were included for consistency with the plankton FECs, while ice-associated fishes are covered in Chapter 3.4.

Taxon group (FEC)	Estimated number of species/OTUs	Bloom (peak) abundance	Key references
Bacteria and Archaea	> 120 at 95% similarity	> 210 cells m ⁻²	This chapter
Microalgae and other protists	1,276	< 109 cells m ⁻²	Philippe 2013; this chapter
Sympagic multicellular meiofauna	> 60	> 400,000 ind. m ⁻²	Bluhm et al. 2017; this chapter
Under-ice macrofauna	> 40 (amphipods: 6-17)	< 5,590 ind. m ⁻³ (I.A. Melnikov unpubl. data)	Arndt and Swadling 2006; this chapter



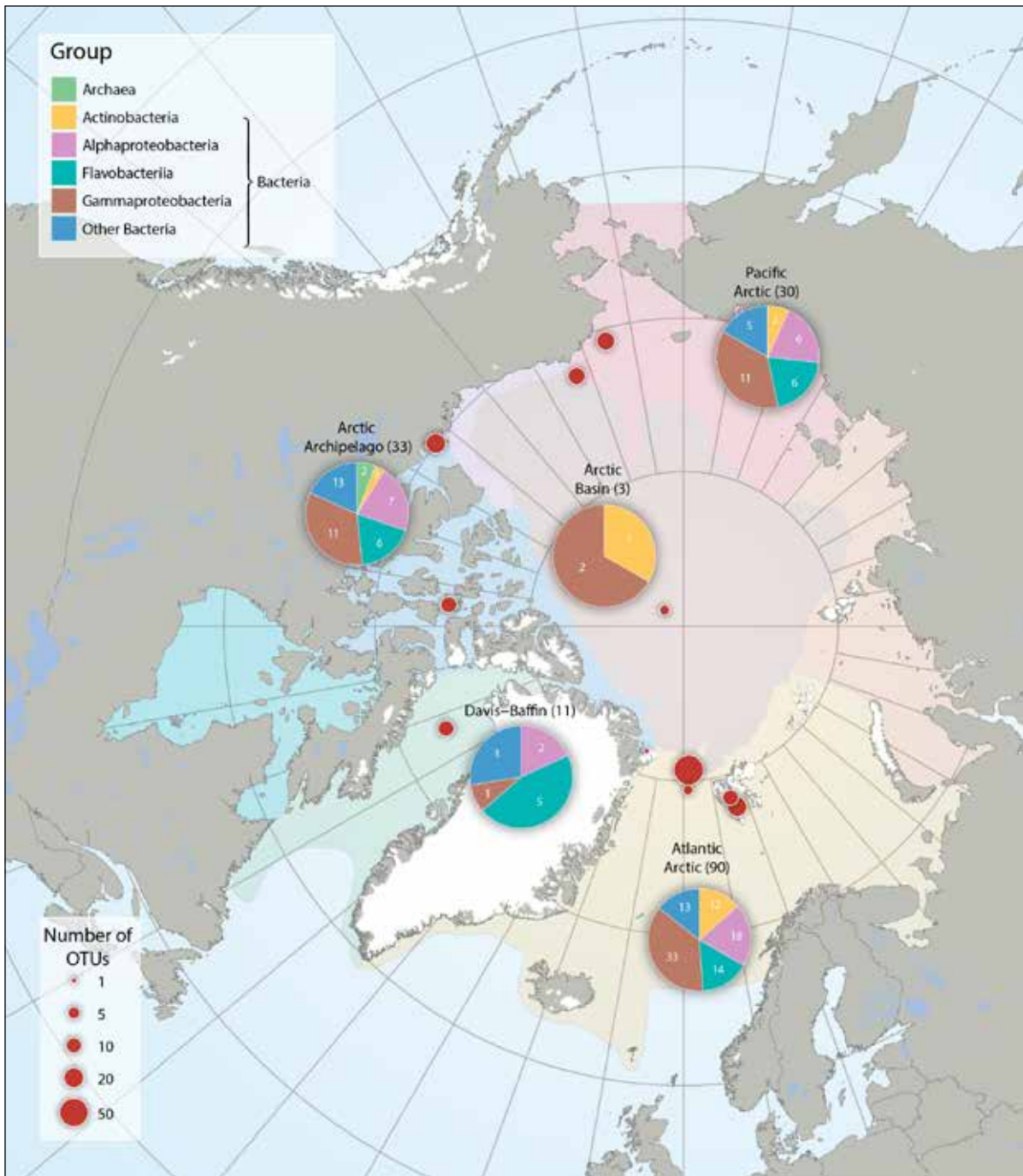


Figure 3.1.2 Bacteria and Archaea across five Arctic Marine Areas (AMAs) based on number of operational taxonomic units (OTUs), or molecular species. Composition of microbial groups, with respective numbers of OTUs (pie charts) and number of OTUs at sampling locations (red dots). Data aggregated by the CBMP Sea Ice Biota Expert Network. Data source: National Center for Biotechnology Information's (NCBI 2017) Nucleotide and PubMed databases.

3.1.2 Current monitoring

Sea ice biota is not monitored regularly at any location and our description is, therefore, based on synthesis of available data from a series of research projects. For each FEC, a brief background and description of data sources and analysis approach is provided. Note that the available historical data sources go back much further in time for morphologically identifiable taxa than for microbial diversity due to morphological studies preceding the development of DNA (or protein) sequencing methodology.

Bacteria and Archaea

Single-celled microorganisms belonging to the domains Bacteria and Archaea are highly diverse and make up a

large fraction of the biomass in the global ocean, including the sea ice habitat. These microbes are principal actors in carbon and nitrogen cycling, making nutrients available to other organisms. DNA (or protein) sequence similarity is the only reliable way to measure the taxonomic diversity of these communities. The most widely used marker for this purpose is found in the ribosome (the cellular structure used for protein synthesis), specifically the small subunit ribosomal RNA gene (16S rRNA gene for Bacteria and Archaea, 18S rRNA gene for Eukarya). Modern phylogenetics highlighting evolutionary relationships of microbes have mostly been developed during the last two decades (e.g., Junge et al. 2002, Collins et al. 2010, Deming 2010, Collins 2015). The relatively few studies available indicate that sea ice harbours an active microbial food web, which comprises high abundances of cold-adapted, halophile (thriving at high

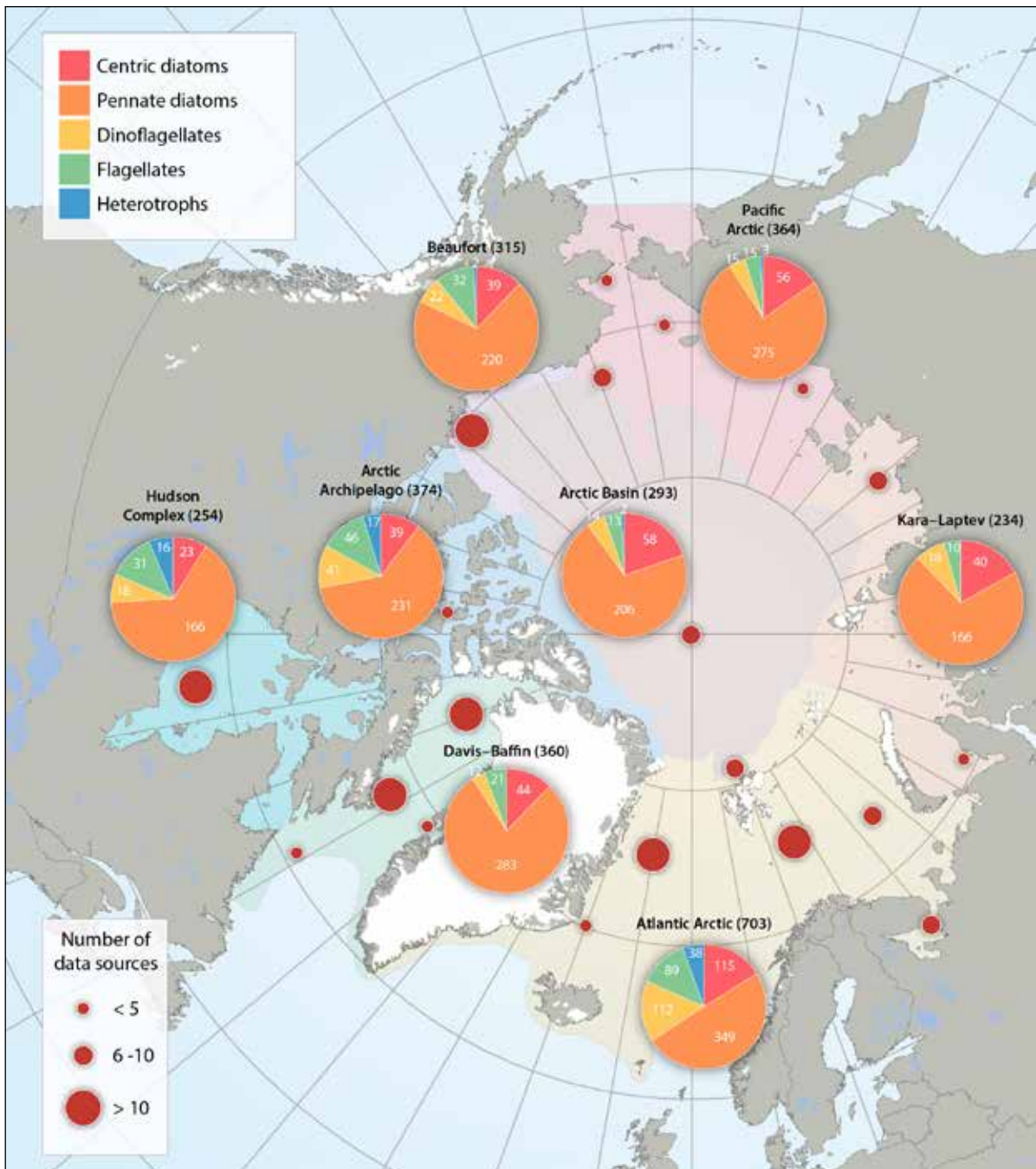


Figure 3.1.3 Numbers and taxonomic composition of five single-celled eukaryote groups for the regional divisions of the Arctic Marine Areas (AMAs, pie charts), as well as the number of data sources reviewed across the Arctic (red circles). Total number of taxa is given in parenthesis after each region. Flagellates include: chlorophytes, chrysophytes, cryptophytes, dictyochophytes, euglenids, prasinophytes, prymnesiophytes, raphidophytes, synurales, and xanthophytes, and- for practical purposes though not flagellates - cyanophytes. Heterotrophs include: choanoflagellates, kinetoplastea, incertae sedis. Updated from Poulin et al. (2011).

salt concentrations) bacteria that typically are most abundant in high concentrations of organic matter. Most of these sea ice-associated bacteria are heterotrophs utilizing organic substances released from the primary producers (autotrophic taxa) at the base of the food web. Patterns in bacterial community composition in Arctic sea ice differ from those of the underlying water column for both first-year (Collins et al. 2010) and multi-year ice (Bowman et al. 2012). Species richness in Bacteria and Archaea is often indicated by the number of operational taxonomic units (OTUs, or molecular species). Typical values of the number of OTUs in sea ice are about half of that in the underlying water column (Bowman et al. 2012). Bacterial abundances in sea ice, however, vary with season and at times exceed those of the water column by three orders of magnitude, when scaled to the brine channels they inhabit within the ice. Ice bacterial biomass

contributes substantially (a third or more) to particulate organic matter produced in sea ice (Gradinger et al. 1999). The ratio between bacterial and primary production in sea ice varies between 10 and 38% (Nguyen et al. 2011).

Synthesis of available data was performed by using searches conducted in the National Center for Biotechnology Information's (NCBI) Nucleotide and PubMed databases. Aligned DNA sequences were clustered into OTUs by maximum likelihood phylogenetic placement, a method that uses the most probable assignment to a reference phylogenetic tree showing the relationship among genetically identified units. The genetic resolution of OTUs in this analysis is approximately at the genus level.

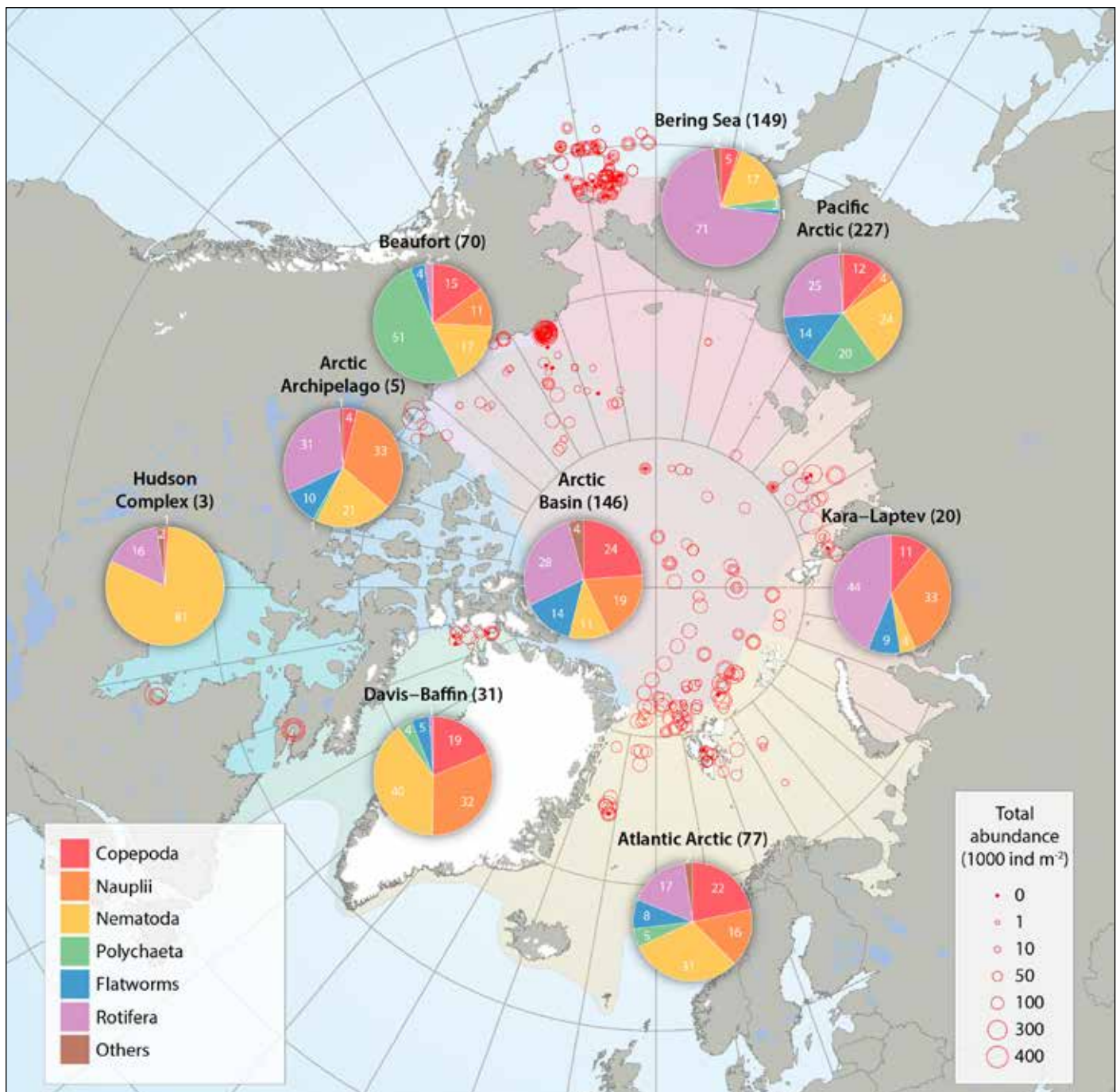


Figure 3.1.4 Sea ice meiofauna composition (pie charts) and total abundance (red circles) across the Arctic, compiled by the CBMP Sea Ice Biota Expert Network from 27 studies between 1979 and 2015. Scaled circles show total abundance per individual ice core while pie charts show average relative contribution by taxon per Arctic Marine Area (AMA). Number of ice cores for each AMA is given in parenthesis after region name. Note that studies were conducted at different times of the year, with the majority between March and August (see 3.1 Appendix). The category 'other' includes young stages of bristle worms (Polychaeta), mussel shrimps (Ostracoda), forams (Foraminifera), hydroid polyps (Cnidaria), comb jellies (Ctenophora), sea butterflies (Pteropoda), marine mites (Acari) and unidentified organisms.

