Chapter 1
The Book, and Ecology of Sea Ice

Abstract This chapter describes the structure of the book and the diverse significance and importance of sea ice. The first section explains how and why the book is structured following the seasonal events governing the abiotic and biotic parameters in sea ice (1.1). The second section places sea ice into a physical and geopolitical perspective with the new and developing international borders in the Arctic Ocean (1.2). Sea ice ecosystems are then compared to other ecosystems (1.3), followed by a section describing the important and global ecological features of sea ice (1.4).

Keywords Seasonal variability · Arctic marine ecosystem · Ecological role of sea ice

1.1 Follow the Seasons

In this book, we emphasize the seasonal sea ice dynamics, highlighting the strong seasonal signal from development of the ice during autumn, all through the winter, and through to the melt and eventual disappearance of the ice in summer. Most ecosystems on Earth experience seasonal variations in the physical environment as with light or temperature, but it is difficult to envisage any other system where such a large part of the ecosystem simply disappears during spring and summer to be regenerated the following autumn and winter. The book is therefore organized differently to a traditional "The Ecology of …." textbook, which in different chapters would focus on the physical, chemical, and biological components. Here we have strongly emphasized the seasonal variation in all parameters, considering that a large part of this ecosystem melts and disappears in spring and summer, and is re-established again in autumn and winter. The physical, optical, biological, and chemical conditions are then described in each chapter according to their seasonal context. For instance, physical ice growth and ice formation are more prominent features during autumn compared to winter when there is solid ice with minor variations in the physical conditions. Accordingly, the book is organized in three seasonal chapters: autumn, winter, and spring/summer, with focus on important and dominant seasonal parameters, and how these affect and relate to the sympagic biota of ice algae, bacteria, and meiofauna. The chapters also include several case studies based on the authors fieldwork

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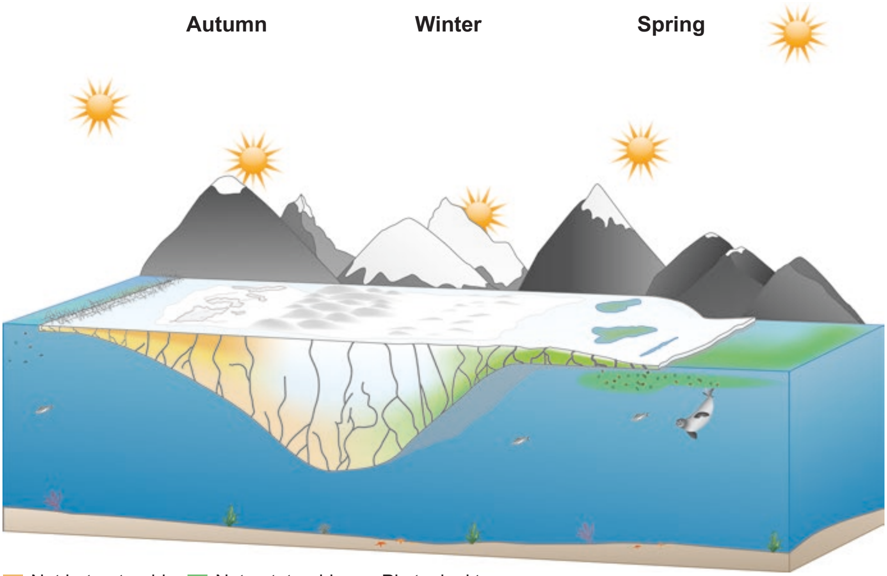

Fig. 1.1 Schematic representation of the evolution of bacterial productivity (net heterotrophic in orange) and algal productivity (net autotrophic in green) in ice-covered seas during all phases of the sea ice formation and decay cycle in the Arctic

in Greenland, the Arctic Ocean, Fram Strait, and Antarctica to exemplify themes and topics from the general text. The final chapter is a methods section, where methods commonly applied in sea ice ecology research are described in more detail, for the benefit of readers seeking a deeper understanding. The scenario of the book is envisaged in Fig. 1.1, which depicts the seasonal progress of the sea ice from its establishment in autumn, through a period of thick ice with a snow cover in winter. This is followed by the decay cycle of thinner ice and snow, and development of melt ponds on the surface of the ice, and finally the complete ice melt. The seasonal succession from yellow/orange colours to greenish depicts the change from a net heterotrophic bacteria-based activity in autumn/winter, to a net autotrophic ice algae-based activity in spring/summer. Grey and branched lines in the ice are the brine channels illustrating that the ice is a porous medium.

