

# Ecosystem Assessment of the Central Arctic Ocean: Description of the Ecosystem

Volume 355 | July 2022

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# ICES Cooperative Research Report

Volume 355 | July 2022

## Ecosystem Assessment of the Central Arctic Ocean: Description of the Ecosystem

Editor

Hein Rune Skjoldal

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## I Summary

The report provides a description of the ecosystem in the Central Arctic Ocean, or CAO. This is a deep-sea area with two main basins of depths to 4–5 km, separated by the Lomonosov Ridge. The CAO is a globally unique ecosystem, characterized by presence of sea ice and very low primary production by phytoplankton and ice algae. Atlantic water flows into the CAO through the deep Fram Strait and across the Barents Sea shelf, and continues as a set of boundary currents anti-clockwise around the slopes of the CAO basins. The circulation of the boundary currents takes place at an intermediate depth of about 200–1000 m, underneath a gradient layer with strong salinity and density stratification, and a seasonally dynamic top layer with two prominent circulation features: the Beaufort Gyre in Canada Basin, and the Transpolar Drift across the North Pole that exits in Fram Strait. A smaller amount of Pacific water (ratio of about 1:5 to Atlantic water) flows north through the Chukchi Sea and into the gradient layer between the surface polar water and the deeper Atlantic water of the boundary currents. The Pacific water exits primarily through Canadian Arctic Archipelago passages into Baffin Bay.

The circulating waters and floating sea ice form the dynamic habitats of the animals and plants that constitute the living part of the CAO ecosystem. Large calanoid copepods, with *Calanus hyperboreus* as the most important species in terms of zooplankton biomass, reproduce successfully mainly in the peripheral parts of the CAO with seasonal ice cover. Sea ice amphipods, with *Gammarus wilkitzkii* and *Apherusa glacialis* as the two most prominent species, are the dominant group among the sea ice invertebrate fauna. An important issue addressed in the report, is how the ice fauna can maintain their populations by recolonizing new sea ice as it forms in autumn and winter.

About 50 species of fish have been either found (39 species), or are considered likely to occur (14 species), in the CAO. Most of them are small species, dominated by eelpouts along the basin slopes, and sculpins on the upper slopes and surrounding shelves. Two small cods, polar cod (*Boreogadus saida*) and Arctic cod (*Arctogadus glacialis*), are assumed to be the most important fishes in the CAO foodwebs. Thirty-five species of birds and 35 species of marine mammals have been recorded in the CAO. Most of them are seasonal visitors, and the CAO plays small roles for their populations overall. Exceptions to this are two species of gulls, ivory gull (*Pagophila eburnea*) and Ross's gull (*Rhodostethia rosea*), for which the marginal ice zone of the CAO in late summer provides a habitat for large parts of their global populations. Polar bear (*Ursus maritimus*) is the marine mammal with strongest dependence on sea ice habitats in the CAO. Considerable parts of several subpopulations of polar bear (Barents Sea, Laptev Sea, Chukchi Sea, Southern and Northern Beaufort Sea subpopulations) move seasonally with the retreating sea ice into the CAO in summer.

There has been a large loss in sea ice since the 1990s in what is termed the “Great melt”, with a pronounced change from heavier multiyear pack ice to thinner annual ice. The report describes some of the associated changes in the CAO ecosystem associated with the loss and change in sea ice habitats. However, the main aim of this report is to provide detailed descriptions of the current CAO ecosystem and its various components, thereby providing a basis for more in-depth assessments on the impacts of climate change and other human activities in future.

## II Foreword

The International Council for the Exploration of the Sea (ICES), together with the Protection of the Arctic Marine Environment (PAME) Arctic Council working group, established the ICES-PAME Working Group on Integrated Ecosystem Assessment of the Central Arctic Ocean (WGICA) in 2016. One year later, the North Pacific Science Organization (PICES) joined as a sponsor of the group, which then became the joint ICES-PICES-PAME WGICA (hereon referred to as WGICA).

As reflected by the name, the purpose of WGICA is to conduct integrated ecosystem assessments (IEA) of the Central Arctic Ocean (CAO). Like other assessments, an IEA is both a process (the process of doing an assessment) and a product (the documented outcome of the assessment). This report is the first output from the WGICA IEA work. It is not a fully-fledged IEA report, but rather, it takes the first important step of providing a description and overview of the CAO ecosystem, the subject (the patient in a medical sense as a metaphor) that is being assessed.

Why are we doing an IEA for the CAO? It is an important step for implementing the ecosystem approach to management [EA, or its synonymous term ecosystem-based management (EBM)]. An expert group in the Arctic Council has established a framework with six elements (IEA being one of them), and a first set of guidelines based on the framework for implementing EA to management of Arctic Large Marine Ecosystems (LMEs). ICES views IEA as an important mechanism for promoting the development of EA, and has established regional working groups to perform IEAs, e.g. for the Barents Sea, Norwegian Sea, and North Sea LMEs.

There is no blueprint for how to do an IEA. What is clear is that it needs to include an assessment of the state of the ecosystem and its various components, and of the impacts of human activities that occur in, or otherwise influence, the ecosystem. The present report deals primarily with the first part, the state of the ecosystem. A second report is being prepared by WGICA which will build on this report and address human activities and impacts, including climate change, pollution, and shipping.



R.V. Polarstern. Photograph credit: Pauline Snoeijjs Leijonmalm.

# 1 Introduction

*Alf Håkon Hoel, David Fluharty, and Hein Rune Skjoldal*

This section explains the geographical scope of this work, and provides a short introduction to the Central Arctic Ocean (CAO) ecosystem, which is the subject of the assessment. This is followed by a short explanation on the structure and content of the current report. The final section of this introduction gives an overview of the governance framework of international agreements that apply to the CAO. This provides a contextual background to the integrated ecosystem assessment (IEA) work that is done by WGICA.

## 1.1 Geographical scope

The Arctic Ocean as a geographical name is used with two different meanings:

1. In a wide sense, it pertains to the entire area of the ice-covered Arctic seas, including peripheral seas such as Baffin Bay, Hudson Bay, Greenland Sea, and the northern Bering Sea.
2. In a narrower sense, it is the sea area north of, and land-locked between, the Eurasian and North American continents.