Ice algae and other single-celled eukaryotes

Different types of biotic communities, namely surface, interior, bottom and sub-ice, have been described for Arctic sea ice based on their vertical occurrence and dominance in the ice matrix (Syvertsen 1991, Horner et al. 1992). However, the bulk of the standing stock and taxonomic diversity is mainly found in the bottom 10 cm of the ice matrix, generally in the lowermost 3–4 cm of the ice during springtime (Rózańska et al. 2009, Duarte et al. 2015, Leu et al. 2015). Often, ice algae and other protists are entrapped in newly formed sea ice during autumn and remain dormant over the winter (Gradinger and Ikävalko 1998, Rózańska et al. 2008). In the spring, increasing light levels trigger the first sign of

growth, which is often followed by rapid ice-algal growth in the dense network of brine pockets and channels in the bottom section of the ice matrix, sustained by nutrient-rich underlying water (von Quillfeldt et al. 2003, Rózańska et al. 2009). These ice algal communities provide early food for sympagic and pelagic herbivorous grazers such as copepod and amphipod crustaceans and contribute to carbon cycling (Michel et al. 2002, 2006, Tamelander et al. 2009, Søreide et al. 2010). The colonial centric diatom, *Melosira arctica*, can form 2 m long strands attached to the underside of the sea ice matrix in densely packed filamentous rows of cells hanging in the water column like curtains (Melnikov 1997, Boetius et al. 2013). This sub-ice community may serve as host substrate for epiphytic algae, such as the diatoms *Attheya*

septentrionalis, *Synedropsis hyperborea*, *Pseudogomphonema arcticum* (von Quillfeldt 1997, von Quillfeldt et al. 2003, Poulin et al. 2014). Ice algae can also form aggregates, which had already been observed during the Norwegian Fram Expedition in 1894 (Gran 1900, Nansen 1906) and the Russian North Pole drift ice station NP-23 in 1977 (Melnikov 1997). Such aggregates of ice-associated pennate diatoms have been found floating below the ice (Assmy et al. 2013) or in melt ponds (Lee et al. 2015). Aggregation of organic material from the ice may also promote the vertical export of material towards the benthos, thus strengthening ice-pelagic-benthic coupling (Tamelander et al. 2006, Renaud et al. 2007, Juul-Pedersen et al. 2008, Morata et al. 2011).

For a pan-Arctic assessment of biodiversity (here as species richness based on presence/absence), the first comprehensive assessments of this FEC from a few years ago (Poulin et al. 2011, Daniëls et al. 2013) have been updated with 134 documents and databases screened and mapped following the eight regional divisions of the Arctic Marine Areas (AMAs) (Gill et al. 2011; Fig. 3.1.4), including standardization of taxonomic names and nomenclature based on original literature. For the analysis of possible interannual trends in the ice algal community, we used a data set from the Arctic Basin, the area most consistently and frequently sampled (Melnikov et al. 2002, I.A. Melnikov unpubl. data). Multivariate community structure was analysed based on a presence-absence matrix of ice protists (autotrophs) from sections of ice cores taken from 1980 to 2013 and mostly identified to species level. The analysis is biased by the varying number of analysed cores taken annually ranging from 1 to 24, with ice thickness varying between 0.6 and 4.2 m, and including both first-year as well as multi-year sea ice. Sampling locations were confined within 74.9 to 90.0°N and 179.9°W to 176.6°E and exact locations varied among years, depending on the drift patterns of the ice stations.

Ice meiofauna

Arctic ice meiofauna is comprised of multi-cellular taxa including flatworms (of the phyla Acoelomorpha and Platyhelminthes), round worms (Nematoda), copepods (Crustacea), wheel animals (Rotifera), and less frequent taxa such as polyps (hydrozoan Cnidaria) and ribbon worms (Nemertea) (e.g., Marquardt et al. 2011, Bluhm et al. 2017). Single-celled ciliates are included in some studies, but are in others referred to as microfauna (< 62 µm; Carey 1985), and are not included in this synthesis. In addition to ice endemic species, both pelagic and benthic meiofauna species occur in sea ice and are included here. Ice meiofauna settle in sea ice through active migration, are scavenged during ice formation, disperse from multi-year ice, or are recruited from resting stages (Carey and Montagna 1982). Many ice meiofauna taxa graze on the abundant and highly concentrated ice algae early in the season (Grainger and Hsiao 1990), allowing for higher growth rates than under concurrent phytoplankton bloom concentrations (McConnell et al. 2012). Yet, meiofauna grazing does not appear to limit ice algal growth despite their seasonally high abundance: estimated ingestion rates by multicellular meiofauna are generally < 10% of ice algal biomass (Gradinger 1999, Michel et al. 2002). The small size of the brine channel system, mostly < 1 mm in a given channel, may restrict some meiofauna from exploiting niches with high ice algal growth (Krembs et al.

2000). This limitation rapidly changes during the onset of melting when brine channels become connected (Gradinger et al. 2010). Direct ingestion of ice-produced dissolved organic matter is an alternative feeding mode suggested for ice meiofaunal nematodes (Tchesunov and Riemann 1995). Meiofaunal predators, however, appear to be rare (Bluhm et al. 2007, Siebert et al. 2009).

Here, the CBMP Sea Ice Biota Expert Network synthesized 27 studies across the Arctic conducted between 1979 and 2015. This extensive effort includes several unpublished sources (see Appendix 3.1.1 and 3.1.2). These studies sampled landfast sea ice and offshore pack ice, both first-year and multi-year ice, using ice cores. Meiofauna abundances from ice cores were converted to individuals m⁻² of sea ice. Due to the generally low taxonomic resolution in the reviewed studies, ice meiofauna were grouped into: copepods (Copepoda), nauplii (i.e., young stages of copepods as well as other taxa with naupliar stages), round worms (Nematoda), bristle worms (Polychaeta) (mostly juveniles, but also the larval stage, trochophores), flatworms (Acoelomorpha and Platyhelminthes; these phyla have mostly been reported as one category), Rotifera and others. The category 'others' includes typically rare groups such as meroplanktonic larvae other than Polychaeta, mussel shrimps (Ostracoda), forams (Foraminifera), hydroid polyps (Cnidaria), comb jellies (Ctenophora), sea butterflies (Pteropoda), marine mites (Acari) and unidentified organisms. Percentage of total abundance for each group was calculated for each ice core, and these percentages were used for regional averages. Maximum available ice-core length was used in data analysis, but 50% of these cores included only the bottom 10 cm of the ice profile, 12% the bottom 5 cm, 10% the bottom 2 cm and 11% the entire ice profile. Data from 728 cores were used. In addition to showing composition and peak abundance ranges, the phenology of ice meiofauna is illustrated over the ice-covered season in data sets from landfast ice near Barrow, Alaska, and in drifting pack ice north of Svalbard.

Under-ice macrofauna

The most prominent members of the under-ice community typically include the gammarid amphipods *Apherusa glacialis*, *Gammarus wilkitzkii*, *Onisimus glacialis* and *O. nanseni*, as well as the polar cod and ice cod (Lønne and Gulliksen 1989, Gradinger and Bluhm 2004, Mecklenburg et al. 2011, Hop and Gjøsaeter 2013). All inhabit the under-ice realm for at least part of their lives (Gulliksen and Lønne 1991, Melnikov 1997, Poltermann et al. 2001). The amphipods have different feeding preferences and longevities, with *G. wilkitzkii* being the most predatory and long-lived, at six to seven years (Poltermann 2000, Beuchel and Lønne 2002). The ice-associated fishes primarily eat crustaceans including under-ice amphipods, copepods, hyperiid amphipods and mysids with proportions varying regionally (Lønne and Gulliksen 1989, Christiansen et al. 2012, Dalpadado et al. 2016). Dozens of other taxa, such as copepods, ctenophores and pteropods, also inhabit the under-ice realm (Arndt and Swadling 2006, Bluhm et al. 2017), but are not included here. Gelatinous zooplankton (ctenophores and jellyfish) have been observed at high densities just below the ice by remotely operated vehicles and scuba divers (Raskoff et al. 2005, 2010, Purcell et al. 2010, H. Hop unpubl. data), where they congregate in turbulence areas created by ridges.

This summary includes 47 data sources of under-ice amphipods published between 1977 and 2012. When available, the CBMP Sea Ice Biota Expert Network collected information on their abundance (individuals m^{-2} , or individuals m^{-3} that were converted to individuals m^{-2}) and biomass ($g\ m^{-2}$, wet weight). If abundance or biomass data were not available, presence/relative abundance information was included. Frequency of occurrence was calculated for regions across the Arctic using integrated data for all available years. Due to large variability, medians and median absolute deviations (MAD) were used to present abundance and biomass data.

The only available time-series of sympagic fauna is based on composite data of ice-amphipod abundance and biomass estimates from 1981 to 2012 for the Svalbard and Fram Strait region (Hop et al. 2013). Samples were obtained by scuba divers that collected amphipods quantitatively with electrical suction pumps under the sea ice (Lønne 1988, Lønne and Gulliksen 1991a, b, Hop and Pavlova 2008).

3.1.3 Status and trends of FECs

Bacteria and Archaea

Forty-five data sets in the NCBI Nucleotide database were analysed for the present synthesis. They included a total of 1,146 sequences of the target gene (small subunit ribosomal RNA) from Arctic sea ice. On average, these sequences consisted of 1,256 base pairs (i.e., the building blocks) and the mean number of sequences per study was 25 (median= 3). These sequences represented 120 bacterial and two archaeal OTUs, of which 95 (81% of sequences) were at the genus level and the remainders were not represented in the database or at higher taxonomic levels. The analysed data sets revealed different groups of species, with an overlap of only one third of the 43 OTUs found to occur in two or more studies.

The total diversity of Bacteria and Archaea found in sea ice spans the phylogenetic tree, but the dominant taxa are concentrated within the Gram-negative bacterial groups Gammaproteobacteria, Bacteroidetes, and to a lesser extent the Alphaproteobacteria (Fig. 3.1.2). Biodiversity was highly dominated by a few taxa: the five most common taxa represented 50% of all sequences in the dataset (*Pseudoalteromonas*, *Colwellia*, *Shewanella*, *Marinomonas* and *Pelagibacter*). There are no known bacterial or archaeal genera unique to sea ice, and at more refined taxonomic levels there is not enough information to determine to what extent microbes found in sea ice are endemic to the ice (Collins 2015).

Ice algae and other single-celled eukaryotes

The species richness of microalgae and other protists in sea ice is high. As with ice microbes, the inventory of these single-celled eukaryotes is incomplete, which makes assessment of temporal changes challenging. A few years ago, a first inventory found 1,027 single-celled eukaryotes inhabiting Arctic sea ice (Poulin et al. 2011, Daniëls et al. 2013). The present synthesis by the CBMP Sea Ice Biota Expert Network documented that increased effort still increases the inventory, which now includes more than

200 additional taxa for a total of 1,276 sympagic algae and other protists (Figure 3.1.3). Cyanobacteria (phototrophic Bacteria) and five supergroups of eukaryotes (cf. Adl et al. 2012) are present in Arctic sea ice (Poulin et al. 2011). Most of this sea ice biota inventory, however, consists of large diatom and dinoflagellate cells ($>20\ \mu m$) that are relatively easily identified through light microscopy (von Quillfeldt et al. 2003, Róžańska et al. 2009, Poulin et al. 2011). Large cells contributed 82% of the known pan-Arctic species numbers, with 82% for the Hudson Bay Complex and Atlantic Arctic, 83% for the Arctic Archipelago, 89% for the Beaufort Sea, 94% for Davis Strait-Baffin Bay, 95% for both the Pacific Arctic and Arctic Basin, and 96% for the Kara-Laptev. The highest inventory, and reporting effort, of sea ice microalgae and other protists has been recorded for the Atlantic Arctic, with an almost two-fold higher number of taxa (700) compared to the other seven regional divisions of the AMAs (Figure 3.1.3).

The Arctic Archipelago and Pacific Arctic had intermediate species richness (>350), whereas the lowest (<300) was reported for the Kara-Laptev Seas, the Hudson Bay Complex and the Arctic Basin. High research effort in the Atlantic Arctic also resulted in the identification of a significant contribution of 18% small-sized cells ($<20\ \mu m$), an otherwise morphologically poorly documented size group. During the algal bloom, the bottom ice communities are predominantly represented by colonial diatoms, e.g., *Nitzschia frigida* and *Fragilariopsis cylindrus*, while some solitary cells are also frequently encountered, e.g., *Cylindrotheca closterium* and *Navicula directa*. Pennate diatoms are the most abundant single-celled eukaryotes across the Arctic, contributing a low 50% in Atlantic Arctic to a high 79% in Davis Strait-Baffin Bay of the eukaryote community in sea ice (Figure 3.1.3).

Standard microscopy counts do not take into account the diversity of smaller mixotrophic and heterotrophic microbial eukaryotes in ice. Molecular techniques indicate these groups in ice may be as diverse as in the water column (Comeau et al., 2013).

Ice meiofauna

On a coarse taxonomic level, most meiofauna taxa occur rather consistently across the Arctic, although their proportions vary with region and season of sampling (Figure 3.1.4). Total abundance of meiofauna can be higher close to land compared to offshore locations. This is partly explained by the contribution of meroplankton, the frequently abundant larval stages of benthic organisms, and the fact that most studies there were conducted during spring. In offshore drift ice, the proportion of species of pelagic origin within the ice meiofauna is higher than in shallow areas where adults of taxa of benthic origin are also found (e.g., Friedrich and De Smet 2000). Regional comparisons are limited by differences in seasonal and taxonomic coverage, but available data indicate that rotifers, for example, dominate in some areas such as the Bering Sea in the Pacific Arctic and the Kara-Laptev. Rotifers can be abundant in these areas, although they are small and therefore contribute much less to the total in-ice meiofauna biomass than other taxa (Friedrich 1997). By comparison, nematodes dominate in Davis Strait-Baffin Bay, Hudson Bay Complex and the Greenland Sea—part of the Atlantic Arctic (Fig. 3.1.4). Copepods are reported in all regions

(although their composition may vary which we do not show here) and their nauplii cause large seasonal fluctuations in meiofauna abundance (Figure 3.1.5). Separating seasonal fluctuations from geographical differences is difficult due to the low number of studies, and because most studies take place during the spring when copepod nauplii are the most abundant. Nauplii, however, appear to be particularly common in the Atlantic-advective inflow area. In coastal fast ice of the Beaufort Sea, in turn, the positive influence of meroplanktonic stages of primarily Polychaeta and Mollusca on diversity and abundance during spring months has been documented (Nozais et al. 2001, Gradinger et al. 2009).

The few studies that provide identification of ice meiofauna taxa beyond the order level suggest nearly pan-Arctic distribution ranges for those taxa (examples shown in Bluhm et al. 2017). A few ice meiofauna species appear to be endemic to the ice, such as the hydroid polyp *Sympagohydra tuuli* and the nematode *Theristus melnikovi* (Riemann and Sime-Ngando 1997, Bluhm et al. 2007), although these taxa may have been overlooked in benthic habitats so far.