1.2 Physical and Geopolitical Perspectives of Sea Ice

Sea ice is an inherent, characteristic, and extremely important entity in polar regions, from physical, chemical, biological, economical, and political perspectives. Sea ice in the Arctic and Antarctic together covers about 10% of the world's oceans at its average winter maximum extent of about 34 million km^2, an area larger than Africa (30.4 million km^2). The Arctic sea ice extent varies between a minimum of

4.7–7.7 million km^2 and a maximum of 14.3–16.3 million km^2 (median values, 1981–2010). The seasonal difference of about 8.0 million km^2 between summer and winter extent is comparable to the total area of the USA (9.6 million km^2). Sea ice cover is also an important indicator and mediator of climate change, as seen from the significant decrease in sea ice extent and volume over recent decades in the Arctic Ocean. Changes in sea ice extent have far-reaching consequences. For example, ice and snow reflect light and radiation back into space, while most of this radiation would otherwise be absorbed in an ice-free water column. It is foreseen that the entire Arctic Ocean will reach an ice-free state for several weeks in summer within three to four decades, except for a few remaining areas of multiyear ice north of Greenland. The sea ice extent during winter is also decreasing, but at a lower rate compared to the rate of the summer ice extent. This decrease in sea ice extent is also driving a growing economical and thereby political interest in the Arctic, with less and less summer ice opening up both the Northeast and Northwest Passages for commercial shipping. These routes are shorter and safer than classical shipping routes and would save expensive fuel. The decreasing extent of summer sea ice has also opened the extensive and shallow (<200 m) Arctic shelf areas, many of which contain huge amounts of oil and gas reserves. Nearly 50% of the Arctic Ocean consists of such shelf areas. Deep-sea mining in the Arctic Ocean for rare elements will also be an issue in the future, and a reduced sea ice cover with more light and more photosynthesis in the water column is predicted to increase fishery catches in the Arctic Ocean. All of the five Arctic countries (USA, Canada, Russia, Greenland, and Norway) have borders in the central Arctic Ocean. These countries have a 200 nautical mile wide zone from their coast and outwards as their sovereign region. However, borders in the central Arctic Ocean have not yet been agreed upon and the countries have specified their territorial claims based on several years of geological exploration in the Arctic Ocean. The UN-founded organization United Nations Law of the Sea Convention (UNCLOS) validates the data presented to support the territorial claims.

1.3 Sea Ice as an Ecosystem

Sea ice ecosystems comprise a physical environment of ice, snow, brine channels and seawater at a particular location with specific pathways and exchanges of energy and matter, and with a variety of organisms that live and thrive there. Organisms living inside the ice in the brine channels or at the bottom of the ice are called sea ice or sympagic biota, and include bacteria, viruses, algae, fungi, ciliates, heterotrophic flagellates, amphipods, copepods, and several others as shown in Fig. 1.2. These organisms form a unique food-web inside the ice, and facilitate specific pathways of matter and transport of energy, as heterotrophic bacteria digest particulate organic material (POM) and or dissolved organic matter (DOM) excreted by the ice algae. Ciliates and flagellates ingest ice algae and bacteria, and their breakdown of organic material also generates inorganic nutrients available for the ice algae and their