We use Arctic Ocean in this latter sense in this report. This sea, the Arctic Ocean, is part of the larger Arctic Mediterranean Sea, which is the sea area north of the ridge running from Scotland via Iceland to Greenland.

The Arctic Ocean consists of two main parts: deep basins and surrounding shelves ([Figure 1.1](#)). The shelves are particularly wide and shallow on the Eurasian side. The total area of the Arctic Ocean is about 9 million km<sup>2</sup>, divided approximately equally between basins and shelves. The name Central Arctic Ocean is used for the basin part of this sea area, not including the shelves. The basins of the CAO are separated from the shelves by continental slopes. The slopes are the walls of the basins, and should be considered integral parts of the basins. The slopes steer ocean currents, which constrain the distribution of water masses in the CAO. The focus of this report, and the IEA work from WGICA, is the CAO, which is thus comprised of the deep basins, including the continental slopes but excluding the surrounding shelves. However, information is included regarding features and processes of the shelves that influence conditions and dynamics of the basins. This is especially the case for the two gateways, Atlantic and Pacific, which connect the CAO to the North Atlantic and North Pacific. Similarly, the conditions and status of the Barents Sea or Northern Bering–Chukchi Sea Large Marine Ecosystems (LME) are not assessed in this report, but information about these adjacent areas is included if it is relevant to conditions in the CAO.

Large-scale migrations of birds, marine mammals, and, to some extent, fish, are very prominent features of Arctic marine ecosystems (AMAP/CAFF/SDWG, 2013). The Arctic is used as a feeding and breeding place during the short and productive summer, whereas most birds and many mammals leave the Arctic to spend winter farther south, including the southern hemisphere for birds. The migrations provide functional links between the Arctic and lower-latitude ecosystems. For migratory birds and mammals, this report takes a broader look to assess the extent to which species currently use habitats in the CAO on a seasonal basis, or could do so in the future as a consequence of the poleward expansion of their ranges.



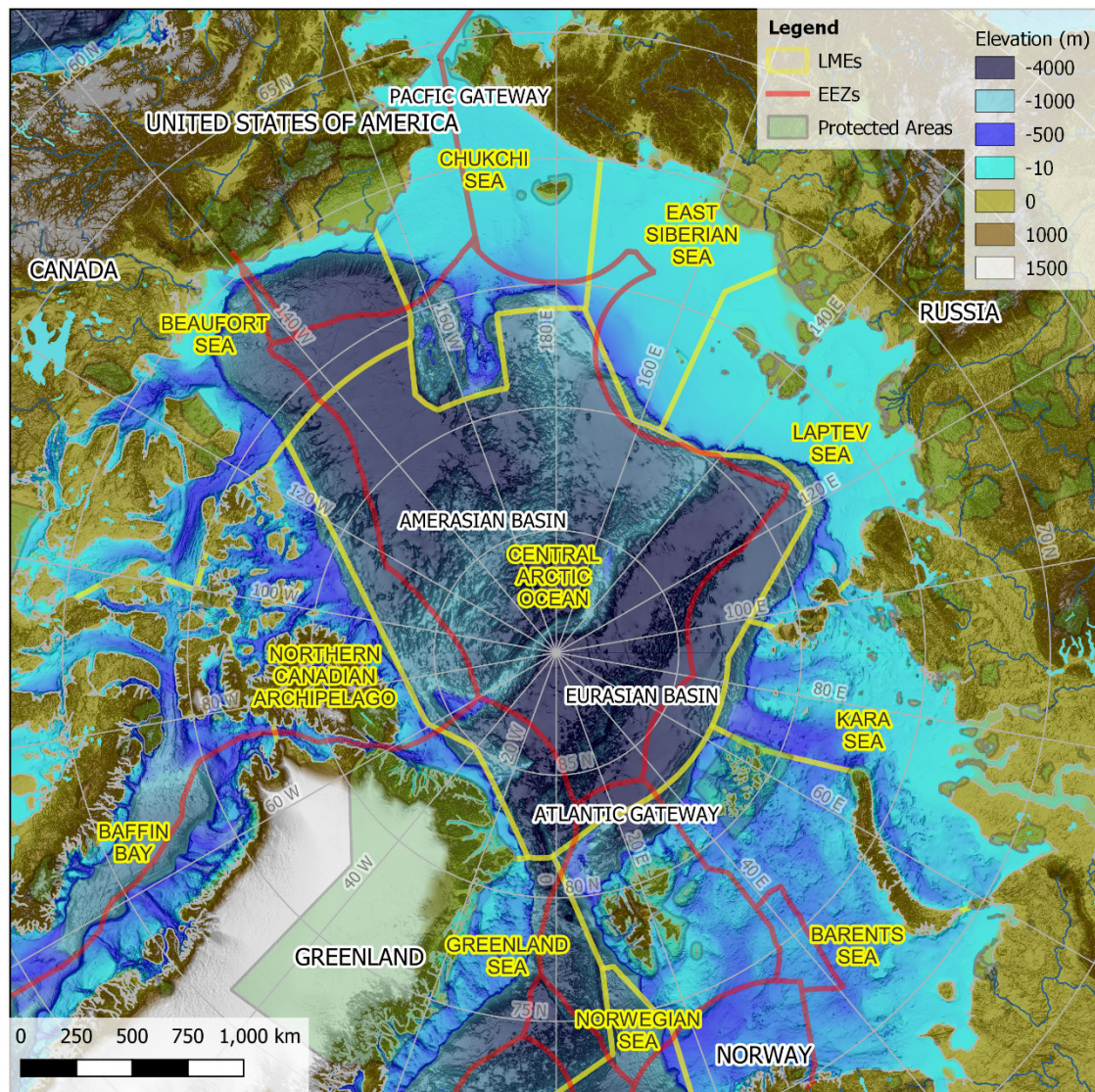


Figure 1.1. Geography and boundaries of the Arctic Ocean consisting of the deep Eurasian and Amerasian basins surrounded by shelf seas. The red lines are political boundaries between areas under national jurisdiction (Exclusive Economic Zones) and high seas areas beyond. The yellow lines are defined boundaries for Large Marine Ecosystems (LMEs) identified for the purpose of applying the ecosystem approach to management.