Macrofauna: under-ice amphipods

A handful of gammarid amphipod species are found in the under-ice habitat across the Arctic (Figure 3.1.6). *Apherusa glacialis* is the most frequent ice amphipod, which is likely related to its herbivorous feeding style and short, two-year life cycle in drift ice (Beuchel and Lønne 2002, Arndt et al. 2005). Though most abundant, this ice amphipod contributes little to the total under-ice amphipod biomass due to its small size (Figure 3.1.7). *Gammarus wilkitzkii* is also a frequently occurring ice-amphipod with circumpolar distribution. Due to its large size (5 cm as adults), *G. wilkitzkii* dominates the ice-amphipod biomass, but tends to occur in lower frequencies than *A. glacialis* (e.g., Hop and Pavlova 2008; Figure 3.1.7). This predatory and omnivorous crustacean preys on smaller ice amphipods, such as *A. glacialis* and *Onisimus glacialis*, as well as zooplankton and detritus (Poltermann 2001). *Gammarus wilkitzkii* is often associated with structurally complex multi-year sea ice, where it can frequently be found hiding in large brine channels and crevices (Hop et al. 2000). This synthesis, however, indicates that *G. wilkitzkii* also frequently inhabits

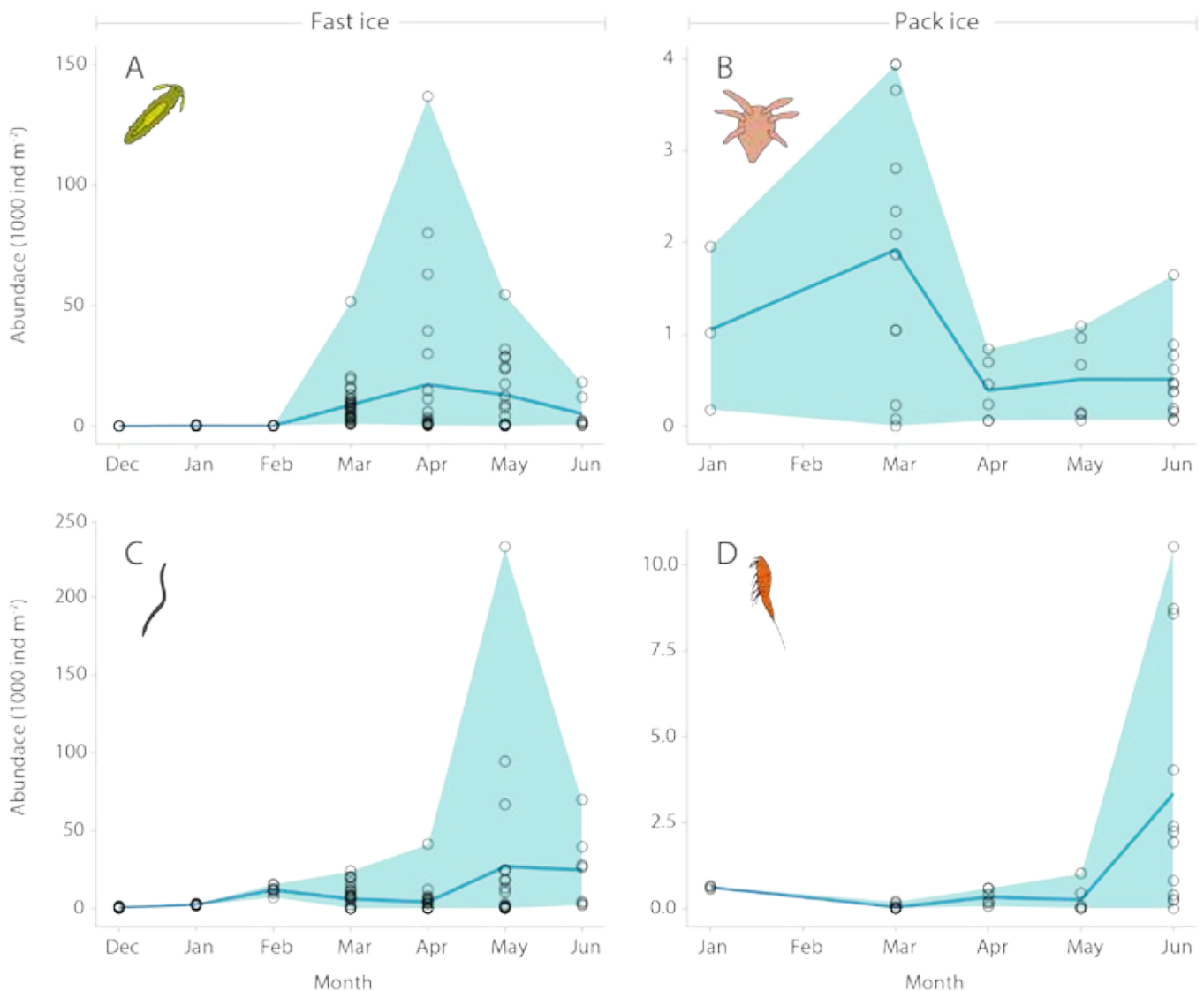


Figure 3.1.5 Seasonal abundance (1000 individuals m⁻²) of sea ice meiofauna at landfast sea ice (Barrow, 2005–2006, A and C) and pack ice (North of Svalbard, 2015, B and D). A and B show larval stages (polychaete juveniles and nauplii, respectively), while C and D show nematodes and harpacticoid copepods, respectively. Circles represent individual cores (n = 107 for A and C, and 39 for B and D), shading the extent of minimum as well as maximum values, and blue line indicates mean values.

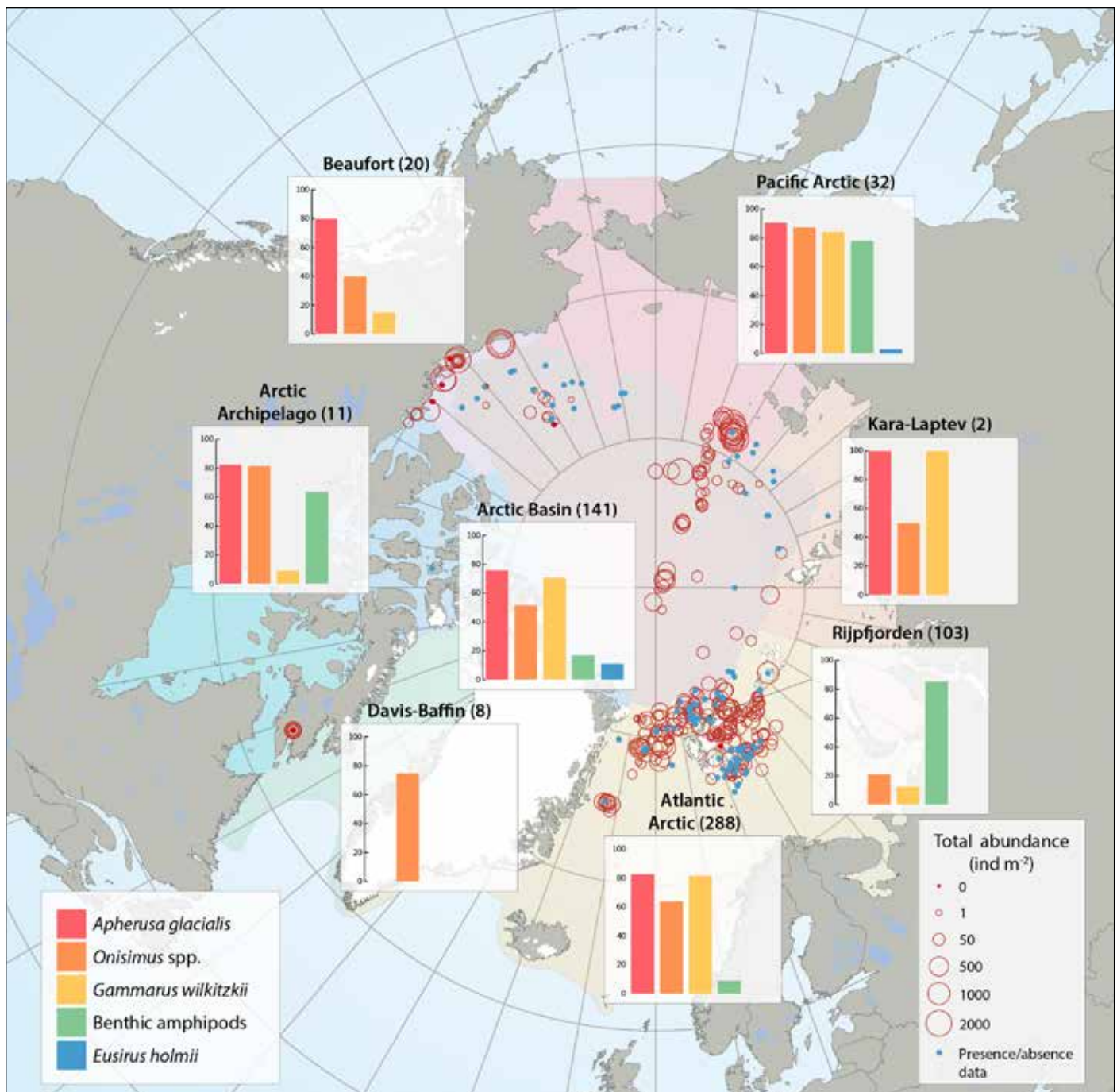


Figure 3.1.6 Sea ice amphipod (macrofauna) distribution and abundance across the Arctic aggregated from 47 sources between 1977 and 2012 by the CBMP Sea Ice Biota Expert Network. Bar graphs illustrate the frequency of occurrence (%) of amphipods in samples that contained at least one ice-associated amphipod. Red circles illustrate the total abundances of all ice-associated amphipods in quantitative samples (individuals m^{-2}) at locations of sampling for each Arctic Marine Area (AMA). Number of sampling efforts for each region is given in parenthesis after region name. Blue dots represent samples where only presence/absence data were available and where amphipods were present.

annual landfast and drift ice, although at lower frequencies than it occurs in the Arctic Basin and the East Siberian Shelf break of the Pacific Arctic (Figure 3.1.6). *Onisimus nanseni* and *O. glacialis* are difficult to distinguish from samples preserved in alcohol and therefore were not separated in most reviewed studies. Genetically, these species are also difficult to separate because of low genetic divergence (Ki et al. 2011). They occur frequently below sea ice but are generally much less abundant than *A. glacialis* and *G. wilkitzkii* (Hop and Pavlova 2008; Fig. 3.1.7). It is noteworthy that no under-ice amphipods were encountered on the Bering and Chukchi Seas and adjacent shelves of the Pacific Arctic, where some of the authors have done extensive sea ice work (R. Gradinger, K. Iken, B.A. Bluhm unpubl.). However, high amphipod abundances have been recorded on the shelf

of the East Siberian Sea as well as in the Beaufort Sea, with values an order of magnitude higher than those recorded in the Atlantic Arctic (Figs. 3.1.6, 3.1.7). High abundance values likely reflect large contributions of newly hatched juveniles and benthic amphipods.

Benthic amphipods are also occasionally encountered under sea ice, particularly over shallow water (e.g., Pike and Welch 1990, Gradinger and Bluhm 2010). Even though their distributions are related to distance to land and water depth, some benthic amphipods drift with sea ice across the Arctic Basin and are present in sea ice far from its origin (Figure 3.1.6). In Rijpfjorden, Northern Svalbard, the benthic amphipods *Anonyx* spp. utilize sea ice as a reproductive habitat during spring (Werner et al. 2004, Nygård et al. 2012).

Most frequently occurring benthic amphipods were *Anonyx* spp. (8% of all samples), *Metopa* spp. (8%), *Gammaracanthus loricatus* (4%), *Weyprechtia pinguis* (2%) and *Gammarus setosus* (2%).

Seasonality in the meiofauna community

Biological communities in the sea ice system exhibit strong seasonality linked to the annual cycle in both sea ice formation and light. Few studies, however, actually cover full seasonal cycles; here two examples of meiofaunal communities are given. Seasonal increase in meiofaunal abundances occurs during spring (Figure 3.1.5), linked to the increase in day light that facilitates the onset of the ice algal bloom, which consequently progresses temporally with increasing latitude (Leu et al. 2015). Nearshore fast ice typically harbours the highest densities of meiofauna during spring peaks in ice algal production (up to 250,000 ind. m⁻²; Nozais et al. 2001, Gradinger et al. 2009; Figure 3.1.5a, c), followed by density peaks observed in shelf pack ice (Gradinger 2009, Marquardt et al. 2011), with the lowest abundances in offshore drift ice and ice pressure ridges (<10,000 ind. m⁻²; Friedrich 1997, Gradinger et al. 2005, 2010, Schünemann and Werner 2005; Figure 3.1.5b, d). Different taxonomic groups show abundance peaks at different times.

For example, meroplanktonic polychaetes and copepod nauplii peak earlier during ice algal blooms (Figure 3.1.5a, b) than nematodes, which spend their entire life cycle in sea ice, and harpacticoid copepods peak even later (Figure 3.1.5c, d). Large variability in abundance indicates patchiness in the spatial distribution of meiofauna, which is related to ice properties, snow depth and sediment load in the ice, known as dirty sea ice (Nürnberg et al. 1994, Gradinger et al. 2009).

Interannual trends in ice algal community structure in the central Arctic Basin

Assessment of interannual changes of the ice-algal community in the central Arctic Basin is challenging, because of introduced biases due to variations in ice types, ice thickness, sampling date, region and number of ice cores collected. Keeping in mind this bias, species numbers recorded and community composition appear to have changed during three periods: early 1980s, late 1990s and the recent period of 2005-2013 (Fig. 3.1.8). This involved a major decrease from 50-70 species in 1980-2006 to <30 in recent years. However, the sampling effort was much greater in the earlier decades, which likely resulted in detection of more species. Community structure also

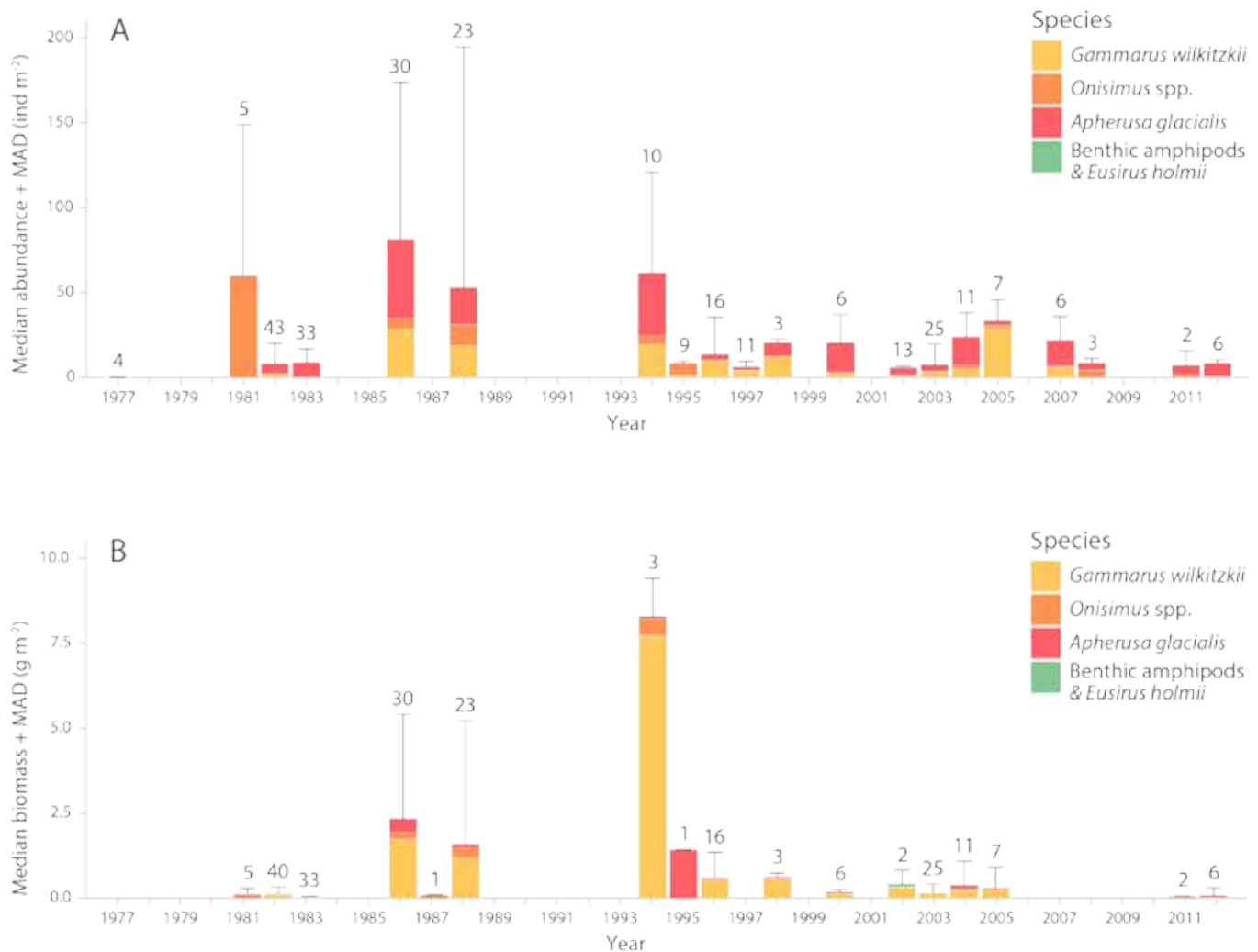


Figure 3.1.7 Multi-decadal time series of A) abundance (individuals m⁻²) and B) biomass (g wet weight m⁻²) of ice amphipods from 1977 to 2012 across the Arctic. Bars and error bars indicate median and median absolute deviation (MAD) values for each year, respectively. Numbers above bars represent number of sampling efforts (n). Modified from Hop et al. (2013).

appears to have shifted from the 1980s to the 2010s (Figure 3.1.8), although it, too, is somewhat influenced by sampling effort. Analysis of similarity¹ suggests that the sampling period had the strongest influence on the similarity of algal community structure followed by ice type, which was moderately influential, with less effect of region or month of sampling. The top characteristic sympagic species in the 1980s, the period where multi-year ice was more abundant than in later decades, included *Thalassiosira nordenskiöldii*, *Fragilariopsis oceanica*, *Chlamydomonas nivalis*, *Trochiscia cryophila* and *Nitzschia* spp. The cores from the 1990s were characterized by *Groenlandiella brevispina*, *Cylindrotheca closterium*, *Fragilariopsis cylindrus* and *Navicula vanhoeffenii*. After the year 2000 when perennial ice declined strongly, mostly *Nitzschia frigida*, *N. polaris*, *F. cylindrus*, *F. oceanica* and *Navicula transitans* characterized the community. For decades, the dominant multi-year ice in the central Arctic Ocean was a relatively stable ecological system with a rather consistent species composition of flora and fauna (Melnikov 1997). The ice thickness of the multi-year pack ice was maintained in equilibrium, with summer melt of the upper layers of ice from above and compensating winter ice growth from below. During the early period of observation (1975–1981), pennate diatoms dominated (56 species) in multi-year ice, while centric diatoms and dinoflagellates were species poor. Dinoflagellate species increased after the mid-1990s despite lower sampling effort, while diatom species numbers (in particular pennate form) declined. In conclusion, the results are not unequivocal, but provide some evidence that ice algal communities have undergone some changes in taxonomic composition in multi-year sea ice.