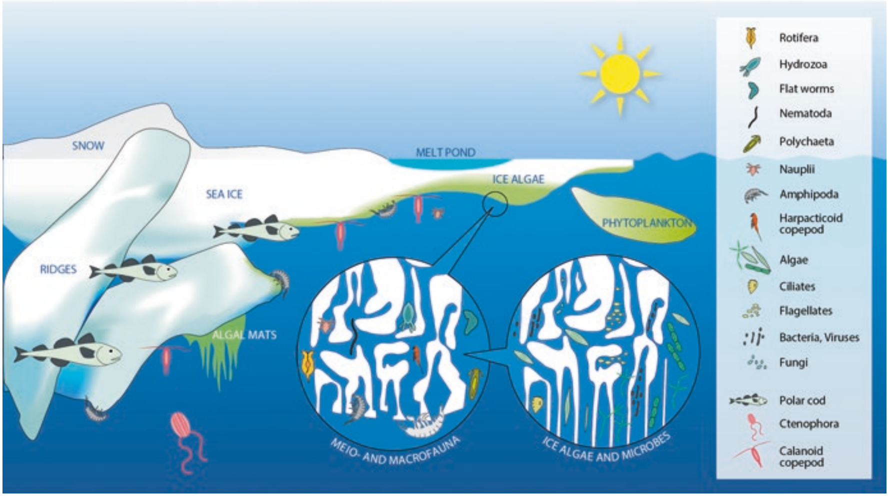

Fig. 1.2 Sea ice ecosystem with microhabitats for a variety of biota including single-celled eukaryotes (labelled algae), meio- and macrofauna, bacteria and viruses, under-ice fauna (amphipods and copepods), and polar cod (*Boreogadus saida*). (Courtesy: State of the Arctic Marine Biodiversity Report, https://www.caff.is/marine/marine-monitoring-publications/state-of-the-arctic-marine-biodiversity-report)

photosynthesis. Metazoans small enough to fit into the brine channel network are termed meiofauna and are mainly herbivores. In addition to the brine channel community, other organisms also inhabit the ice-water interface. Here the in-ice biota interact with other organisms such as larger zooplankton in the water column that also graze on ice algae (Fig. 1.2). The focus of this book is the in-ice biota and especially the ice algae and bacteria. An understanding of the living conditions for ice algae and bacteria implies descriptions of **(1)** the physical growth and structure of the sea ice as a habitat, **(2)** the optical properties of the ice and the overlying snow, especially concerning how much light reaches the ice algae for photosynthesis, and **(3)** the availability and concentrations of nutrients. Sea ice is an extreme environment where survival is challenging for most organisms, though bacteria and ice algae are both halophiles i.e. can live at very high salinities and cryophiles i.e. can live at very low temperatures. Oceans covered with ice are also found elsewhere in the solar system, such as on Saturn's moon Enceladus, and given this resemblance, sea ice is also of great interest in an astrobiological context given that sampling there is not an option yet (Martin and McMinn 2018). Ice algae attached to the sea ice or inside the brine channels are species of microalgae that have adapted to this high saline, low light, and cold environment. Some of the ice algae species also occur as drifting organisms in the water column below termed phytoplankton, where the main difference is that ice algae are fixed in position in or on the ice. It is estimated that sea ice algae account for a modest 4–6% of the pelagic primary production in the entire Arctic Ocean, but their major importance is being the only carbon source during late winter and early spring for higher trophic levels in the Arctic food chain (i.e. ice algae → zooplankton → fish → seals → polar bears). The pelagic carbon production is based on phytoplankton in the water column and commences after sea-ice surface melt and ice break-up. The important role of the sea ice algae is illustrated in a recent study suggesting that 70–100% of the polar bear diet is derived from sympagic ice algae rather than pelagic phytoplankton, meaning that 70–100% of their food intake occurs during the ice-covered season, and further emphasizes the animals dependence on sea ice (Brown et al. 2018).