## 1.2 The CAO as an ecosystem

The first element of the framework to implement the ecosystem approach to management (EA) is to identify the ecosystem (PAME, 2017, 2019). This has been done by delineating 18 Arctic LMEs based on ecological criteria (PAME, 2013). The criteria are general and include bathymetry, hydrography, productivity, and trophic linkages.

The Central Arctic Ocean LME ([Figure 1.1](#)) includes the main basins of the CAO, but is defined as a more geographically restricted area than the CAO considered in this report. The upper slope (down to 1000 m depth) along the Eurasian continent was included with the adjacent shelf LMEs (Barents Sea, Kara Sea, Laptev Sea, and East Siberian Sea). The reason for this is the strong ecological connections between the upper slopes and shelves, which made it preferable to include the upper slope as part of the shelf ecosystems. The deep extensions of the Chukchi shelf (Chukchi Rise and Northwind Ridge) were included as part of the Northern

Bering–Chukchi Sea LME. The southeastern part of the Canada Basin (north to 76°N) was included as part of the Beaufort Sea LME, based on productivity considerations (PAME, 2013). The choice of LME boundaries is, in the end, based on pragmatic and practical considerations. WGICA considered that the Central Arctic Ocean LME was too narrow for the purpose of this work, and, therefore, also included the upper slope, the Chukchi Borderland, and the Beaufort Sea portion of the Canada Basin in the area considered as the CAO in this report.

The CAO ecosystem is not clearly recognizable as an integrated and consistent functional ecological unit. It is a unit in a geophysical sense, made up of basins and surrounding slopes. What makes it unique is the drifting pack ice with its associated biota. The multiyear ice pack, which is now declining, is found only in the CAO and its exits through the northern Canadian Arctic Archipelago and the Fram Strait. Ice algae, ice amphipods, and other ice biota constitute unique components of the ecosystem from both productivity and biodiversity perspectives. The plankton of the CAO are mostly of Atlantic origin, and the species are inhabitants of the Arctic Mediterranean Sea. The CAO portion of this larger sea area is an extreme environment in terms of seasonal variation (e.g. polar night) and low productivity, which the species living there need to cope with.

The CAO ecosystem has distinctive hydrography and productivity features that are related to the bathymetry of the system. Although there is considerable spatial heterogeneity, the unique characteristics of the CAO (e.g. sea ice and hydrographic stratification) impose some degree of uniformity on the ecosystem. For the algae, microorganisms, and invertebrates that comprise ice biota and plankton, the concept of populations is unclear and diffuse. There may not be distinct spatial populations for these groups, but rather distributions of species over wide areas that comprise populations in an ecological sense. With migratory animals, including fish, the situation is very different. The ability to migrate leads to the emergence of spatial migratory patterns and population units that possess the knowledge of migratory patterns. Over long evolutionary time periods, this may lead to genetic differentiation into distinct subspecies, which is a characteristic feature of many migratory Arctic-breeding birds (AMAP/CAFF/SDWG, 2013).

There are few, if any, distinct animal populations that live and interact with other species inside the CAO ecosystem. It is possible (based on some observations) that Arctic cod (*Arctogadus glacialis*) forms a migratory population in the Amerasian Basin, but this has not yet been confirmed. There is also a subpopulation of polar bear (*Ursus maritimus*; Arctic Ocean subpopulation) that may reside in the CAO, although it is also possible that these bears are associated with the northernmost part of the Canadian Arctic Archipelago and North Greenland. Therefore, the CAO is not an ecosystem where distinct animal populations live as permanent residents, interact through trophic linkages in foodwebs, and contribute to the system characteristics. Instead, there are many populations of birds and marine mammals that frequent the CAO on a seasonal basis, where they use habitats for feeding and possibly over-summering when sea ice is at its seasonal minimum. The system characteristics – what ties the CAO together as an ecosystem – is primarily related to the interactions among lower trophic levels and their dependencies on the physical realm, where sea ice is a prominent feature.

### 1.3 The content of this report

In this report, the CAO ecosystem is characterized through descriptions of the main compartments and components of the ecosystem. This follows a traditional structure with sections on bathymetry (the "landscape"), oceanography and sea ice, plankton, ice biota, microorganisms, benthos, fish, birds, and mammals. The descriptions are detailed and summarize what we know from the literature on CAO studies over many decades. For plankton

and ice biota, descriptions of general patterns are provided, with a focus on the most important species. One main aspect covered is the level of primary production (PP) by phytoplankton and ice algae, and how production is constrained by physical conditions, notably the presence of sea ice.

All species of fish, birds, and marine mammals that are known to occur, or might occur, in the CAO are described. Emphasis is given to the spatial aspects of species distribution and to trophic linkages, by summarizing information on feeding ecology and likely food sources for the species in the CAO. For fish, all the known species from the CAO are described, as well as from the surrounding Arctic shelves. Some of these species are coastal and are unlikely to expand into the deep CAO. For other species that live on the shelves, there are gradients regarding the degree to which they extend their range over the shelf edge and down the slope to the deep basins.

For birds and mammal species, which are migratory on a seasonal basis, overviews are provided with information on all species that are known to occur, or have been recorded from, the CAO area. For these groups, information is included on subspecies (which are distinct races or forms of the species) and populations or stocks, to the extent that such subdivisions exist and are known. A broad view is taken of species and populations around the CAO, on both the Atlantic and Pacific sides, to evaluate the potential for expansion into the CAO.

The information from the various chapters on ecosystem components is brought together in a synthesis section called “Key characteristics of the CAO ecosystem” ([Section 2](#)). This is a version of a conceptual model of the CAO ecosystem. The ecosystem is both simple and complex. It is simple in that there are small numbers of dominant species of ice biota and other components that carry out much of the action in the ecosystem (e.g. energy flow), and in that there are very prominent annual cycles in physical conditions, between polar night and polar day, that have overriding influence on biological conditions. It is complex in its spatial heterogeneity, which is partly related to its large size (about 4.5 million km<sup>2</sup>) that stretches between the Atlantic and Pacific gateways.