Ice amphipods around Svalbard: decadal trends

Under-ice amphipod abundance demonstrates large seasonal and interannual variability, partly due to the patchiness of their habitats and heterogeneous distribution below ice floes (Lønne and Gulliksen 1991a, b, Werner and Gradinger 2002; Figure 3.1.7). Despite the variability, a decline in ice-amphipod abundance and biomass is apparent, from high values until mid-1990s and to lower values during recent years, and very low values after 2010 (Figure 3.1.7). This trend is equally evident from regional observations: in the 1990s, the area north of Svalbard was dominated by multi-year sea ice and quantitative ice-amphipod sampling was possible to conduct at most ice stations. After mid-2000, the amount of multi-year ice in the Arctic Ocean including the area north of Svalbard declined dramatically (Polyakov et al. 2012, Perovich et al. 2015), and quantitative collections of ice amphipods are no longer possible at many ice stations in that area because of extremely low abundances of these crustaceans, with typical catches of < 1 ind. m⁻² (H. Hop pers. obs.).

Ice-amphipod abundance seems to be connected to the amount of ice structures and the age of the ice. As shown, with decreasing extent of multi-year sea ice, abundance and biomass of ice amphipods have declined in the Eurasian Arctic. The same trend has been independently observed in the central Arctic (I.A. Melnikov pers. comm.). Multi-year sea ice is described as preferred habitat of the long-lived *G. wilkitzkii* (Lønne and Gulliksen 1991b), although this

species also occurs in other ice types, as well as planktonic or benthic habitats for some parts of the summer season (Poltermann 1998, Werner et al. 1999; Fig. 3.1.6). Interestingly, some researchers have reported *A. glacialis* deep (100–2000 m) in the Arctic Basin (Berge et al. 2012), indicating that these organisms are capable of inhabiting the water column in absence of sea ice, at least for part of the year. Future projections for the under-ice associated fauna are uncertain. The multi-year ice ecosystem is capable of supporting a relatively constant species composition of permanent ice biota, while the species composition of the biota of the seasonal sea ice ecosystem largely depends on the biota of the water column for recruitment. In the current sea ice cover situation in the Arctic, these two situations co-exist.

3.1.4 Drivers of observed trends

Abundance and biomass, diversity and distribution of sea ice biota are highly variable in space and time. This variability can largely be attributed to the physical and chemical conditions in and under the sea ice. Light availability, ice and snow conditions, ice temperature, brine salinity, nutrient concentrations (for primary producers), carbon sources (for heterotrophic Bacteria and Archaea) or general food availability (for heterotrophic eukaryotes) are among the main drivers that explain the horizontal and vertical patchiness of sympagic biota. Biodiversity studies should therefore provide auxiliary information for at least the aforementioned variables. At a minimum, ice temperature as well as bulk salinity of melted samples should be determined. On larger spatial scales, ice (extent, thickness, type) and snow cover data are desirable. Below we describe briefly the influences of critical environmental factors on ice biota under the current conditions.

Light conditions under the ice are modulated by day length (i.e., seasonally) as well as by snow depth, ice thickness and particle content in the ice (Leu et al. 2015). During the melt season, ponds develop on top of the ice and increase light transmission from 5–15% to 40–70% (Ehn et al. 2011). A continuation of the observed decline in sea ice extent and thickness will increase the amount of light penetrating into the Arctic Ocean, which will further enhance melting and alter the upper ocean ecosystem (Nicolaus et al. 2012). Thinner ice may facilitate higher production and biomass of ice algae in the Arctic Ocean, but because some areas will have less ice and stratification of the upper water column may increase, the net effect for the Arctic is uncertain (Barber et al. 2015, Leu et al. 2015).

Ice properties, such as thickness, structure, drift, age and stage of freezing/melting, largely influence the seasonal occurrence of sea ice biota (Barber et al. 2015). **Ice and snow properties** as well as seasonal development of melt ponds on the ice are important for the energy budget of sea ice (Hudson et al. 2013). On larger scales, the ice extent, ice type (first-year versus multi-year ice, landfast ice versus drift ice) and ridging influence the abundance and distribution of sea ice biota. Snow layer thickness and duration on top of the ice are important for light transmission and onset of the primary production of ice algae, since snow blocks out to > 80% of the radiation whereas bare ice reflects < 70% and ponded ice < 40% (Gerland et al. 2007).

¹ Analysis of similarity (ANOSIM) was done in the software package PRIMER (Clarke, K.R., Gorley RN (2006) PRIMER v6: user manual/tutorial PRIMER-E Ltd, Plymouth)

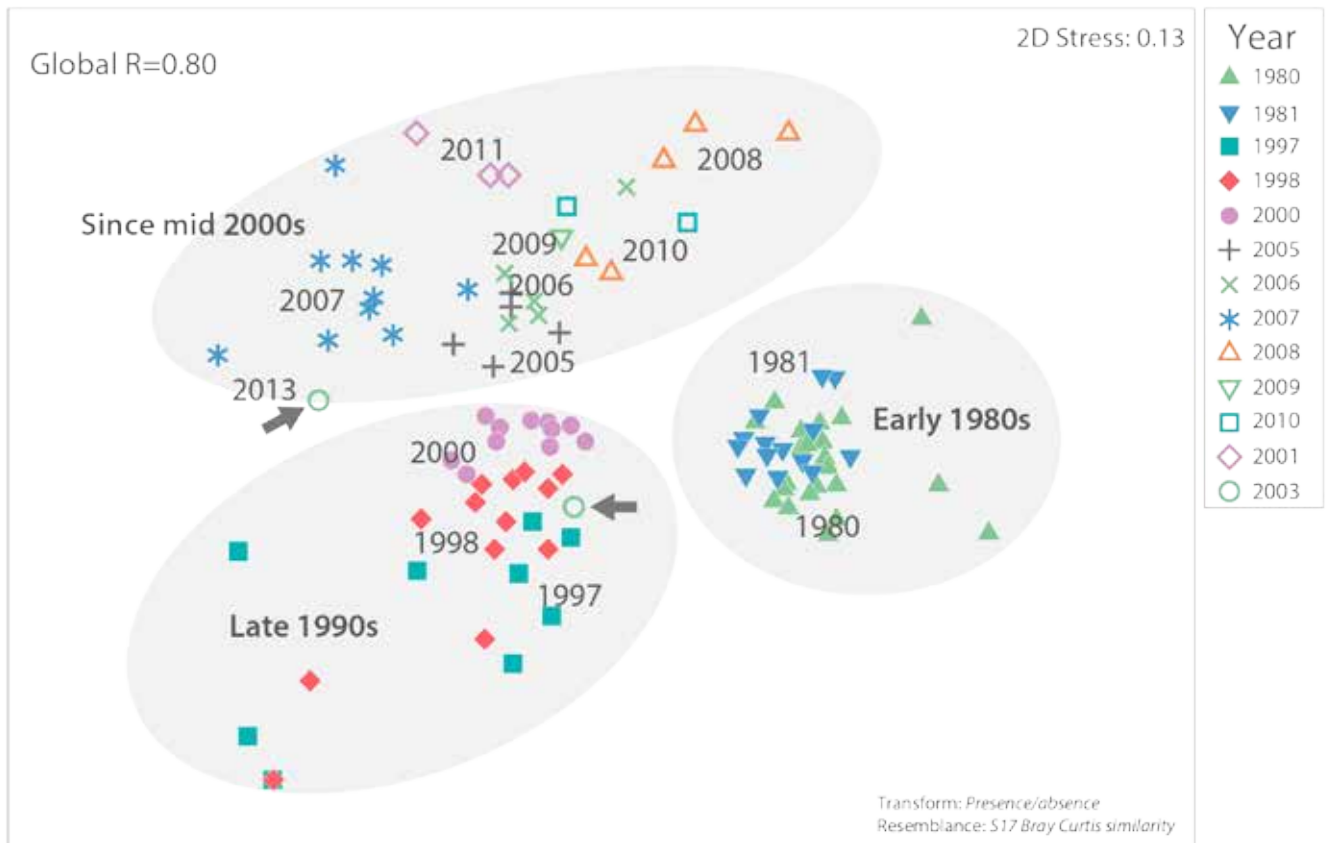


Figure 3.1.8 Ice algal community similarity of central Russian Arctic drifting stations from the 1980s to the 2010s based on unpublished data by I.A. Melnikov, Shirshov Institute of Oceanology. The closer two samples (symbols) are to each other in this multi-dimensional scaling plot, the more similar their algal communities were, based on presence/absence of algal species. Samples from the same year tend to be similar and group together on the plot, with some exceptions. Dispersion across the plot suggests that community structure has changed over the decades, although sampling locations in the central Arctic have also shifted, thus introducing bias. An analysis of similarity (PRIMER version 6) with a high Global $R=0.80$ indicates strong community difference among decades (global $R=0$ indicates no difference, $R=1$ indicates complete dissimilarity). Regional differences were low (global $R=0.26$) and difference by ice type moderate (global $R=0.38$). Grey arrows point to the very different and only two samples from 2013.

Spatial scales in the **ice structure** relevant for ice biota range from the size of a brine channel to the extent of the pan-Arctic ice cover. At small scales, the sea ice brine channel network with dimensions $< 1 \mu\text{m}$ to several mm, depending on temperature, influences biotic distributions (Krembs et al. 2000; Figure 3.1.1). Sea-ice pressure ridges provide niches where larger biota, including fishes, find refuge from predatory vertebrates (Hop et al. 2000, Gradinger and Bluhm 2004). In areas with multi-year ice floes, sea ice fauna can complete their life cycles in the ice habitat, allowing for the evolution of sea-ice endemic taxa (Arndt and Swadling 2006). In coastal Arctic fast ice, however, ice-endemic fauna appears to be sparser due to the habitat loss during the ice-free period.

Temperature, salinity and inhabitable space within sea ice are closely related (Mundy et al. 2011). Temperatures in the sea ice decrease from the ice-water towards the ice-snow interface, with concurrent decrease in brine volume and increase in brine salinity (Ehn et al. 2011). Temperature and brine salinity are similar to open water conditions near the sea water-ice interface. The coldest ice ($< -10^\circ\text{C}$) and highest brine salinities ($> 100 \text{ psu}$) occur near the snow-ice interface of Arctic multi-year ice floes; this ice type with extreme salinity conditions has been decreasing during the last decades. Very low salinities (1 to 2 psu, near freshwater

conditions) are found in melt ponds and the upper part of melting ice floes, and a thin meltwater layer of 30 to 50 cm brackish water (salinity 5 to 25 psu) typically develops below the ice during early summer (Hop et al. 2011). Melt ponds with variable salinity conditions have become more common and may occur for a longer time during the year. They harbour characteristic biota depending on their salinity (Lee et al. 2011). Adaptations to low temperatures and high and variable brine salinities are already prerequisites for the survival of sympagic organisms in sea ice and influence their biodiversity (Gradinger and Schnack-Schiel 1998). Very low salinities are only tolerated by few marine taxa, but ice amphipods show low osmotic response to hyposmotic stress indicating that they are tolerant to salinity fluctuations in melting sea ice environment (e.g., Aarset and Aunaas 1987). Riverine influence also reduces the salinity so that typical brackish-water (rather than marine) species thrive in some coastal ice areas when the ice is formed (von Quillfeldt et al. 2003).

Water depth and distance from land affect the community types recorded in sea ice. The presence of a large number of typically neritic (shallow water) species and freshwater species (e.g., *Asterionella formosa* and *Tabellaria flocculosa*) indicates a coastal formation of the ice (von Quillfeldt et al. 2003). Comeau et al. (2013) also found differences in

the microbial flagellates in landfast versus drift ice. Water depth and distance from land also affect the contribution of benthic taxa to the under-ice habitat (von Quillfeldt et al. 2003, Nygård et al. 2012, Bluhm et al. 2017; Figure 3.1.4, 3.1.6). Some of the fauna associated with drifting sea ice may also stay in shallow benthic areas during the ice-free season (Poltermann 1998). The temporary ice fauna, which may include larvae and juveniles of benthic taxa, can drift with sea ice far from shallow regions and increase the diversity and biomass of sea ice biota, although such organisms are most frequently found nearshore.