1.4 Ecological Role of Sea Ice

Sea ice algae primary production in the Arctic Ocean is about 20 Tg C year^{-1} (Arrigo 2017) compared to a pelagic primary production in the Arctic Ocean of 350–500 Tg C year^{-1} (Sakshaug 2004). Primary production rates in Arctic sea ice vary between 0.2 and 463.0 mg C m^{-2} day^{-1} (Arrigo 2017) which is low compared to e.g., estuarine ecosystems with rates up to 4101.0 mg C m^{-2} day^{-1} (Stiling 1996). The highest ice algal production rates are comparable to the 342.0 mg C m^{-2} day^{-1} reported for oligotrophic open oceans (Stiling 1996). There is, on the other hand, considerable spatial variation in rates of ice algae primary production in the Arctic, with average rates of 116.8 mg C m^{-2} day^{-1} and 93.7 mg C m^{-2} day^{-1} reported for the Canadian Arctic Archipelago and the North Water polynya area in Northern Baffin Bay, respectively (Arrigo 2017). Much lower rates of 0.1 mg C m^{-2} day^{-1}, 8.6 mg C m^{-2} day^{-1} and 21 mg C m^{-2} day^{-1} have been reported from various areas around Greenland (Rysgaard et al. 2001; Mikkelsen et al. 2008; Lund-Hansen et al. 2018). Ice algae production data in Fig. 1.3 comprise mostly coastal and shelf areas, based on the ^{14}C incubation method (Sect. 6.6). These differences in production rates between Greenland and the Canadian Arctic Archipelago are significant despite possible minor methodological variations. The reasons for the differences

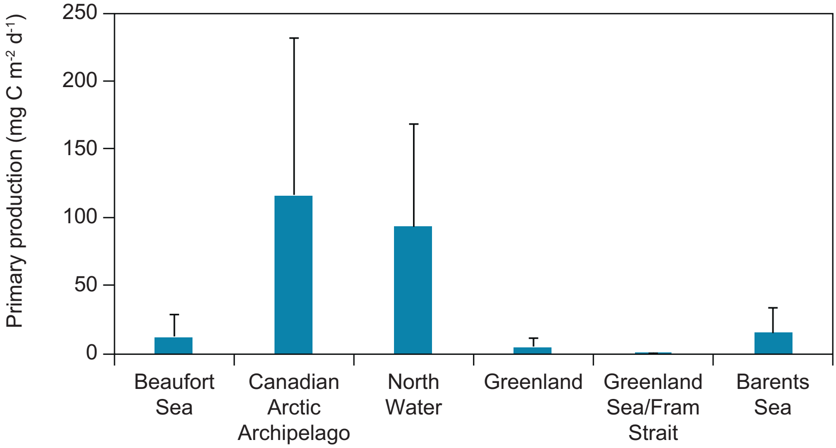

Fig. 1.3 Ice algae primary production in different Arctic regions. Data points represent treatment mean ± SD (Compiled from Barber et al. 2015; Leu et al. 2015; Arrigo 2017)

are unknown but studies have pointed towards the effects of nutrient availability and differences in water column stratification. A strong stratification inhibits vertical mixing and transport of nutrients from below to the surface layer (Schuback et al. 2017), and is important at points in time when the surface layer is depleted of nutrients. Exchange of sea ice brines and seawater between the ice and the water column induced by under-ice currents may additionally transport nutrients into the ice, and may be a key driver of productivity in land-fast sea ice regimes open to coastal currents and tidal influence (Cota and Horne 1989; Meiners and Michel 2017). Areas with high primary production rates as in the Canadian Arctic Archipelago (Fig. 1.3) are generally also areas of high Chlorophyll *a* (Chl *a*) concentrations as a proxy for ice algae biomass, which also varies between sites and over time (Fig. 1.4). Ice algal