The CAO is undergoing climate change, with a substantial loss of sea ice that has been taking place since the 1990s in what has been called the “great melt”. The changes in sea ice and some of the associated changes in oceanography are described. Biological and ecological changes are also noted that have taken place in recent decades, likely as a result of warming and loss of sea ice. However, the temporal changes in physics and biology related to warming will be dealt with more thoroughly in the next report from WGICA, which will address impacts of climate change as well as other human activities.

## 1.4 The international governance framework for the CAO

The CAO area is under the jurisdiction of the five coastal states to the Arctic Ocean (Russian Federation, USA, Canada, Denmark/Greenland, and Norway), except for a high seas area of 2.8 million km<sup>2</sup> in the middle of the CAO.

The 1982 United Nations (UN) Convention on the Law of the Sea (UNCLOS; Law of the sea, 1982; entered into force in 1994) is the “Constitution of the oceans” and provides the ground rules for how countries are to relate to each other in all marine matters. It contains provisions for the establishment of maritime zones, and principles for the management of natural resources, conduct of marine science, and protection of the marine environment. An implementing agreement to UNCLOS, the 1995 UN Fish Stocks Agreement (UNFSA; UN Fish stocks agreement, 1995; entered into force in 2001), provides additional global rules concerning fisheries management on the high seas and in transboundary areas.



This global framework applies to the Arctic Ocean in the same way that it applies elsewhere on the planet. The Arctic Ocean is nothing special as far as the Law of the Sea is concerned. The most important aspect of UNCLOS is perhaps the establishment of 200-mile Exclusive Economic Zones (EEZ), where coastal states have jurisdiction over natural resources. This means that most of the natural resources in the CAO are already under the control of coastal states (e.g. oil, gas, fisheries, and minerals). In the high seas area beyond the EEZs (currently covered by sea ice during most of the year) UNCLOS provides that flag states are responsible for vessels flying their flag, ensuring that they comply with international obligations that the flag states have over shipping and other activities.

The UNCLOS is ratified by four of the CAO coastal states. USA is not party to the convention, but nevertheless considers customary international law and, therefore, abides by its provisions.

The UNCLOS provides rules for the management of living marine resources, and requires that they be managed sustainably and utilized in an optimal manner. There are also rules pertaining to the management of continental shelf resources, the marine environment, and marine science. With regard to living marine resources, the main rule is that a coastal state decides on the management of such resources inside the 200-mile EEZ off its coast. On the high seas beyond the EEZs, UNCLOS and UNFSA stipulate that states are to establish regional fisheries organizations or arrangements for managing fisheries on the high seas.

Regarding continental shelf resources, it is notable that the continental shelves and slopes in many areas of the Arctic extend beyond the EEZs. In such situations, UNCLOS provides that coastal states are to submit information on their claims to outer limits of the extended continental shelf to the UN Continental Shelf Commission, which provides recommendations on the final limits. In the context of the CAO, it should be noted that continental shelf resources are within coastal state jurisdiction, and that the management of shelf resources is thus a matter for the coastal states.

With respect to environmental protection, UNCLOS rules are vague beyond stipulating a general obligation to protect the environment. For marine scientific research, the main thrust from the regulations in UNCLOS is that scientific activity is to be promoted, subject to certain requirements relating to seeking permission for access to EEZs, and to the publication of results.

The CAO governance regime has been expanded considerably over the last decade through numerous other international agreements, such as the Port State Measures Agreement (FAO, 2009) against IUU (illegal, unreported, and unregulated) fishing, the Arctic Council agreements on international scientific cooperation (Arctic Council, 2017), oil spill prevention (Arctic Council, 2013), and search and rescue (Arctic Council, 2011), as well as the International Maritime Organization (IMO) Polar Code (IMO, 2017), and the agreement to prevent unregulated fishing in the CAO (2018) among the five coastal states as well as the EU and four distant-water fishing countries<sup>1</sup>. Of these agreements, the 2016 agreement on scientific cooperation and the 2018 agreement on prevention of unregulated fishing bring new arenas and opportunities for strengthened research and monitoring in the CAO.

In addition, there is a large number of international agreements besides those mentioned above that pertain to the CAO (PAME, 2012). With regard to science, the International Arctic Science Committee (IASC) represents the scientific community, and the Arctic Council science cooperation agreement, the recent Arctic science ministerials, ICES, and PICES have important roles in these areas. ICES has had an Arctic Fisheries Working Group (AFWG) for about 50

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<sup>1</sup> <https://www.dfo-mpo.gc.ca/international/agreement-accord-eng.htm>. Last accessed 13 June 2022.



years. A recent development is the establishment of WGICA for the cooperation between ICES, PICES, and PAME on an integrated ecosystem assessment for the CAO.

Finally, it is important to note that most of the actual governance of the Arctic takes place on the territories and maritime areas of the Arctic countries and by the Arctic countries. The international aspects of governance can be considered more of a framework or frameworks within which the Arctic states govern the areas under their jurisdiction.

## 2 Key characteristics of the CAO ecosystem

*Hein Rune Skjoldal*

The CAO is a globally unique ecosystem due to its high-latitude location at the "top of the world", the presence of sea ice, the strong vertical stratification from freshwater input, and its low primary production (PP) during a short summer season. It is a large geographical area, with the CAO LME spreading over 3.3 million km<sup>2</sup>.

The CAO consists of two deep basins (around 4000 m deep), the Eurasian and Amerasian (Canadian) basins, separated by the Lomonosov Ridge (about 1000 m deep), and extending from central Siberia to northern Greenland and Canada ([Figure 1.1](#)). The basin slopes are generally steep, separating the basins from wide, shallow shelves on the Eurasian side and narrower shelves on the American side.