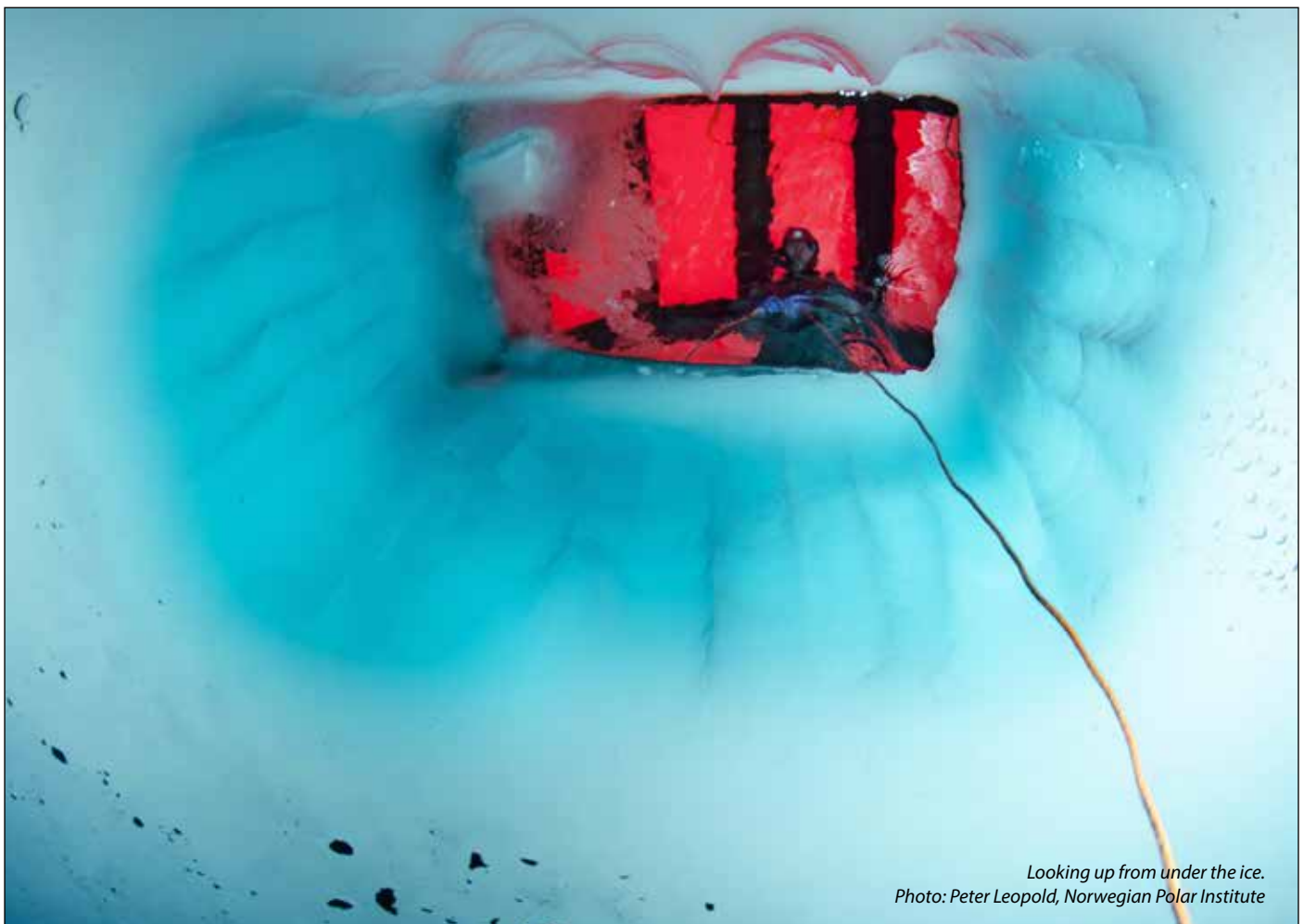
Nutrient concentrations available to sea ice biota are primarily a function of three factors: (1) nutrient concentrations in the ice and underlying water masses after the winter; (2) nutrients supplied by advection; and (3) biological uptake and remineralization processes (Gradinger 2009). Nutrient concentrations in surface water of a given region thus constitute a reservoir for ice algal growth (Tremblay et al. 2011). Accumulation of high ice-algal biomass (measured as chlorophyll *a*) within sea ice cannot be explained by the initial nutrient concentrations during ice formation alone, which are typically ~30% of surface water concentrations (Gradinger and Ikävalko 1998). Rather, advection of underlying, nutrient-rich water or upwelling is required to achieve high accumulation of ice algae. Upwelling of nutrient-rich water along the shelf break towards surface water layers has become more common in parts of the Arctic as ice retreats and can result in increased nutrient supplies supporting algal blooms (Carmack and Chapman 2003, Tremblay et al. 2011). Autumn blooms have also become more common through this process (Ardyna et

al. 2014). Continued supply of nutrients can result in a thick layer of bottom ice algae, particularly in the shallow region of the Laptev Sea and the shelf break in the western sector of the Canadian Arctic Archipelago (Boetius et al. 2013).

Several of the above described environmental variables are currently changing in the Arctic. Sea ice extent and thickness have declined, and, with this change, the light regime is changing. Thinner ice, or more leads in the ice, result in more light available for ice algae and under-ice blooms, and therefore the potential for higher production (Arrigo et al. 2011, 2012), provided that nutrients are available and snow thickness does not increase substantially. Other processes may counteract increased algal production including the shorter ice-covered period, less extensive ice extent as well as increased stratification through increased freshwater content resulting in diminished vertical mixing, as for example in the Canada Basin (Tremblay et al. 2015).

3.1.5 Knowledge and monitoring gaps

No monitoring program currently exists for sea ice biota, and the figures presented here are based on amalgamated data collected by many different researchers. Various research groups around the Arctic, however, have regular field activities involving select sampling of one or several FECs as part of short-term funded projects. The accumulated knowledge base in this chapter can serve as a baseline for monitoring of sea ice biota. However, monitoring requires coordinated plans for sampling at set locations, with consistent sampling and analyses to ensure comparability



Looking up from under the ice.
Photo: Peter Leopold, Norwegian Polar Institute

(Gill et al. 2011). For sea ice, standardized sampling techniques have for example been summarized by Eicken et al. (2009, 2014) and Miller et al. (2015). Proper monitoring requires seasonal and annual field campaigns as well as sufficient, long-term financial support.

Most (but not all) sea ice sampling for ice biota living *within* the brine channels has been done using ice cores (methods described for example in Gradinger and Bluhm 2009). The thickness of the ice sections studied in this synthesis, however, showed high variation, depending on the goals of each study, time constraints and ambient ice thickness to name a few, resulting in different thickness horizons sampled. Often the bottom 0-4 cm or 0-10 cm were sampled (with 0 cm representing the ice-water interface), sometimes the bottom 20-30 cm and occasionally whole cores. Here, a recommendation is given to sample (at least) the bottom 10 cm of ice cores (which can be split into the lowermost 3-4 cm bottom ice and the next 6-7 cm of the core), because the bottom 10 cm often includes the majority of the biomass and abundance of ice biota (~65 % of ice meiofauna, up to 95% for algae based on the here compiled data sets). The CBMP Sea Ice Biota Expert Network also recommends the 10-30 cm section be included (separately) where feasible, as an average 12% of the meiofauna have been observed in this ice section. Microbes, particularly bacteria, are distributed ubiquitously throughout the ice column and are generally sampled in 10 -cm increments using sterile procedures to avoid contaminating the ice cores (e.g., Collins et al. 2010). Ice algal communities and biomass (chlorophyll *a*) are concentrated in the bottom few centimeters, but have in some studies been determined in 20 cm sections up to the surface of the ice (e.g., Mundy et al. 2011). The need for sampling the entire ice column will depend on project goals, which may also include modelling aspects of biota in sea ice (Duarte et al. 2015).

Under-ice sampling has been more variable in approach. Regularly used tools have included (1) SCUBA-operated suction pumps (Lønne 1988), (2) under-ice *in situ* or surface-operated still photos (Mundy et al. 2007), (3) video in a fixed location or video transects (SCUBA diver or ROV operated) (Gradinger and Bluhm 2004), (4) under-ice traps (Nygård et al. 2012) and (5) under-ice trawl nets (David et al. 2016; approaches summarized by Gradinger and Bluhm 2009). The most quantitative samples appear to be based on SCUBA-operated sampling of squares with electrical suction pump (Hop et al. 2000) and the under-ice trawl net SUIT (van Franeker et al. 2009), as well as imagery with sufficient resolution.

In terms of seasonal and annual sampling at selected stations, the most frequently sampled locations (and ice types) in the past have included: (1) Central Arctic pack ice during Russian ice drifting stations, historically in multi-year sea ice and more recently increasingly in first-year ice; (2) Barrow area, landfast ice; (3) Resolute Bay area, landfast ice, and; (4) Svalbard fjords and offshore pack ice (Figure 3.1.3, 3.1.4, 3.1.6). Not all of these locations, however, may be the most promising locations to implement monitoring at, because both the ice cover and research arenas are changing rapidly. The central Arctic Russian ice-drift stations are no longer regular events because ice conditions have become less stable. The ice camp Barneo near the North Pole, however, is still active, though partly used as a tourist location. The use of Resolute



Dive photographer.
Photo: Peter Leopold, Norwegian Polar Institute

Bay facility may be shifting towards the newly constructed Canadian High Arctic Research Station (CHARS) in Cambridge Bay planned to open in 2017. However, Resolute Bay offers better conditions for sampling of Arctic ice biota based on the higher diversity of sea ice organisms at this more northern location, combined with access to a laboratory run by the Canadian Polar Continental Shelf Program. Thus, the Resolute station should be maintained as a Canadian monitoring site for sea ice biota. In Greenland, new research activities and facilities may provide opportunities to monitor ice biota in the future at Station Nord (north Greenland), Zackenberg Station (northeast Greenland) or Arctic Station (west Greenland). At Svalbard, much recent sampling has focused on fast ice in fjords, with seasonal sampling in e.g., Billefjorden. Norwegian research cruises will likely continue in the areas north of Svalbard and in the Arctic Ocean, with possibilities to incorporate monitoring elements in their sampling programs.

Regarding the choice of taxa, communities or habitats to monitor, the studies reviewed have usually focused either on a sub-habitat (e.g., ice biota inside brine channels) or on a taxonomic group (e.g., ice meiofauna), a particular method (e.g., morphological taxonomy or genetic analysis), or a combination of the three. Ice biota has rarely been studied as a whole at a given location and time period. The Russian ice-drift studies have likely been the most extensive and comprehensive studies (Melnikov 1997), and there has also been coordinated sampling of ice biota and sea ice physics at some locations in Arctic Canada and Alaska (e.g., Ehn et al.

2011, Hop et al. 2011, Mundy et al. 2011), and more recently during the N-ICE2015 campaign by the Norwegian Polar Institute to the Arctic Ocean. Indicator taxa are sometimes useful and the following could be suitable for monitoring: (1) the arborescent colonial endemic *Nitzschia frigida*, which regularly occurs in bottom sea ice and has been recorded all across the Arctic (Róžańska et al. 2009, Poulin et al. 2011); (2) the diatom *Melosira arctica* based on its ability to grow to long curtains under the ice under favourable conditions; (3) the under-ice amphipod *Gammarus wilkitzkii* due to its association with multi-year ice (although certainly not exclusively, as this synthesis demonstrates). This species may be gradually replaced by the more pelagic, but also ice-associated amphipod *Eusirus holmi*, which is of similar large size as adult. Both amphipod species should therefore be monitored, since changes in their relative abundance may reflect changes in sea ice conditions.

Main challenges for monitoring include the relatively low number of people working on sea ice biota and the loss of taxonomic expertise for groups such as ice algae and other protists, but also ice-associated fauna (e.g., meiofauna and ice-associated zooplankton). Another great challenge in attempting to monitor sea ice biota is the large variability of the dynamic sea ice habitat. Ice biota composition and abundance are, as detailed above, highly dependent upon light availability (modulated by day length, ice and snow thickness, sediments in ice, etc.), nutrient availability, temperature, salinity and location. These factors modify the habitat seasonally, even in the same place or the same ice floe. This variability, in combination with historic variability in sampling approach and timing, obscure potential temporal trends. Thus, actual changes in ice biota diversity and community structure need to be substantial enough to rise beyond the existing variability in order to be detected.



Eusirus holmi.
Photo: Peter Leopold, Norwegian Polar Institute

3.1.6 Conclusions and key findings

Temporal trends in sea ice biota diversity and/or abundance/biomass are very challenging to detect for two main reasons: the large natural variability within the sea ice system and the lack of systematic and consistent sea ice biota monitoring. The data sets aggregated in this synthesis suggest that changes in community structure of ice algae have occurred in the central Arctic since the 1980s, although this suspected change is coincident with a shift in the region sampled and decreased sampling effort. Over a similar period, ice amphipod abundance and biomass appear to have declined in at least the Svalbard region and perhaps elsewhere in the Arctic. Sea ice biota in general, however, is able to cope with extreme environmental conditions inherent to their habitat in terms of large variations in temperature and salinity, nutrient and space limitations and the ephemeral nature of the habitat. Regular ice biota sampling of the four FECs analysed here should be conducted in the future.

Key findings are:

- Sea ice is a species-rich habitat.
- Inventories of sea ice biota are incomplete.
- Many sea ice biota taxa are widespread across the Arctic ice cover.
- Sea ice houses some species endemic to the Arctic and species endemic to sea ice. Other taxa occur more widely.
- The ice biota generally copes with extreme conditions, although little is known about the tolerance limits and preferences of individual species in this habitat.
- Sea ice algal community structure has possibly changed in the central Arctic between the 1980s and 2010s. Identified shifts in community structure in decadal time series are confounded by shifts in sampling region and effort. Simultaneously, this shift occurred when ice conditions changed, i.e. both multi-year sea ice and ice extent declined.
- Ice amphipod abundance and biomass have declined in the Svalbard area since the 1980s. Amphipods appear to have been more abundant in the late 1970s to mid-1990s than afterwards.
- The occurrence and distribution of ice biota is highly variable in time and space related to a suite of environmental conditions. Consequently, monitoring the biota in this variable habitat is challenging.
- Regions with most frequent or consistent sampling over time (though for different FECs) include the central Arctic, Svalbard, the Barrow, Alaska area and the Canadian Arctic. New sites are evolving in Greenland. These locations are recommended for monitoring ice biota in the future.
- Consistent methodology is required for monitoring of ice biota. Available protocols need to be more widely implemented for monitoring. Monitoring should be standardized with regard to gear, collections, timing, sample preservation and processing, storage, and data management. A central receiving place as well as long-term funding for monitoring should be considered. Data should be deposited in existing databases and made available to researchers and beyond.

Appendix 3.1.1: Meiofauna References

Reference	Title	Authors	Journal	Pub. year	Volume	Pages	Place	url	doi	Temporal coverage
BEST 2008	Bering Sea Ecosystem survey 2008	Bluhm B.A. & Gradinger R.R	unpub.							2008
BEST 2009	Bering Sea Ecosystem survey 2009	Bluhm B.A. & Gradinger R.R	unpub.							2009
BEST 2010	Bering Sea Ecosystem survey 2010	Bluhm B.A. & Gradinger R.R	unpub.							2010
Bluhm & Gradinger unpubl., 2005	Barrow seasonal meiofauna study 2005	Bluhm B.A. & Gradinger R.R	unpub.							2005-2006
Bluhm & Gradinger unpubl., 2007	Barrow seasonal meiofauna study 2007	Bluhm B.A. & Gradinger R.R	unpub.							2007
Carey & Montagna 1982	Arctic sea ice fauna assemblage: first approach to description and source of the underice meiofauna	Carey, A. G. & Montagna, P. A.	Mar. Ecol. Prog. Ser.	1982	8	1-8		www.int-res.com/articles/meps/8/m008p001.pdf		1979
Friedrich 1997	Ökologische Untersuchungen zur Fauna des arktischen Meerereises = Ecological investigations on the fauna of the Arctic sea-ice	Friedrich, C.	Berichte zur Polarforschung (Reports on Polar Research)	1997		211	Bremerhaven, Alfred Wegener Institute for Polar and Marine Research	http://epic.awi.de/26424/		1993-1994
Friedrich & De Smet 2000	The rotifer fauna of arctic sea ice from the Barents Sea, Laptev Sea and Greenland Sea	Friedrich, C. & De Smet, W.H.	Hydrobiologia	2000	432	73-89			10.1023/A:1004069903507	1993-1994
Gradinger et al. 2005	Abundance and composition of the sea-ice meiofauna in off-shore pack ice of the Beaufort Gyre in summer 2002 and 2003	Gradinger, R.R, Meiners, K., Plumley, G., Zhang, G. & Bluhm, B.A.	Polar Biol.	2005	28	171-181			10.1007/s00300-004-0674-5	2002-2003
Gradinger & Bluhm 2005	Susceptibility of sea ice biota to disturbance in the shallow Beaufort Sea. Phase 1: Biological coupling of sea ice with the pelagic and benthic realms	Gradinger R.R & Bluhm B.A.	OCS Study MMS 2005-062 Final Report			87				2002-2003
Gradinger et al. 2009	Pivotal role of sea ice sediments in the seasonal development of near-shore Arctic fast ice biota	Gradinger, R.R., Kaufman, M.R. & Bluhm, B.A.	Mar. Ecol. Prog. Ser.	2009	394	49-63			10.3354/meps08320	2002-2003
Gradinger et al. 2010	Arctic sea-ice ridges—Safe heavens for sea-ice fauna during periods of extreme ice melt?	Gradinger, R.R., Bluhm, B.A. & Iken, K.	Deep-Sea Res. Pt. II	2010	57	86-95			10.1016/j.dsr2.2009.08.008	2005
Grainger 1985	The sea ice fauna of Frobisher Bay, Arctic Canada	Grainger, E.H., Mohammed, A.A. & Lovrity, J.E.	Arctic	1985	38	23-30			10.14430/arctic2103	1981-1982
Grainger 1988	The influence of a River Plume on the Sea-ice Meiofauna in South-eastern Hudson Bay	Grainger, E.H.	Estuar. Coast. Shelf S.	1988	27	131-141			10.1016/0272-7714(88)90086-8	1983
Kern & Carey 1983	The faunal assemblage inhabiting seasonal sea ice in the nearshore Arctic Ocean with emphasis on copepods	Kern, J.C. & Andrew Jr., C.G.	Mar. Ecol. Prog. Ser.	1983	10	159-167		www.int-res.com/articles/meps/10/m010p159.pdf		1980
Kramer & Kiko 2011	Brackish meltponds on Arctic sea ice—a new habitat for marine metazoans	Kramer, M. & Kiko, R.	Polar Biol.	2011	34	603-608			10.1007/s00300-010-0911-z	2007
Marquardt et al. 2011	Vertical distribution of sympagic meiofauna in sea ice in the Canadian Beaufort Sea	Marquardt, M., Kramer, M., Carnat, G. & Werner, I.		2011	34	1887-1900			10.1007/s00300-011-1078-y	2008