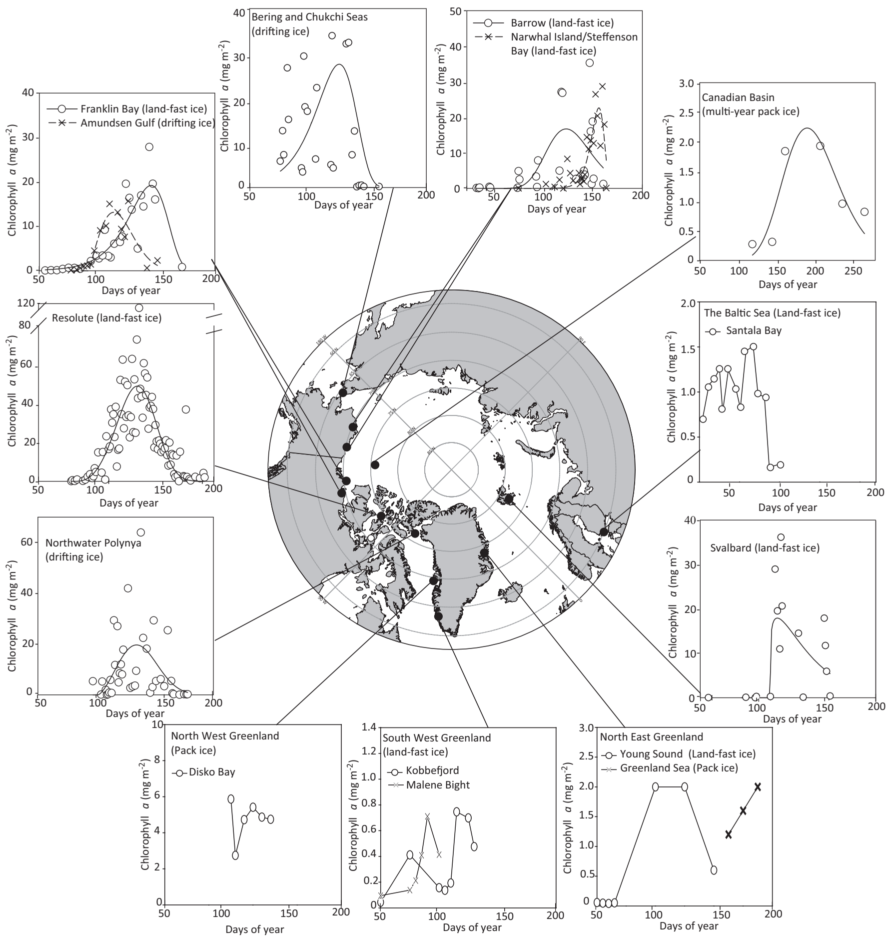

Fig. 1.4 Seasonal development of Chl *a* concentrations in sea ice in different regions of the Arctic. (Modified from: Leu et al. 2015) with additional data from the Baltic Sea (Kaartokallio 2004), Young Sound (Søgaard et al. 2019, Rysgaard and Glud 2007), Greenland Sea (Gradinger 1999), Disko Bay (Buck et al. 1998) and Malene Bight (Søgaard et al. 2010). (Note different ordinate scales for Chl *a*)

production, and the increase in biomass, can potentially start at first light and depends on snow and sea ice thickness as well as latitude. Time-series of seasonal irradiance (PAR) from three research stations at 81°, 74° and 64° N in Greenland demonstrate how the sun rises later and sets earlier with increasing latitude (Fig. 1.5). PAR is the photosynthetic active radiation between 400 and 700 nm (visible light)