### 2.1 The physical realm – the “stage”

Hydrographically, the water masses of the CAO consist of four vertical layers (see [Figure 3.3](#) and [Section 3](#)):

- A top layer, about 50 m thick on average (varying from about 30 to > 100 m), that exhibits large seasonal change. Homogenization occurs in winter due to ice formation and brine rejection, and stratification occurs in summer due to ice melt and stronger riverine input.
- A gradient layer (including the cold halocline) located from about 50 to 200 m depth. The cold halocline is a strong gradient in salinity without a corresponding gradient in temperature (near freezing), which is interpreted to reflect horizontal transport of water from adjacent shelves along density isolines. Pacific water, of lower salinity than Atlantic water by around 2 salinity units, is found in the upper and mid-part of the halocline in the Amerasian Basin, with Pacific summer water layered above Pacific winter water.
- An Atlantic layer at about 200–1000 m depth, with circulating Atlantic water from two main sources, the Barents Sea and Fram Strait branches.
- A deep layer below about 1000 m depth, with water of Atlantic origin that fills the deep basins.

Floating above the top layer is sea ice, which forms a special habitat for a unique biota. Sea ice is broadly classified into first-year ice, formed during the preceding winter, and multiyear ice, which is thicker and may be several years old. Sea ice is a heterogeneous environment with build-up of pressure ridges and opening of leads as it moves around as drifting pack ice.

Sea ice and the different layers of water move in different and partly opposing patterns ([figures 3.4](#) and [3.5](#)). The sea ice and top water layer move with two prominent features: the clockwise Beaufort Gyre in Canada Basin, and the Transpolar Drift across the central ocean towards Fram Strait. The Atlantic layer moves in a system of boundary currents in an anticlockwise direction around the margins of the basins. The Lomonosov Ridge influences the circulation and contributes to establishing sluggish circulation cells in the main basins.

The Arctic Ocean is openly connected to the North Atlantic through the deep Fram Strait. About half of the Atlantic water (approx. 5 Sv; 1 Sv = 10<sup>6</sup> m<sup>3</sup> s<sup>-1</sup>) that enters the Nordic Seas (north of the ridge between Scotland and Iceland) continues into the CAO through the Atlantic gateway.

The residence time of Atlantic water is about 10–60 years, depending on the route, and most of the water leaves through Fram Strait. Pacific water (about 1 Sv) that enters through the Pacific gateway (which is about 1000 km of very shallow water, around 50 m deep, from the northern Bering Sea through the Chukchi Sea), spreads out in the upper halocline layer in the Amerasian Basin, and drains out mainly through the openings of the Canadian Arctic Archipelago and, to a lesser extent, through Fram Strait. The residence time of the halocline water is from one to a few decades, while that of the deep water is several hundred years.

## 2.2 The living part of the ecosystem – the “actors”

The CAO is geologically a relatively new ocean, only about 50 million years old. Due to the open and deep connection through Fram Strait, the CAO is biogeographically an extension of the North Atlantic (as part of the Arctic Mediterranean Sea), and most species are of Atlantic origin. The number of species that are adapted to and capable of living in the harsh Arctic conditions is limited compared to other marine ecosystems, although several thousand species are found among lower trophic-level organisms. There are more than 150 species of zooplankton recorded from the CAO, many of them deep-water species found in the deep basins. About 50 species of fish have been recorded from the CAO (or are expected to occur there), while eight species of marine mammals are found more or less regularly in the CAO. Most animals at higher trophic levels are seasonal visitors to the CAO, and there is no clear evidence of any species populations that are resident and found only in the CAO (except perhaps for Arctic cod and a polar bear subpopulation).

The primary producers are unicellular algae, growing as phytoplankton in the upper lighted water layer or as ice algae in the sea ice or attached to the underside of ice (see [Section 4](#)). Small flagellates and diatoms make up most of the phytoplankton. The ice algae community is dominated by diatoms of various types and species. Among the latter, *Melosira arctica* is an important and characteristic species, forming meter long tufts suspended from the underside of ice floes.

Four species of copepods make up most of the mesozooplankton biomass (see [Section 5](#)): three species of *Calanus* (*C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*) and *Metridia longa*. However, small copepods, including *Oithona* and *Microcalanus* species, are also important components of the CAO ecosystem. The *Calanus* species are predominantly herbivores and feed only during the short summer period, whereas *M. longa* is more of an omnivore. *C. hyperboreus* is a relatively large copepod (ca. 6 mm cephalothorax length) and has a multiannual life cycle (up to four years or even more), which allows it to live in the CAO. It appears to reproduce successfully only in the southern and peripheral areas of the CAO with lighter sea ice conditions. The same is the case for *C. glacialis* which is more common on the surrounding shelves and less important over the deep basins. *C. finmarchicus* is an expatriate (it does not reproduce in the CAO) transported with Atlantic water, primarily through the Fram Strait branch, into the Eurasian Basin.

Amphipods are an important group among the sea ice biota (see [Section 5](#)). *Gammarus wilkitzkii*, *Apherusa glacialis*, *Onisimus nansenii* and *O. glacialis* are common species. *G. wilkitzkii* is the largest (up to 6 cm in length). Another large-sized amphipod recorded on sea ice is *Eusirus holmi*, which has a more pelagic life style and may have become more abundant in the thinner ice regime of the CAO.

The majority of fish classified biogeographically as Arctic species are benthic or demersal, living more or less closely associated with the seabed (see [Section 8](#)). Two dominant groups, by number of species, are sculpins (Cottidae), which tend to dominate on Arctic shelves, and eelpouts (Zoarcidae), which are more common on Arctic slopes. Two small cod are found in the

CAO, polar and arctic cod. Polar cod (*Boreogadus saida*) presumably has migratory populations on surrounding shelves (Barents, Laptev, Chukchi, and Beaufort seas). It is also found under the ice in the CAO, but it is unclear to what extent this represents spillover of larvae and juveniles from the surrounding shelf populations. Arctic cod (*Arctogadus glacialis*) has been found under sea ice primarily in the Amerasian Basin, where it possibly forms a migratory population. Little is known about the species, but it has been speculated (based on observations from previous ice-floe drift stations) that it may migrate to spawn in the Chukchi Borderland region. Greenland halibut (*Reinhardtius hippoglossoides*) is found in the slope region north of the Barents and Kara seas. They belong to the Barents Sea stock, with a spawning area on the western slope into the Norwegian Sea. This species is also found in the Amundsen Gulf region in the eastern Beaufort Sea.