Reference	Title	Authors	Journal	Pub. year	Volume	Pages	Place	url	doi	Temporal coverage
N-ICE 2015	N-ICE 2015 meiofauna data	Hop, H.	unpublished							2015
Nozais et al. 2001	Abundance, biomass, composition and grazing impact of the sea-ice meiofauna in the North Water, northern Baffin Bay	Nozais, C., Gosselin, M., Michel, M. & Tita, G.	Mar. Ecol. Prog. Ser.	2001	217	235-250		www.int-res.com/abstracts/meps/v217/p235-250/		1998-1999
PSEA 2009	Beaufort Sea cruise meiofauna data	Bluhm B.A. & Gradinger R.R	unpublished							2009
Schünemann & Werner 2005	Seasonal variations in distribution patterns of sympagic meiofauna in Arctic pack ice	Schünemann, H. & Werner, I.	Mar. Biol.	2005	146	1091-1102			10.1007/s00227-004-1511-7	2002-2003

Appendix 3.1.2: Macrofauna References

Reference	Title	Authors	Journal	Pub. Year	Volume	Issue	Pages	Place	url	doi	Data type	Temporal Coverage
Aarset 1987	Osmotic Responses to Hyposmotic Stress in the Amphipods <i>Gammarus wilkitzkii</i> , <i>Onisimus glacialis</i> and <i>Parathemisto libellula</i> from Arctic waters	Aarset, A.V.; Aunaas, T.	Polar Biology	1987	7	4	189-193			10.1007/BF00287415	p	1984
Aarset 1990	Effects of osmotic stress on oxygen consumption and ammonia excretion of the Arctic sympagic amphipod <i>Gammarus wilkitzkii</i>	Aarset, A.V.; Aunaas, T.	Marine Ecology Progress Series	1990	58		217-224			10.3354/meps058217	p	1986, 1988
Arctic Ocean 1967	Arctic non-copepod Zooplankton T3 Ice Island 1966-1967	ArcOD/AOOS	IOBIS database	2012					http://www.iobis.org/		p, am3	1967
Arndt 2005a	Moutpart-atlas of Arctic sympagic amphipods-- trophic niche separation based on mouthpart morphology and feeding ecology	Arndt, C., Berge, J., Brandt, A.	Journal of Crustacean Biology	2005	25	3	401-412				p	1998, 2000, 2002
Arndt 2005b	Origin and fate of ice fauna in the Fram Strait and Svalbard area	Arndt, C.; Pavlova, O.	Marine Ecology Progress Series	2005	301		55-66			10.3354/meps301055	p, am2	2002
AWI 1997	ARK13/1a cruise 14 May -29 Sept 1997	Werner, I.	unpublished								am2	1997
AWI 2007	ARK22/2.28 July-10 October 2007	Werner, I.; Siebert, S.; Kramer, M.; Kiko, R.	unpublished								p, am2	2007
Beaufort Sea 1971	An analysis of the zooplankton community structure of the Western Beaufort Sea. WEBSEC 1971	ArcOD/AOOS	IOBIS database	2012					http://www.iobis.org/		p, am3	1971
Beuchel 2002	Population dynamics of the sympagic amphipods <i>Gammarus wilkitzi</i> and <i>Apherusa glacialis</i> in the sea ice north of Svalbard	Beuchel, F.; Lonne, O.J.	Polar Biology	2002	25		241-250			10.1007/s00300-001-0329-8	p	1998
Canada Basin 2002	Ice amphipods Canada Basin	ArcOD/AOOS	IOBIS database	2012					http://www.iobis.org/		p	2002
Canadian Arctic 2007	The pre-winter 2007 vertical distribution of zooplankton in the Cape Bathurst and North Water polynyas, and Lancaster Sound, Canadian Arctic	ArcOD/AOOS	IOBIS database	2012					http://www.iobis.org/		p, am3	2007
Fram Strait 1997	Seasonal dynamics of sub-ice fauna below pack ice in the Arctic (Fram Strait)	ArcOD/AOOS	IOBIS database	2012					http://www.iobis.org/		p, am3	1997
Franz Josef Land 1994	Biology and Ecology of Cryopelagic Amphipods from Arctic Sea Ice Collected near Franz Josef Land in the summer of 1994	ArcOD/AOOS	IOBIS database	1994					http://www.iobis.org/		p	1994
Gradinger 2004	In-situ observations on the distribution and behavior of amphipods and Arctic cod (<i>Boreogadus saida</i>) under the sea ice of the High Arctic Canada Basin	Gradinger, R.; Bluhm, B.	Polar Biology	2004	27		595-603			10.1007/s00300-004-0630-4	p, am2	2002

Reference	Title	Authors	Journal	Pub. year	Volume	Issue	Pages	Place	url	doi	Data type	Temporal Coverage
Grainger 1985	The sea ice fauna of Frobisher Bay, Arctic Canada	Grainger, E.H.; Mohammed, A.A.; Lovrity, J.E.	Arctic	1985	38	1	23-30			10.14430/arctic2103	p, am2, ww	1981, 1982
Grainger 2011	FRB Eastern Arctic Investigations: The <i>Calanus</i> Series (OBIS Canada)	Grainger, E.H.; Dunbar, M.J.	IOBIS database	2011					http://www.iobis.org/		p	1947-1951
Gulliksen 1984	Under-ice fauna from Svalbard waters	Gulliksen, B.	Sarsia	1984	69		17-23			10.1080/00364827.1984.10420585	p, am2, ww	1982
Honer 1985	Species Composition and Abundance of Zooplankton in the Nearshore Beaufort Sea in Winter-Spring 1978-1980	Honer, R.; Murphy, D.	IOBIS database	1985					http://www.iobis.org/		p, am3	1978, 1980
Hop 2000	Ice amphipod distribution relative to ice density and under-ice topography in the northern Barents Sea	Hop, H.; Poltermann, M.; Lonne, O. J.; Falk-Peterson, S.; Korsnes, R.; Budgell, W.	Polar Biology	2000	23		357-367			10.1007/s003000050456	p, am2, ww	1996
Hop 2008	Distribution and biomass transport of ice amphipods in drifting sea ice around Svalbard	Hop, H.; Pavlova, O.	Deep Sea Research II	2008	55		2292-2307			10.1016/j.dsr2.2008.05.023	p, am2, ww	2003-2005
Hop 2011	Zooplankton boom and ice amphipod bust below melting sea ice in the Amundsen Gulf, Arctic Canada	Hop, H.; Mundy, C.J.; Gosselin, M.; Rossnagel, A.L.; Barber, D.G.	Polar Biology	2011	34		1947-1958			10.1007/s00300-011-0991-4	p, am2	2008
Hopky 1994a	Zooplankton data from the Canadian Beaufort Sea Shelf 1984 and 1985, Zooplankton Beaufort Sea NOGAP1	Hopky, G.E.; Lawrence, M.J.; Chiperzak, D.B.	Can Data Report Fish Aquat Sci, Central and Arctic Region Dept Fish & Oceans	1994	922			Winnipeg, Canada	http://www.iobis.org/		p, am3	1984, 1985
Hopky 1994b	Zooplankton Data from the Canadian Beaufort Sea Shelf 1986, ZooplanktonBeaufortSeaNOGAP2	Hopky, G.E.; Lawrence, M.J.; Chiperzak, D.B.	Can Data Report Fish Aquat Sci, Central and Arctic Region Dept Fish & Oceans	1994	923			Winnipeg, Canada	http://www.iobis.org/		p, am3	1987
Hopky 2004b	Zooplankton Data from the Canadian Beaufort Sea Shelf 1986, ZooplanktonNOGAP32b1986	Hopky, G.E.; Lawrence, M.J.; Chiperzak, D.B.	Can Data Report Fish Aquat Sci, Central and Arctic Region Dept Fish & Oceans	2004	923			Winnipeg, Canada	http://www.iobis.org/		p	1986
Honer 1985	Species composition and abundance of zooplankton in the nearshore Beaufort Sea in winter-spring	Honer, R.; Murphy, D.	Arctic	1985	38	3	201-209				p, am3	1980
Lonne 1991a	On the distribution of sympagic macro-fauna in the seasonally ice covered Barents Sea	Lonne, O.J.; Gulliksen, B.	Polar Biology	1991	11		457-469			10.1007/BF00233081	p, am2, ww	1983, 1985, 1986, 1988
Lonne 1991b	Sympagic macro-fauna from multiyear sea-ice near Svalbard	Lonne, O.J.; Gulliksen, B.	Polar Biology	1991	11		471-477			10.1007/BF00233082	p, am2, ww	1986, 1988

Reference	Title	Authors	Journal	Pub. year	Volume	Issue	Pages	Place	url	doi	Data type	Temporal Coverage
Sameoto 2013	Zooplankton datasets collected using the BIONESS sampler ring and an Icelandic high speed sample 1967-2006	Sameoto, D.D.; Kennedy, M.; Spry, J.S.; Spry, J.M.	OBIS Canada Digital Collections. Biochem: Sameoto zoo-plankton collection	2013					http://www.iobis.org/		p, am3	1980, 1983
Svalbard 2000	Ice Amphipods Svalbard, 2000	ArcOD/AOOS	IOBIS database	2000					http://www.iobis.org/		p	2000
UNIS 1998a	Distribution and abundance of zooplankton and sympagic fauna in Svalbard waters	Hoem, T.; Dahl T.; König S.M.	In "Report of AB-202 Course at UNIS"	1998			21-38	Longyearbyen, Norway			p	1998
UNIS 1998b	Distribution of the sympagic fauna at three different locations north of Svalbard	Beuchel, F.; Borgå, K.; Karlsson, S.; Lillekval, G.	In "Report of AB-310 course at UNIS"	1998			1-31	Longyearbyen, Norway			p, am2, ww	1998
UNIS 1999	Vertical and horizontal distribution of zooplankton and sympagic fauna in north-western Svalbard waters	Daase, M.; Martinsson, P.; Siwertson, A.M.C.; Skoglund, H.; Verreault, J.C.N.	In "Report of AB-202 Course at UNIS"	1999			79-101	Longyearbyen, Norway			p	1999
UNIS 2000	Abundance of sympagic amphipods north of Svalbard considering the ice conditions	Arndt, C.E.; Kanapathippillai, P.; Kluge, R.; Krapp, R.	In "Report of AB-320 Course at UNIS"	2000			14	Longyearbyen, Norway			p, am2, ww	2000
UNIS 2002	Sympagic fauna in Fram Strait and Svalbard waters	Backman, J.; Klette, M.; Krey, A.; Luodekari, K.; Vestheim, H.	In "Report of AB-310 Course at UNIS"	2002			5-22	Longyearbyen, Norway			p, am2, ww	2002
UNIS 2004	AB320 UNIS report 2004		In "Report of AB-320 Course at UNIS"	2004				Longyearbyen, Norway			p	2004
UNIS 2006	AB320 UNIS report 2006		In "Report of AB-320 Course at UNIS"	2006				Longyearbyen, Norway			p	2006
UNIS 2008	Zooplankton and sympagic fauna in Svalbard fjords and adjacent waters focussing on taxonomy, distribution and basic ecology	Rabindranath, A.; Baczewska, A.; Losham, E.K.; Nielsen, D.L.	In "Report of AB-320 Course at UNIS"	2008			46	Longyearbyen, Norway			p	2008
UNIS 2012	Amphipods and their interactions in the sympagic food web in the Arctic Ocean	Berthold, M.; Kallevik, I.H.F.; Marquardt, M.; Rekdal, S.	In "Report of AB-330 Course at UNIS"	2012			39	Longyearbyen, Norway			p	2012
Werner 1999	The sub-ice fauna of the Laptev Sea and the adjacent Arctic Ocean in summer 1995	Werner, I.; Arbizu, P.M.	Polar Biology	1999	21		71-79				p, am2, ww	1995
Werner 2002	Carnivorous feeding and respiration of the Arctic under-ice amphipod <i>Gammarus wilkitzkii</i>	Werner, I.; Auel, H.; Friedrich, C.	Polar Biology	2002	25		523-530				p, am2	1994, 1995, 1997, 2000
Werner 2005	Living conditions, abundance and biomass of under-ice fauna in the Storfford area (western Barents Sea, Arctic) in late winter (March 2003)	Werner, I.	Polar Biology	2005	28	4	311-318				p	2003
Werner unpubl.	AKR1/1 cruise 7.juli-20.Sept 1995	Werner, I.	unpublished								p, am2	1995