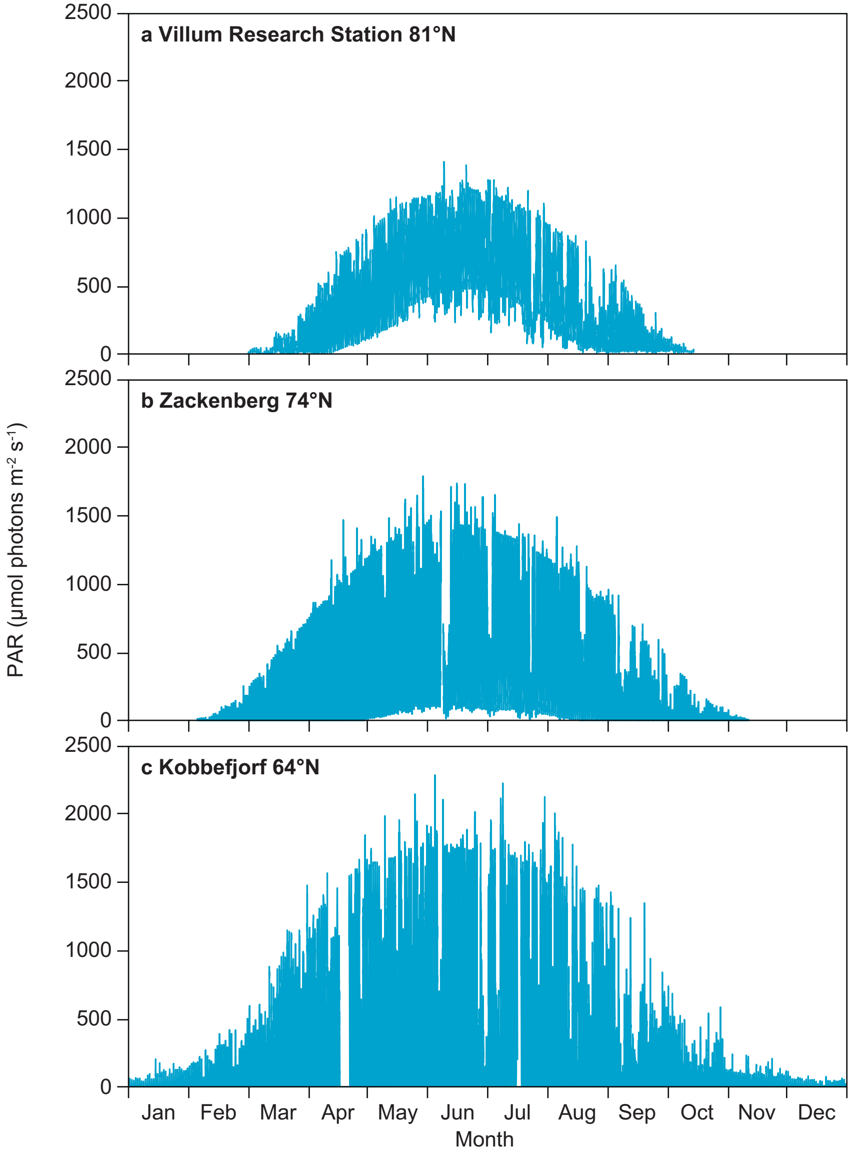

Fig. 1.5 Seasonal irradiance (PAR) at Villum Research Station, NE Greenland (81°N) (**a**), at Zackenberg Research Station, NE Greenland (74°N) (**b**), and at Kobbefjord, SW Greenland (64°N) (**c**)