Ringed seal (*Pusa hispida*; see [Section 10.2.2](#)) is a true Arctic species found scattered in small numbers in sea ice of the CAO. Satellite-tracking has shown that individuals from surrounding shelves (Barents, Chukchi, and Beaufort seas) make seasonal excursions in summer into the CAO, presumably to feed on sea ice amphipods and polar and Arctic cod. It is not known whether there is a component of ringed seals that live permanently and breed on pack ice in the CAO.

Polar bears (*Ursus maritimus*; see [Section 10.2.1](#)) of several subpopulations can be found on sea ice in the CAO (Barents Sea, Kara Sea, Laptev Sea, Chukchi Sea, and southern and northern Beaufort Sea subpopulations). A common pattern is that after spending winter breeding in core areas of the respective shelf seas, large fractions of individuals from the various subpopulations migrate north with the seasonally retreating sea ice into the CAO. In addition, there is an Arctic Ocean subpopulation that possibly breeds mainly in the northernmost part of the Canadian Arctic Archipelago. Ringed seal is probably the main prey for polar bears in the CAO.

Bowhead whales (*Balaena mysticetus*; see [Section 10.2.11](#)) of the endangered Spitsbergen population live in the waters north of Svalbard and use the marginal ice zone in Nansen Basin as a foraging habitat in summer. Bowheads of the much larger Bering–Chukchi–Beaufort stock migrate seasonally to feed in the eastern and southern Beaufort Sea. *Calanus hyperboreus* is possibly the main prey item for bowheads of both stocks.

Beluga whales (*Delphinapterus leucas*; see [Section 10.2.9](#)) of the Karskaya stock complex (Barents–Kara–Laptev) and the Beaufort and Chukchi stocks may extend their seasonal feeding migrations into the CAO basins, where they presumably seek polar cod and Arctic cod. Narwhal (*Monodon monoceros*; see [Section 10.2.10](#)) use the slope region north of the Barents and Kara seas and the marginal ice zone of Nansen Basin as habitat, possibly feeding on Greenland halibut and the squid *Gonatus fabricii*. Harp seals (*Pagophilus groenlandicus*; see [Section 10.2.6](#)) from stocks in the Greenland and Barents seas may use the same area to feed in summer, as may some hooded seals (*Cystophora cristata*; see [Section 10.2.7](#)) from the Greenland Sea stock.

There is a limited number of seabird species that are found in the CAO, and they usually occur in small numbers (see [Section 9](#)). These include black-legged kittiwake (*Rissa tridactyla*), thick-billed murre (*Uria lomvia*), and black guillemots (*Cepphus grylle*). There are two gull species for which the marginal ice zone of the CAO constitutes an important habitat for major parts of the populations: ivory and Ross's gull. Ivory gull (*Pagophila eburnea*) breeds on remote cliffs and nunataks in northern Greenland, on islands in the northern Kara and Barents seas, and, in smaller numbers, in Arctic Canada. In late summer and autumn, the population use the ice habitat in Nansen Basin before moving south with the advancing ice in winter. Ross's gull (*Rhodostethia rosea*) breeds on tundra in eastern Siberia. After breeding, the population moves north, and the gulls spread out in the marginal ice zone of the CAO.



## 2.3 Spatial, seasonal, and trophic dynamics – the “play”

Primary production (PP) by phytoplankton and ice algae in the CAO is generally low, reflecting strong light and nutrient limitation. Sea ice and snow cover reduce the light that reaches the water by a factor of 10–1000 (light transmission of 10%–1‰). Nutrients are limited due to the cycle of ice freezing and thawing, which leads to an impoverished upper-water layer with limited nutrient replenishment through vertical mixing. The growing season is short (2–4 months) and seasonally skewed towards late summer, when minimum sea ice cover occurs. The level of annual PP is very low (1–5 g C m<sup>-2</sup> year<sup>-1</sup>) in areas with heavy pack ice, low (10–15 g C m<sup>-2</sup> year<sup>-1</sup>) in areas with lighter ice conditions, and somewhat higher (20–30 g C m<sup>-2</sup> year<sup>-1</sup>) in slope areas. Overall, the area-specific (per m<sup>2</sup>) PP in the CAO is an order of magnitude lower than in adjacent subarctic and boreal seas with open waters (typically 100–200 g C m<sup>-2</sup> year<sup>-1</sup>). There are probably four hot spots of relatively high PP: (i) southwestern Nansen Basin with inflow of Atlantic water, (ii) Laptev sector with the Great Siberian Polynya, (iii) Amundsen Gulf region with the Bathurst Polynya and associated leads, and (iv) Chukchi Borderland region with inflow of nutrient-rich Pacific water. In contrast, the Beaufort Gyre is a region of very low PP due to doming and downwelling in the clockwise gyre.

Phytoplankton and ice algae nourish the growth and reproduction of zooplankton and ice fauna. The coupling between algae and grazers can be complex and involve microorganisms and protozoans in the so-called microbial loop. *Calanus hyperboreus* is predominantly a herbivore that is restricted to feeding on larger phytoplankton since it cannot filter the smallest forms (pico- and nanoplankton < 5 µm in size). Some of the sea ice amphipods can graze on layers of ice algae, while other species are mostly carnivorous. The trophic transfer efficiency from primary producers to herbivores, and then further up the foodweb, is poorly known for the CAO. It could be low due to the apparent large role of small phytoplankton cells, which requires more steps in the microbial loop, with associated metabolic loss, before production can be channeled to larger consumers. However, some parts of the foodweb can be effective, such as sea-ice amphipods grazing on mats of ice algae and being, in turn, eaten by ringed seal.

The four regions indicated with relatively high PP are probably also core areas for reproduction for large herbivorous or omnivorous copepods (e.g. *Calanus hyperboreus*). From these core areas, new cohorts of zooplankton can spread and be transported with currents into less productive parts of the CAO. Advective transport of zooplankton with the inflowing Atlantic water (notably *C. hyperboreus* and the expatriate *C. finmarchicus*) is a major process for sustained production and the energy budget of the CAO. In contrast, transport of Pacific expatriates with inflowing Pacific water is not a significant contribution to the budget for the Pacific sector of the CAO.