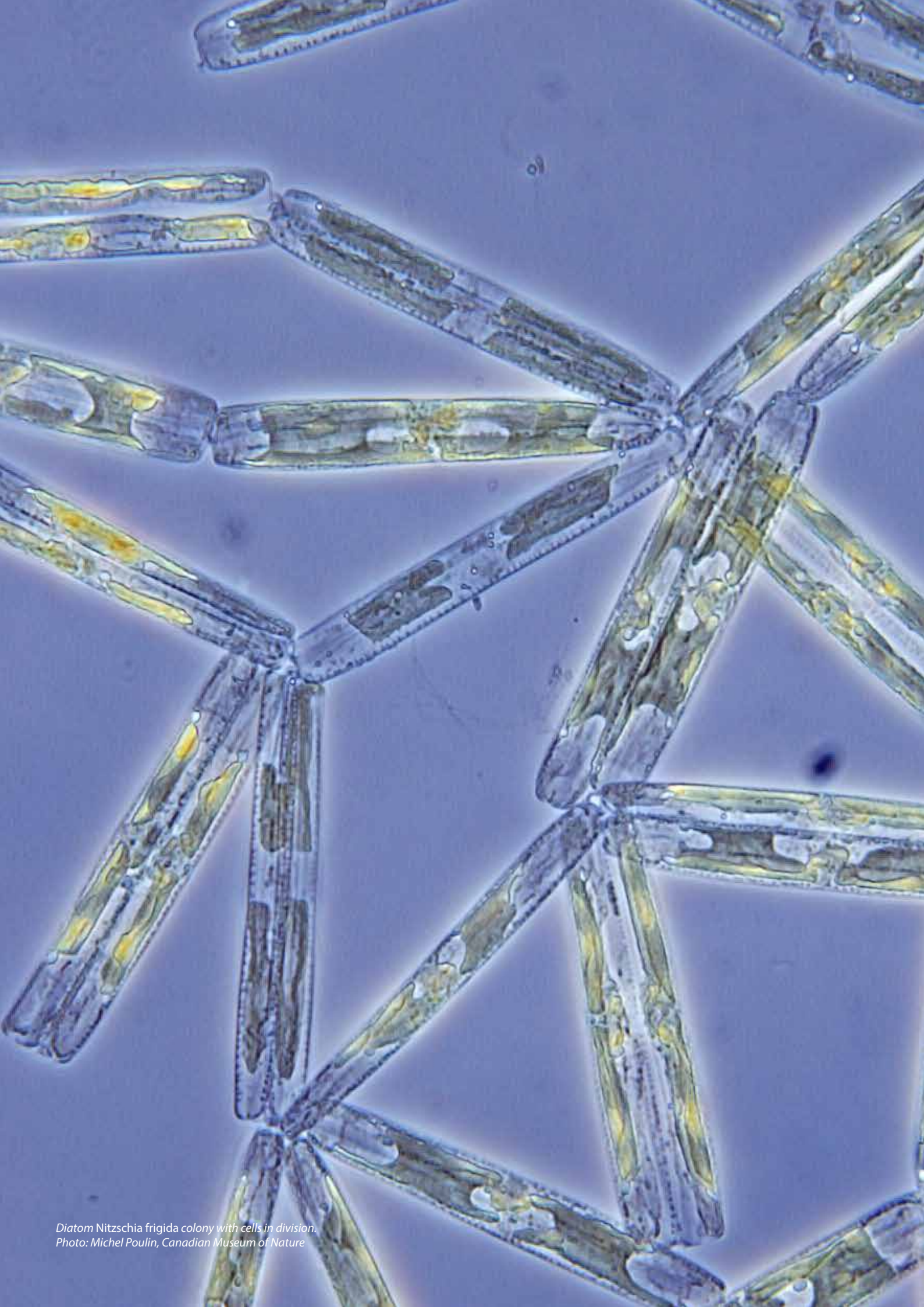
References

- Aarset, A.V. and Aunaas, T. 1987. [Osmotic responses to hyposmotic stress in the amphipods *Gammarus wilkitzkii*, *Onisimus glacialis* and *Parathemisto libellula* from Arctic waters](#). *Polar Biology*, 7: 189-193.
- Adl, S.M., Simpson, A.G.B., Lane, C.E., Lukes, J., Bass, D., Bowser, S.S., Brown, M.W., Burki, F., Dunthorn, M., Hampl, V., Heiss, A., Hoppenrath, M., Lara, E., Gall, L.L., Lynn, D.H., McManus, H., Mitchell, E.A.D., Mozley-Stranridge, S.E., Parfrey, L.W., Pawlowski, J., Rueckert, S., Shadwick, L., Schoch, C.L., Smirnov, A. and Spiegel, F.W. 2012. [The revised classification of eukaryotes](#). *Journal of Eukaryotic Microbiology*, 59(5): 429-493.
- Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L. and Tremblay, J.-É. 2014. [Recent Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms](#). *Geophysical Research Letters*, 41(17): 6207-6212.
- Arndt, C.E. and Swadling, K.M. 2006. [Crustacea in Arctic and Antarctic sea ice: Distribution, diet and life history strategies](#). *Advances in Marine Biology*, 51: 197-315.
- Arndt, C.E., Berge, J. and Brandt, A. 2005. [Mouthpart-atlas of Arctic sympagic amphipods—Trophic niche separation based on mouthpart morphology and feeding ecology](#). *Journal of Crustacean Biology*, 25: 401-412.
- Arrigo, K., Matrai, P.A. and van Dijken, G.L. 2011. [Primary productivity in the Arctic Ocean: Impacts of complex optical properties and subsurface chlorophyll maxima on large-scale estimates](#). *Journal of Geophysical Research Oceans*, 116: C11022.
- Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M., Palmer, M.A., Balch, W.M., Bahr, F., Bates, N.R., Benitez-Nelson, C., Bowler, B., Brownlee, E., Ehn, J.K., Frey, K.E., Garley, R., Laney, S.R., Lubelczyk, L., Mathis, J., Matsuoka, A., Mitchell, B.G., Schieber, B., Sosik, H.M., Stephens, M. and Swift, J.H. 2012. [Massive phytoplankton blooms under Arctic sea ice](#). *Science*, 336(6087): 1408.
- Assmy, P., Ehn, J.K., Fernández-Méndez, M., Hop, H., Katlein, C., Sundfjord, A., Bluhm, K. and Wiktor, J. 2013. [Floating ice-algal aggregates below melting Arctic sea ice](#). *PLoS ONE*, 8: e76599.
- Barber, D.G., Hop, H., Mundy, C.J., Else, B., Dmitrenko, I.A., Tremblay, J.-É., Ehn, J.K., Assmy, P., Daase, M., Candlish, L.M. and Rysgaard, S. 2015. [Selected physical, biological and biogeochemical implications of a rapidly changing Arctic Marginal Ice Zone](#). *Progress in Oceanography*, 139: 122-150.
- Berge, J., Varpe, Ø., Moline, M.A., Wold, A., Renaud, P.E., Daase, M. and Falk-Petersen, S. 2012. [Retention of ice-associated amphipods: possible consequences for an ice-free Arctic Ocean](#). *Biology Letters*, 8: 1012-1015.
- Beuchel, F. and O.J. Lønne. 2002. [Population dynamics of the sympagic amphipods *Gammarus wilkitzkii* and *Apherusa glacialis* in sea ice north of Svalbard](#). *Polar Biology*, 25: 241-250.
- Bluhm, B. and Gradinger, R. 2008. [Regional variability in food availability for Arctic marine mammals](#). *Ecological Applications*, 18(sp2): 577-596.
- Bluhm B.A., Gradinger, R. and Piraino, S. 2007. [First record of sympagic hydroids \(Hydrozoa, Cnidaria\) in Arctic coastal fast ice](#). *Polar Biology*, 30: 1557-1563.
- Bluhm, B.A., Swadling, K. and Gradinger, R. 2017. Chapter 16: Sea ice as habitat for macrograzers. *In*: D.N. Thomas (ed.). [Sea ice 3rd edition](#), Wiley Blackwell, pp 394-414.
- Boetius, A., Albrecht, S., Bakker, K., Bienhold, C., Felden, J., Fernandez-Mendez, M., Hendricks, S., Katlein, C., Lalande, C., Krumpen, T., Nicolaus, M., Peeken, I., Rabe, B., Rogacheva, A., Rybakova, E., Somavilla, R., Wenzhofer, F. and RV Polarstern ARK27-3-Shipboard Science Party. 2013. [Export of algal biomass from the melting Arctic sea ice](#). *Science*, 339(6126): 1430-1432.
- Bowman, J.S., Rasmussen, S., Blom, N., Deming, J.W., Rysgaard, S. and Sicheritz-Ponten, T. 2012. [Microbial community structure of Arctic multiyear sea ice and surface seawater by 454 sequencing of the 16S RNA gene](#). *The ISME Journal*, 6(1): 11-20.
- Brinkmeyer, R., Knittel, K., Jürgens, J., Weyland, H., Amann, R. and Helmke, E. 2003. [Diversity and structure of bacterial communities in Arctic versus Antarctic sea ice: a comparison](#). *Applied and Environmental Microbiology*, 69(11): 6610-6619.
- Carey, A.G. 1985. Marine ice fauna: Arctic. *Sea ice biota*. CRC Press, Boca Raton: 173-190.
- Carey, A.G. and Montagna, P.A. 1982. [Arctic sea ice fauna assemblage: first approach to description and source of the underice meiofauna](#). *Marine Ecology Progress Series*, 8: 1-8.
- Carmack, E. and Chapma, D.C. 2003. [Wind-driven shelf/basin exchange on an Arctic shelf: The joint roles of ice cover and shelf-break bathymetry](#). *Geophysical Research Letters*, 30(14): 1778.
- Christiansen, J.S., Hop, H., Nilssen, E.M. and Joensen, J. 2012. [Trophic ecology of sympatric Arctic gadoids, *Arctogadus glacialis* \(Peters, 1872\) and *Boreogadus saida* \(Lepechin, 1774\), in NE Greenland](#). *Polar Biology*, 35(8): 1247-1257.
- Clarke K.R. and Gorley, R.N. 2006. *PRIMER v6: user manual/tutorial* PRIMER-E, Plymouth: 1-126.
- Collins, R.E. 2015. Microbial Evolution in the Cryosphere. *In*: C. Bakermans (ed.). [Microbial Evolution Under Extreme Conditions](#), De Gruyter: 31-55.
- Collins, R.E., Rocap, G. and Deming, J.W. 2010. [Persistence of bacterial and archaeal communities in sea ice through an Arctic winter](#). *Environmental Microbiology*, 12(7): 1828-1841.
- Comeau, A.M., Philippe, B., Thaler, M., Gosselin, M., Poulin, M. and Lovejoy, C. 2013. [Protists in Arctic drift and land-fast sea ice](#). *Journal of Phycology*, 49(2): 229-240.
- 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 importance as key prey in a warming marine ecosystem](#). *Polar Biology*, 39(10): 1765-1784.
- Daniëls, F.J.A., Gillespie, L.J. and Poulin, M. 2013. [Plants](#). *In*: H. Meltofte (ed.). [Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity](#), Conservation of Arctic Flora and Fauna, Akureyri, Iceland, pp 310-353.
- David, C., Lange, B., Krumpen, T., Schaafsma, F., van Franeker, J.A. and Flores, H. 2016. [Under-ice distribution of polar cod *Boreogadus saida* in the central Arctic Ocean and their association with sea-ice habitat properties](#). *Polar Biology*, 39(6): 919-994.
- Deming, J.W. 2010. Sea ice bacteria and viruses. *In*: D.N. Thomas and G. Dieckmann (eds.). [Sea ice, 2nd edition](#), Wiley Blackwell pp 247-282.
- Duarte, P., Assmy, P., Hop, H., Spreen, G., Gerland, S. and Hudson, S.R. 2015. [The importance of vertical resolution in sea ice algae production models](#). *Journal of Marine Systems*, 145: 69-90.
- Ehn, J.K., Mundy, C.J., Barber, D.G., Hop, H., Rossnagel, A. and Stewart, J. 2011. [Impact of horizontal spreading on light propagation in melt pond covered seasonal sea ice in the Canadian Arctic](#). *Journal of Geophysical Research*, 116(C9): C00G02.
- Ehrenberg, C.G. 1853. [Über neue Anschauungen des kleinsten nördlichen Polarlebens. Berichte über die zur Bekanntmachung geeigneten Verhandlung](#). Königlich-Preußischen Akademie der Wissenschaften zu Berlin: 522-533.
- Eicken, H., Bluhm, B.A., Collins, R.E., Gradinger, R.R., Haas, C., Ingham, M., Mahoney, A., Nicolaus, M. and Perovich, D. 2014. Field techniques in sea ice research. *In*: H. Shen (ed.). *Cold Regions Science and Marine Technology in Encyclopedia of Life Support Systems (EOLSS)*, UNESCO, Paris, France.
- Eicken, H., Gradinger, R., Salganek, M., Shirasawa, K., Perovich, D. and Leppäranta M. (eds.). 2009. [Handbook on field techniques in sea ice research \(a sea ice system services approach\)](#). University of Alaska Press, Fairbanks.
- Friedrich, C. 1997. [Ökologische Untersuchungen zur Fauna des arktischen Meereises](#). Reports on Polar Research, Alfred Wegener Institute for Polar and Marine Research, 246: 1-211
- Friedrich, C. and De Smet, W.H. 2000. [The rotifer fauna of arctic sea ice from the Barents Sea, Laptev Sea and Greenland Sea](#). *Hydrobiologia*, 432(1): 73-89.
- Fuhrmann, M.M., Nygård, H., Krapp, R.H., Berge, J. and Werner, I. 2011. [The adaptive significance of chromatophores in the](#)

- [Arctic under-ice amphipod *Apherusa glacialis*](#). *Polar Biology*, 34(6): 823–832.
- Gerland, S., Aars, J., Bracegirdle, T., Carmack, E., Hop, H., Hovelsrud, G.K., Kovacs, K., Lydersen, C., Perovich, D.K., Richter-Menge, J., Rybråten, S., Strøm H. and Turner, J. 2007. Ice in the sea. In: *Global Outlook for Ice and Snow*, United Nations Environment Programme, Nairobi, pp 63–96.
- 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.
- Gradinger, R. 1999. [Integrated abundances and biomass of sympagic meiofauna from Arctic and Antarctic pack ice](#). *Polar Biology*, 22(3): 169–177.
- 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 Research Part II*, 56(17): 1201–1212.
- Gradinger, R.R. and Bluhm, B.A. 2004. [In situ observations on the distribution and behavior of amphipods and Arctic cod \(*Boreogadus saida*\) under the sea ice of the high Arctic Canadian Basin](#). *Polar Biology*, 27(10): 595–603.
- Gradinger, R. and Bluhm, B.A. 2009. Assessment of the abundance and diversity of sea ice biota. In: H. Eicken, R. Gradinger, M. Salganek, K. Shirasawa, D. Perovich and M. Leppäranta (eds.). [Handbook on field techniques in sea ice research \(a sea ice system services approach\)](#). University of Alaska Press, Fairbanks: 283–300.
- Gradinger, R. and Bluhm, B.A. 2010. [Timing of ice algal grazing by the Arctic nearshore benthic amphipod *Onisimus littoralis*](#). *Arctic*, 63(3): 355–358.
- Gradinger, R. and Ikävalko, J. 1998. [Organism incorporation into newly forming Arctic sea ice in the Greenland Sea](#). *Journal of Plankton Research*, 20(5): 871–886.
- Gradinger, R. and Schnack-Schiel, S.B. 1998. [Potential effect of ice formation on Antarctic pelagic copepods: salinity induced mortality of *Calanus propinquus* and *Metridia gerlachei* in comparison to sympagic acocel turbellarians](#). *Polar Biology*, 20(2): 139–142.
- Gradinger, R., Bluhm, B. and Iken, K. 2010. Arctic sea-ice ridges—Safe havens for sea-ice fauna during periods of extreme ice melt? *Deep-Sea Research Part II*, 57(1–2): 86–95.
- Gradinger, R., Friedrich, C. and Spindler, M. 1999. [Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice](#). *Deep-Sea Research Part II*, 46(6–7): 1457–72.
- Gradinger, R.R., Kaufman, M.R. and Bluhm, B.A. 2009. [Pivotal role of sea ice sediments in the seasonal development of near-shore Arctic fast ice biota](#). *Marine Ecology Progress Series*, 394: 49–63.
- Gradinger, R., Meiners, K., Plumley, G., Zhang, Q. and Bluhm, B.A. 2005. [Abundance and composition of the sea ice meiofauna in off-shore pack ice of the Beaufort Gyre in summer 2002 and 2003](#). *Polar Biology*, 28(3): 171–181.
- Grainger, E.H. and Hsiao, S.I.C. 1990. [Trophic relationship of the sea ice meiofauna in Frobisher Bay, Arctic Canada](#). *Polar Biology*, 10(4): 283–292.
- Gran, H.H. 1900. Diatomaceae from the ice-floes and plankton of the Arctic Ocean. *Scientific Results, The Norwegian North Polar Expedition, 1893–1896*, 11: 1–74.
- Grunow, A. 1884. Die Diatomeen von Franz Josefs-Land. *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe, Wien*, 48: 53–112.
- Gulliksen, B. and Lønne, O.J. 1991. [Sea ice macrofauna in the Antarctic and the Arctic](#). *Journal of Marine Systems*, 2(1–2): 53–61.
- Hassett, B.T. and Gradinger, R. 2016b. [Chytrids dominate arctic marine fungal communities](#). *Environmental Microbiology*, 18(6): 2001–2009.
- Hassett, B.T., Ducluzeau, A.L., Collins, R.E. and Gradinger, R. 2016a. [Spatial distribution of aquatic marine fungi across the western Arctic and sub-Arctic](#). *Environmental Microbiology*.
- Hop, H. and Gjøsaeter, H. 2013. [Polar cod \(*Boreogadus saida*\) and capelin \(*Mallotus villosus*\) as key species in marine food webs of the Arctic and the Barents Sea](#). *Marine Biology Research*, 9(9): 878–894.
- Hop, H. and Pavlova, O. 2008. [Distribution and biomass transport of ice amphipods in drifting sea ice around Svalbard](#). *Deep-Sea Research Part II*, 55(20–21): 2292–2307.
- Hop, H., Bluhm, B.A., Gradinger, R. and Poulin, M. 2013. [Arctic sea ice biota](#). Arctic Report Card, National Oceanic and Atmospheric Administration (NOAA).
- Hop, H., Mundy, C.J., Gosselin, M., Rossnagel, A.L. and Barber, D.G. 2011. [Zooplankton boom and ice amphipod bust below melting sea ice in the Amundsen Gulf, Arctic Canada](#). *Polar Biology*, 34(12): 1947–1958.
- Hop, H., Poltermann, M., Lønne, O.J., Falk-Petersen, S., Korsnes, R. and Budgell, W.P. 2000. [Ice amphipod distribution relative to ice density and under-ice topography in the northern Barents Sea](#). *Polar Biology*, 23(5): 357–367.
- Horner, R. 1985. Ecology of sea ice microalgae. In: R. Horner (ed.). *Sea Ice Biota*, CRC Press, Boca Raton, Florida, pp 83–103.
- Horner, R., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Hoshiai, T., Legendre, L., Melnikov, I.A., Reeburgh, W.S., Spindler, M. and Sullivan, C.W. 1992. [Ecology of sea ice biota. 1. Habitat, terminology, and methodology](#). *Polar Biology*, 12(3): 417–427.
- Hudson, S.R., Granskog, M.A., Sundfjord, A., Randelhoff, A., Renner, A.H.H. and Divine, D.V. 2013. [Energy budget of first-year Arctic sea ice in advanced stages of melt](#). *Geophysical Research Letters*, 40(11): 2679–2683.
- Hsiao, S.I.C. 1983. A checklist of marine phytoplankton and sea ice microalgae recorded from Arctic Canada. *Nova Hedwigia*, 37: 225–313.
- Josefson, A.B. and Mokievsky, V. 2013. [Marine invertebrates](#). In: H. Meltofte (ed.). [Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity](#), Conservation of Arctic Flora and Fauna, Akureyri, Iceland: 277–309.
- Junge, K., Imhoff, F., Staley, T. and Deming, W. 2002. [Phylogenetic diversity of numerically important Arctic sea-ice bacteria cultured at subzero temperature](#). *Microbial Ecology*, 43: 315–328.
- Juul-Pedersen, T., Michel, C., Gosselin, M. and Seuthe, L. 2008. [Seasonal changes in the sinking export of particulate material under first-year sea ice on the Mackenzie Shelf \(western Canadian Arctic\)](#). *Marine Ecology Progress Series*, 353: 13–25.
- Ki, J.-S., Dahms, H.-U., Kim, I.-C., Park, H.G., Hop, H. and Lee, J.-S. 2011. [Molecular relationships of gammaridean amphipods from Arctic sea ice](#). *Polar Biology*, 34(10): 1559–1569.
- Krembs, C., Gradinger, R. and Spindler, M. 2000. [Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice](#). *Journal of Experimental Marine Biology and Ecology*, 243(1): 55–80.
- Lee, S.H., Kim, B.K., Joo, H.T., Park, J.W., Lee, J.H., Joo, H.M., Lee, D.B., Kang, C.K. and Kang, S.H. 2015. [Carbon contribution of sea ice floes in the Arctic Ocean](#). *Deep-Sea Research Part II*, 120: 35–42.
- Lee, S.H., McRoy, C.P., Joo, H.M., Gradinger, R., Cui, X.H., Yun, M.S., Chung, K.H., Kang, S.H., Kang, C.K., Choy, E.J., Son, S.H., Carmack, E. and Whitley, T.E. 2011. [Holes in progressively thinning Arctic sea ice lead to new ice algae habitat](#). *Oceanography*, 24(3): 302–308.
- Legendre, L., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Horner, R., Hoshiai, T., Melnikov, I.A., Reeburgh, W.S., Spindler, M. and Sullivan, C.W. 1992. [Ecology of sea ice biota 2](#). Global significance. *Polar Biology*, 12: 429–444.
- Leu, E., Mundy, C.J., Assmy, P., Campbell, K., Gabrielsen, T.M., Gosselin, M., Juul-Pedersen, T. and Gradinger, R. 2015. [Arctic spring awakening—Steering principles behind the phenology of vernal ice algal blooms](#). *Progress in Oceanography*, 139: 151–170.
- Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S. and Berge, J.