utilized by the algae for photosynthesis. Midnight sun prevails between mid-April and the middle of August at 81° N but for a shorter period at Zackenberg at 74° N. In comparison there is no midnight sun at lower latitudes (64° N), but the sun is always above the horizon during winter. The summer PAR maximum decreases with latitude from a maximum of 1800 μmol m^{-2} s^{-1} at 64° N in Kobbefjord near Nuuk to about 1200 μmol m^{-2} s^{-1} at Station North. In accordance, there is a general increase in Chl *a* concentrations from mid to late April between latitudes 70°–80° N, and earlier at lower latitudes (Leu et al. 2015) (Fig. 1.4). This is exemplified by the beginning of April increase in Chl *a* in the Northwater Polynya (76° N), which starts in late February further south (64° N) in the Godthåbsfjord (Fig. 1.4). There is an average time span of about 90 days (3 months) between the initial increase in Chl *a* and when Chl *a* once again decreases to minimum concentrations. The size of the bloom varies significantly between a maximum of nearly 120 mg Chl *a* m^{-2} in Resolute Bay, Canada, and around 0.5 mg Chl *a* m^{-2} in Young Sound, NE Greenland. Organisms living inside the ice together form the sympagic communities and comprise taxonomically diverse groups including Eubacteria, Archaea, ice algae, viruses, fungi, ciliates, heterotrophic flagellates, amphipods, copepods, polychaetes, nematodes and more (Fig. 1.2). The communities can be divided into three main groups based on the size of the organisms (Bluhm et al. 2017). The first group is sea ice microbes including ice algae, Eubacteria, and Archaea; the second group is sea ice meiofauna consisting of multicellular organisms in the range 62–500 μm such as rotifers and nematodes; the third group comprises sea ice macrofauna organisms >500 μm such as amphipods and large copepods. The Eubacteria and Archaea use and decompose the organic material produced by ice algae, thereby remineralizing nutrients for primary production by the ice algae (Deming and Collins 2017). The sea ice meiofauna grazes on the ice algae as observed in Arctic Canada, where Grainger and Hsiao (1990) estimated that the meiofauna in the ice could consume about a quarter of the ice algal biomass. Typical estimates of meiofauna biomass from other areas in the Arctic and Antarctic are lower and often below 10% of the algal biomass (Gradinger 1999). Amphipods such as *Gammarus wilkitzkii*, *Onisimus glacialis* and *Apherusa glacialis* also graze directly on the ice algae, with relatively high grazing rates for all three species, e.g., *Gammarus wilkitzkii* can graze up to 73% of the ice algae biomass (Brown et al. 2017). The zooplankton species grazing on ice algae are generally *Calanus hyperboreus, C. finmarchius*, and *C. glacialis,* which are dominant species in the Arctic (Espinasse et al. 2017) but with different ecologies (Scott et al. 2000) (Fig. 1.6). Lønne and Gulliksen (1991) gave a comprehensive study of the sympagic fauna and food chain in the Barents Sea. Ice algae grazed by amphipods and zooplankton are consumed and establish a secondary pathway of organic material in the ice-pelagic-benthic coupling. Studies have established organic carbon budgets for the various components in the Arctic marine food web of the Barents Sea (Reigstad et al. 2011; Kortsch et al. 2015), where stable isotope compositions are often applied in carbon budget and food web structure analyses (Pineault et al. 2013). The zooplankton and the amphipods are again consumed by fish and especially the polar cod (*Boreogadus saida*), a circum-Arctic

Fig. 1.6 The Arctic copepod *Calanus hyperboreus*. (Photograph by: Authors)

Fig. 1.7 A deep sea cucumber (*Kolga hyalina*) (5–6 cm) feeding on clumps of the ice algae *Melosira arctica* at 3569 m depth in the Arctic Ocean. (Photograph by: Antje Boetius)

species that occurs in high numbers near sea ice (David et al. 2016). The polar cod is strongly dependent on the occurrence of ice algae, as stable isotope analyses have shown that between 34% and 65% of the carbon taken up by polar cod is derived from ice algae through grazing on amphipods and copepods (Kohlbach et al. 2017). Much of the organic material produced by the ice algae and not grazed by the zooplankton sinks towards the ocean bottom (Juul-Pedersen et al. 2008; Szymanski and Gradinger 2016) where it is available for benthic organisms on the shelf (Tamelander et al. 2006) and in the fjords (McMahon et al. 2006). It was recently observed that ice algae contribute organic material to the deep sea where invertebrates (*Kolga hyalina*) feed on clumps of the ice algal diatom *Melosira arctica* at 3569 m depth in the Arctic Ocean (Boetius et al. 2013) (Fig. 1.7). During late spring or early summer when the sea ice starts to break up, some of the ice algae leave the ice, either due to formation of larger brine channels and flushing at increased sea ice temperatures, or due to melting of the ice at the bottom. This transfer of ice algae from the sea ice to the pelagic water seeds the water column, and can initiate the pelagic primary production (Gradinger 2009; Selz et al. 2018). It was until very recently assumed that the pelagic primary production below the ice was extremely low and insignificant during the ice covered period, but several recent observations of pelagic phytoplankton blooms below sea ice have changed this view (e.g. Mundy et al. 2009; Arrigo et al. 2014). With younger and thinner sea ice, coupled with an earlier onset of snow melt and increased melt pond formation, it is foreseen that such under-ice blooms will be more frequent in the future (Arrigo et al. 2014; Horvat et al. 2017). It is, on the other hand, unknown how the under-ice blooms will affect ice algae communities and if this bloom is driven by seeding from the sea ice to the underlying water column.

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