There is limited knowledge of the distribution and amount of polar and Arctic cod in the CAO, but it is known that they are present with a wide distribution under the ice. Sea ice amphipods and large zooplankton (such as *C. hyperboreus*, *C. glacialis*, and *Themisto libellula*) are presumably the main food items for these two small cod species. They are, in turn, probably the main prey for ringed seal, which again is the principle food for polar bear while they are summering on the pack ice of the CAO. Sea ice amphipods and other small ice biota and zooplankton are also probably the main prey for ivory and Ross's gulls when they forage in the marginal ice zone of the CAO in late summer. The gulls also feed on faeces and remnants of polar bear kills (e.g. ringed seal). Bowhead whales have fine-meshed baleen and can feed on large copepods including *Calanus glacialis*. It is likely that *C. hyperboreus* is the main prey for bowheads when they are feeding offshore in the Beaufort Sea and, for the Spitsbergen stock, in Nansen Basin. Narwhals are deep divers and may feed on Greenland halibut and *Gonatus fabricii* in Nansen Basin north of the Barents and Kara seas.

### 3 The physical setting: topography, oceanography, and sea ice

*Hein Rune Skjoldal, Randi Ingvaldsen, Vladimir Ivanov, Shigeto Nishino, James Overland, and Muyin Wang*

#### 3.1 Introduction

The physical setting, with the seabed, water masses, and sea ice, is the "stage" where the ecological "play" of the CAO is performed by all the "actors", in this case the interacting species. While the seabed is stationary (at least on ecological time-scales), the water masses and sea ice are moving around, creating very much a dynamic stage. Ocean currents transport plankton into and around the CAO, while seasonal waves of migratory birds and marine mammals come to feed and reproduce in the Arctic during the short summer season, some of them using the CAO 'stage'. A very informative integrated perspective on the physical setting and biology of the CAO was provided recently by Bluhm *et al.* (2015).

In this section, an introductory overview is provided of the CAO physical setting. In [Section 3.2](#), the geomorphology and geographical settings of the CAO are described, i. e. the large-scale seabed topography with deep basins and ridges and the continental shelves that surround the CAO. [Section 3.3](#) addresses water circulation, water masses, and sea ice, which are closely connected aspects of the physical setting of the CAO. Inflow water from the Atlantic and Pacific sides through the two major gateways constitute the basic water masses of the CAO, with major consequences for oceanography. Ice formation and melting in both the CAO and on the surrounding shelves have, in turn, major influences on the water masses. Finally, [Section 3.4](#) deals with atmospheric conditions, and recent changes in CAO oceanography and sea ice related to ongoing warming associated with climate change. The latter is an aspect that will be treated in more detail in later reports from WGICA.

#### 3.2 Topography and geography

The CAO, with its basins, has a roughly rectangular shape with a tapering end towards Alaska and northwestern Canada ([Figure 3.1](#); Jakobsson *et al.*, 2012). It consists of two main basins separated by Lomonosov Ridge: Eurasian Basin (including the Amundsen and Nansen basins) and the Canadian or Amerasian Basin (including the Canada and Makarov basins).

##### **Lomonosov Ridge**

Lomonosov Ridge is a prominent geological feature extending between the New Siberian Islands and the Lincoln Sea area (between northern Ellesmere Island and North Greenland), along the 140°E and 50°W longitudes (Poselov *et al.*, 2014). It is about 1700 km long and 60–200 km wide, with fairly steep slopes on each side, including canyon structures. It is roughly 1000 m deep and rises about 3 km above the seabed of the basins on either side. The minimum depth is about 950 m, and there are deeper passes or saddle points which provide passages for the exchange of deep water between the basins. There is one pass approximately 1700 m deep at about 80.4°N on the Russian side (Woodgate *et al.*, 2001), and another pass approximately 1870 m deep via an intra-basin at about 88.5°N (Bjørk *et al.*, 2007). There is also a relatively deep gap north of Ellesmere Island (roughly 1500 m deep) which connects the Canadian and Eurasian basins. Lomonosov Ridge lies close to the North Pole, which is on the Eurasian side in Amundsen Basin, at about 4200 m depth.

## Eurasian Basin

Eurasian Basin is elongated in shape and bounded to the south by the continental slope from north of Svalbard to the western Laptev Sea, and to the north by Lomonosov Ridge. The short ends of the basin are the slope of northern Greenland to the west, and the slope of the central Laptev Sea to the east. Eurasian Basin is separated by Gakkel Ridge into northern Amundsen Basin and southern Nansen Basin (or Fram Basin). The deep Gakkel Ridge (also known as Nansen–Gakkel Ridge or formerly Nansen Cordillera) is a part of the Mid-Atlantic Ridge that continues north from Jan Mayen as Mohn Ridge, and then as Knipovich Ridge through Fram Strait into the Arctic Ocean. Gakkel Ridge rises 2–2.5 km above the surrounding abyssal plains and is a divergent tectonic plate boundary between the North American and Eurasian plates. It has the form of a rift valley and is the slowest spreading of all oceanic ridges, with a rate of about 1 cm year<sup>-1</sup> (Jokat *et al.*, 2003; Jokat and Schmidt-Aursch, 2007). Gakkel Ridge has been shown to be volcanic, and to have hydrothermal vents and associated mats of very special microbial communities (Edwards *et al.*, 2001; Edmonds *et al.*, 2003; Sohn *et al.*, 2008).

Nansen Basin is located south of Gakkel Ridge, stretches for nearly 2000 km in an east–west direction off the continental slope from north of Svalbard to north of Taymyr Peninsula, and is fairly deep, with an abyssal plain located at 3–4 km depth. Amundsen Basin runs parallel with Nansen Basin between Gakkel Ridge and Lomonosov Ridge and is the deepest of the basins with an abyssal plain deeper than 4 km (Jakobsson *et al.*, 2012). A deposit of sediments of glacial origin is distributed as a geological structure (North Pole Submarine Fan), extending from a source area in the Lincoln Sea and sloping very gently from the northern side at the base of Lomonosov Ridge into Amundsen Basin (Kristoffersen *et al.*, 2004). The Nansen and Amundsen basins are both roughly 300–400 km wide. Yermak Plateau is a geological structure extending north from Spitsbergen and curving east into the western end of Nansen Basin, while Morris Jessup Rise extends north from Greenland and about 200 km into the western end of Amundsen Basin.