2011. [Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity and quality](#). *Progress in Oceanography*, 90(1-4): 18-32.
- Lønne, O.J. 1988. [A diver-operated electric suction sampler for sympagic \(=under-ice\) invertebrates](#). *Polar Research*, 6: 135-136.
- Lønne, O.J. and Gulliksen, B. 1989. [Size, age and diet of polar cod, *Boreogadus saida* \(Lepechin 1773\), in ice covered waters](#). *Polar Biology*, 9(3): 187-191.
- Lønne, O.J. and Gulliksen, B. 1991a. [On the distribution of sympagic macro-fauna in the seasonally ice covered Barents Sea](#). *Polar Biology*, 11(7): 457-469.
- Lønne, O.J. and Gulliksen, B. 1991b. [Sympagic macro-fauna from multiyear sea-ice near Svalbard](#). *Polar Biology*, 11: 471-477.
- Lovejoy, C. 2013. [Microorganisms](#). In: H. Meltofte (ed.). *Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity*, Conservation of Arctic Flora and Fauna, Akureyri, Iceland: 373-382.
- Maranger, R., Bird, D.F. and Juniper, S.K. 1994. [Viral and bacterial dynamics in Arctic sea ice during the spring algal bloom near Resolute, N.W.T., Canada](#). *Marine Ecology Progress Series*, 111: 121-127.
- Marquardt, M., Kramer, M., Carnat, G. and Werner, I. 2011. [Vertical distribution of sympagic meiofauna in sea ice in the Canadian Beaufort Sea](#). *Polar Biology*, 34(12): 1887-1900.
- McConnell, B., Gradinger, R., Iken, K. and Bluhm, B. 2012. [Growth rates of arctic juvenile *Scolecopsis squamata* \(Polychaeta: Spionidae\) isolated from Chukchi Sea fast ice](#). *Polar Biology*, 35(10): 1487-1494.
- Mecklenburg, C.W., Møller, P.R. and Steinke, D. 2011. [Biodiversity of arctic marine fishes: taxonomy and zoogeography](#). *Marine Biodiversity*, 41: 109-140.
- Mehlum, F. and Gabrielsen G.W. 1993. [The diet of high-arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago](#). *Polar Research*, 12(1): 1-20.
- Melnikov, I.A. 1997. *The Arctic Sea ice ecosystem*. Gordon and Breach Science Publisher, Amsterdam.
- Melnikov, I.A., Kolosova, E.G., Welch, H.E. and Zhitina, L.S. 2002. [Sea ice biological communities and nutrient dynamics in the Canada Basin of the Arctic Ocean](#). *Deep-Sea Research Part I*, 49(9): 1623-1649.
- Michel, C., Ingram, R.G. and Harris, L.R. 2006. [Variability in oceanographic and ecological processes in the Canadian Arctic Archipelago](#). *Progress in Oceanography*, 71: 379-401.
- Michel, C., Nielsen, T.G., Nozais, C. and Gosselin, M. 2002. [Significance of sedimentation and grazing by ice micro- and meiofauna for carbon cycling in annual sea ice \(northern Baffin Bay\)](#). *Aquatic Microbial Ecology*, 30(1): 57-68.
- Miller, L.A., Fripiat, F., Else, B.G.T., Bowman, J.S., Brown, K.A., Collins, R.E., Ewert, M., Fransson, A., Gosselin, M., Lannuzel, D., Meiners, K.M., Michel, C., Nishioka, J., Nomura, D., Papadimitriou, S., Russell, L.M., Sørensen, L.L., Thomas, D.N., Tison, J.-L., van Leeuwe, M.A., Vancoppenolle, M., Wolff, E.W. and Zhou, J. 2015. [Methods for biogeochemical studies of sea ice: The state of the art, caveats, and recommendations](#). *Elementa Science of the Anthropocene*, 3(38): 000038.
- Morata, N., Poulin, M. and Renaud, P.E. 2011. [A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor](#). *Polar Biology*, 34(1): 101-112.
- Mundy, C.J., Barber, D.G., Michel, C. and Marsden, R.F. 2007. [Linking ice structure and microscale variability of algal biomass in Arctic first-year sea ice using an in situ photographic technique](#). *Polar Biology*, 30(9): 1099-1114.
- Mundy, C.J., Gosselin, M., Ehn, J.K., Belzile, C., Poulin, M., Alou, E., Roy, S., Hop, H., Lessard, S., Papakyriakou, T.N., Barber, D.G. and Stewart, J. 2011. [Characteristics of two distinct high-light acclimated microbial communities during advanced stages of sea ice melt](#). *Polar Biology*, 34(12): 1869-1886.
- Nansen, F. 1906. Protozoa on the ice-floes of the North Polar Sea. Longmans, Green, and Company.
- National Center for Biotechnology Information's (NCBI) [Nucleotide and PubMed databases 2017](#).
- Nghiem, S.V., Rigor, I.G., Perovich, D.K., Clemente-Colón, P., Weatherly, J.W. and Neumann, G. 2007. [Rapid reduction of Arctic perennial sea ice](#). *Geophysical Research Letters*, 34(19): L19504.
- Nguyen, D. and Maranger, R. 2011. [Respiration and bacterial carbon dynamics in Arctic sea ice](#). *Polar Biology*, 34(12): 1843-1855.
- Nicolaus, M., Katlein, C., Maslanik, J. and Hendricks, S. 2012. [Changes in Arctic sea ice result in increasing light transmittance and absorption](#). *Geophysical Research Letters*, 39(24): L24501.
- Nozais, C., Gosselin, M., Michel, C. and Tita, G. 2001. [Abundance, biomass, composition and grazing impact of the sea-ice meiofauna in the North Water, northern Baffin Bay](#). *Marine Ecology Progress Series*, 217: 235-250.
- Nürnberg, D., Wollenburg, I., Dethleff, D., Eicken, H., Kassens, H., Letzig, T., Reimnitz, E. and Thiede, J. 1994. [Sediments in Arctic sea ice: Implications for entrainment, transport and release](#). *Marine Geology*, 119(3-4): 185-214.
- Nygård, H., Berge, J., Søreide, J.E., Vihtakari, M. and Falk-Petersen, S. 2012. [The amphipod scavenging guild in two Arctic fjords: seasonal variations, abundance and trophic interactions](#). *Aquatic Biology*, 14: 247-264.
- Perovich, D., Meier, W., Tschudi, M., Farrell, S., Gerland, S. and Hendricks, S. 2015. *Sea Ice. 2015 Arctic Report Card*, National Oceanic and Atmospheric Administration (NOAA).
- Philippe, B. 2013. [Changements récents dans la dynamique des algues de glace dans le secteur canadien de la mer de Beaufort](#). Université du Québec à Rimouski, Institut des sciences de la mer de Rimouski (ISMER), Rimouski: 1-87.
- Pike, D. and Welch, H.E. 1990. [Spatial and temporal distribution of sub-ice macrofauna in the Barrow Strait area, Northwest Territories](#). *Canadian Journal of Fisheries and Aquatic Sciences*, 47(1): 81-91.
- Piraino, S., Bluhm, B.A., Gradinger, R. and Boero, F. 2008. [*Sympagohydra tuuli* gen. nov. et sp. nov. \(Cnidaria: Hydrozoa\) a cool hydroid from the Arctic sea ice](#). *Journal of the Marine Biological Association of the United Kingdom*, 88(8): 1637-1641.
- Poltermann, M., 1998. [Abundance, biomass and small-scale distribution of cryopelagic amphipods in the Franz Josef Land area \(Arctic\)](#). *Polar Biology*, 20(2): 134-138.
- Poltermann, M. 2000. [Growth, production and productivity of the Arctic sympagic amphipod *Gammarus wilkitzkii*](#). *Marine Ecology Progress Series*, 193: 109-116.
- Poltermann, M. 2001. [Arctic sea ice as feeding ground for amphipods—food sources and strategies](#). *Polar Biology*, 24(2): 89-96.
- Polyakov, I.V., Walsh, J.E. and Kwok, R. 2012. [Recent changes of Arctic multiyear sea-ice coverage and the likely causes](#). *Bulletin of the American Meteorological Society*, 93: 145-151.
- 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.
- Poulin, M., Underwood, G.J. and Michel, C. 2014. [Sub-ice colonial *Melosira arctica* in Arctic first-year ice](#). *Diatom Research*, 29(2): 213-221.
- Purcell, J.P., Hopcroft, R.R., Kosobokova, K.N. and Whitledge, T.E. 2010. [Distribution, abundance, and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean](#). *Deep-Sea Research Part II*, 57(1-2): 127-135.
- Raskoff, K.A., Hopcroft, R.R., Kosobokova, K.N., Purcell, J.E. and Youngbluth, M. 2010. [Jellies under ice: ROV observations from the Arctic 2005 hidden ocean expedition](#). *Deep-Sea Research Part II*, 57(1-2): 111-126.
- Raskoff, K.A., Purcell, J.E. and Hopcroft, R.R. 2005. [Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice](#). *Polar Biology*, 28(3): 207-217.
- Renaud, P., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T. and Chiuchiollo, A. 2007. [Seasonal variation in benthic community oxygen demand: A response to an ice algal](#)

- [bloom in the Beaufort Sea, Canadian Arctic?](#) *Journal of Marine Systems*, 67(1-2): 1-12.
- Riemann, F. and Sime-Ngando, T. 1997. [Note on sea-ice nematodes \(*Monhysteroidea*\) from Resolute Passage, Canadian High Arctic](#). *Polar Biology*, 18(1): 70-75.
- Rózańska, M., Gosselin, M., Poulin, M., Wiktor, J.M. and Michel, C. 2009. [Influence of environmental factors on the development of bottom ice protist communities during the winter-spring transition](#). *Marine Ecology Progress Series*, 386: 43-59.
- Rózańska, M., Poulin, M. and Gosselin, M. 2008. [Protist entrapment in newly formed sea ice in the Coastal Arctic Ocean](#). *Journal of Marine Systems*, 74(3-4): 887-901.
- Schünemann, H. and Werner, I. 2005. [Seasonal variations in distribution patterns of sympagic meiofauna in Arctic pack ice](#). *Marine Biology*, 146(6): 1091-1102.
- Siebert, S., Anton-Erxleben, F., Kiko, R. and Kramer, M. 2009. [Sypagohydra tuuli \(Cnidaria, Hydrozoa\): First report from sea ice of the central Arctic Ocean and insights into histology, reproduction and locomotion](#). *Marine Biology*, 156(4): 541-554.
- Søreide, J.E., Leu, E., Berge, J., Graeve, M. and Falk-Petersen, S. 2010. [Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic](#). *Global Change Biology*, 16: 3154-3163.
- Syvrtsen, E.E. 1991. [Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom](#). *Polar Research*, 10(1): 277-288.
- Tamelander, T., Reigstad, M., Hop, H. and Ratkova, T. 2009. [Ice algal assemblages and vertical export of organic matter from sea ice in the Barents Sea and Nansen Basin \(Arctic Ocean\)](#). *Polar Biology*, 32: 1261-1273.
- Tamelander, T., Renaud, P.E., Hop, H., Carroll, M.L., Ambrose, W.G. and Hobson, K.A. 2006. [Trophic relationships and pelagic-benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements](#). *Marine Ecology Progress Series*, 310: 33-46.
- Tchesunov, A.V. and Riemann, F. 1995. Arctic sea ice nematodes (*Monhysteroidea*) with descriptions of *Cryonema crassum* gen. n. sp. n. and *C. tenue* sp. n. *Nematologica*, 41(1-5): 35-50.
- Tremblay, J.E., Anderson, L.G., Matrai, P., Coupel, P., Bélanger, S., Michel, C. and Reigstad, M. 2015. [Global and regional drivers of nutrient supply, primary production and CO₂ drawdown in the changing Arctic Ocean](#). *Progress in Oceanography*, 139: 171-196.
- Tremblay, J.É., Bélanger, S., Barber, D.G., Asplin, M., Martin, J., Darnis, G., Fortier, L., Gratton, Y., Link, H., Archambault, P., Sallon, A., Michel, C., Williams, W.J., Philippe, B. and Gosselin, M. 2011. [Climate forcing multiplies biological productivity in the coastal Arctic Ocean](#). *Geophysical Research Letters*, 38(18): L18604.
- van Franeker, J.A., Flores, H. and Van Dorssen, M. 2009. The Surface and Under Ice Trawl (SUIT). In: H. Flores (ed.). [Frozen Desert alive—the role of sea-ice for pelagic macrofauna and its predators: implications for the Antarctic pack-ice food web](#). University of Groningen, Groningen, Netherlands.
- von Quillfeldt, C.H. 1997. [Distribution of diatoms in the Northeast Water Polynya, Greenland](#). *Journal of Marine Systems*, 10(1-4): 211-240.
- von Quillfeldt, C.H., Ambrose Jr., W.G. and Clough, L.M. 2003. [High number of diatom species in first-year ice from the Chukchi Sea](#). *Polar Biology*, 26(12): 806-818.
- Werner, I. 2007. [Seasonal dynamics, cryo-pelagic interactions and metabolic rates of Arctic pack-ice and under-ice fauna – A review](#). *Polarforschung*, 75(1): 1-19.
- Werner, I. and Gradinger, R. 2002. [Under-ice amphipods in the Greenland Sea and Fram Strait \(Arctic\): environmental controls and seasonal patterns below the pack ice](#). *Marine Biology*, 140: 317-326.
- Werner, I., Auel, H. and Kiko, R. 2004. [Occurrence of *Anonyx sarsi* \(Amphipoda: Lysianassoidea\) below Arctic pack ice: an example for cryo-benthic coupling?](#) *Polar Biology*, 27(8): 474-481.
- Werner, I., Auel, H., Garrity, C. and Hagen, W. 1999. [Pelagic occurrence of the sympagic amphipod *Gammarus wilkitzkii* in ice free waters of the Greenland Sea - dead end or part of life cycle?](#) *Polar Biology*, 22(1): 56-60.



Diatom Nitzschia frigida colony with cells in division.
Photo: Michel Poulin, Canadian Museum of Nature