## Amerasian Basin

Amerasian Basin (or Canadian Basin) is located between Lomonosov Ridge and the coasts of Alaska and Canada. It has an irregular rectangular shape measuring roughly 1500 by 2000 km, and is divided into two parts, the Makarov and Canada basins, by the Mendeleev and Alpha ridges. Mendeleev Ridge (or Mendeleev Rise) is a broad and irregular ridge, extending north from the Siberian shelf along about 180°W (Dove *et al.*, 2010). Alpha Ridge is a similar broad ridge extending north and west from the shelf north of Ellesmere Island and parallel with Lomonosov Ridge (Weber and Sweeney, 1990). The geological history of the two ridges is not well understood, but a recent study suggests they are contiguous and share a common geologic origin (Jackson and Chian, 2019). The two ridges are located relatively deep, with portions deeper than 2000 m (Weber and Sweeney, 1990; Jakobsson *et al.*, 2012).

Makarov Basin lies between the Mendeleev and Alpha ridges and Lomonosov Ridge, extends for about 1500 km from the East Siberian Sea to Canada, and is about 300–500 km wide. It is 3–4 km deep, and the seabed is more irregular than in Eurasian Basin. Wrangel Abyssal Plain lies between the Lomonosov and Mendeleev ridges off the Siberian shelf, while the Siberia Abyssal Plain lies farther north, closer to the North Pole.

Canada Basin is the largest and widest of the basins in the Arctic Ocean and measures roughly 1000 by 1500 km, and has a depth of 3–4 km. The slope south off Alaska is steep, while the slope off the northern Canadian Archipelago is more moderate. Chukchi Borderland is a prominent and complex extension from the Chukchi Shelf consisting of Chukchi Plateau and Northwind Ridge with a deeper area (Northwind Abyssal Plain) in between (Jakobsson *et al.*, 2008, 2012). Much of the Canada Basin consists of the vast Canada Abyssal Plain that stretches north toward

Alpha Ridge. The geomorphology of this part of the Arctic Ocean has been shaped and influenced by large glacial ice masses that extended into the CAO from surrounding ice sheets over North America and Eurasia during previous ice ages (Jakobsson *et al.*, 2008).

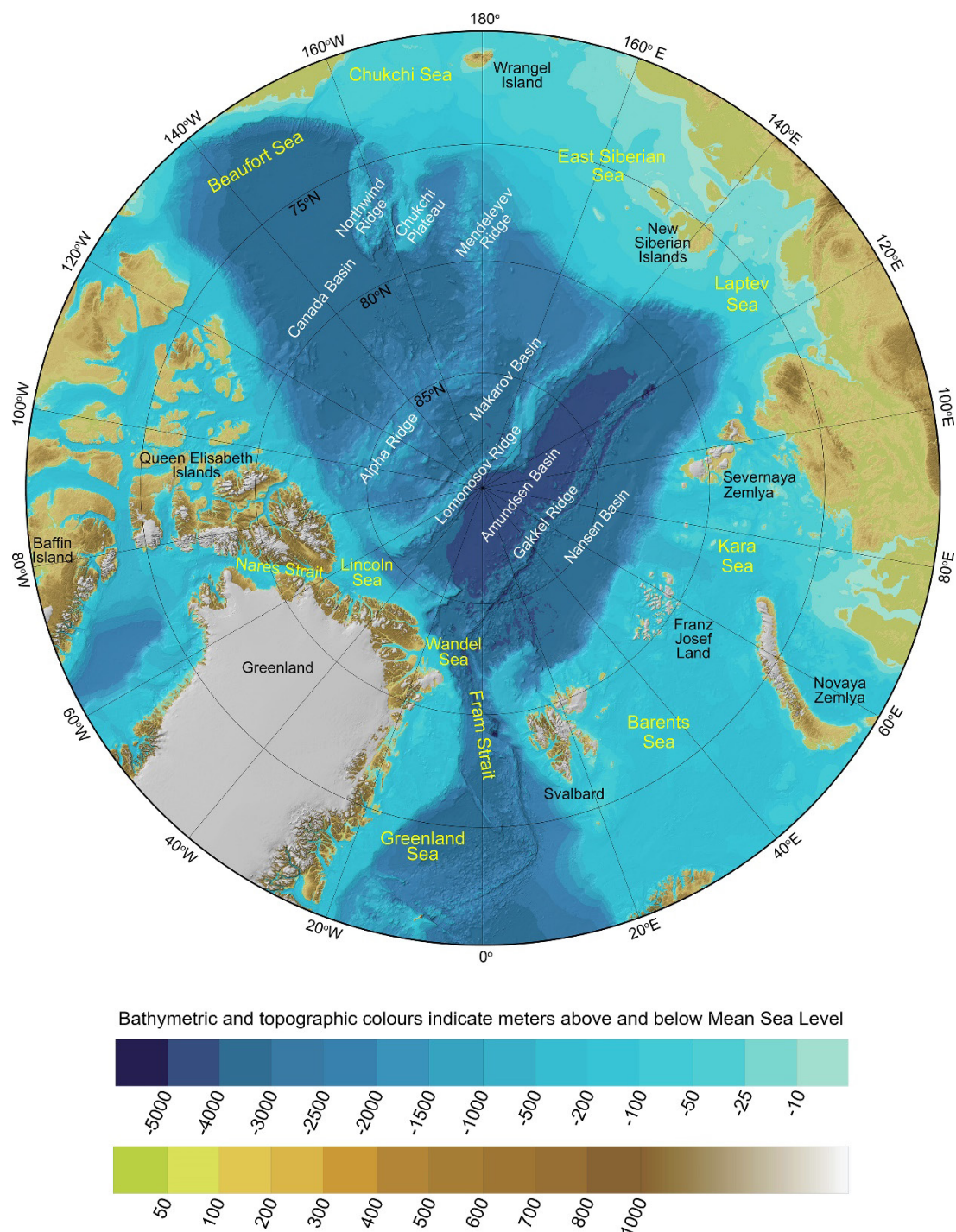


Figure 3.1. Map of the central Arctic Ocean (CAO) showing topographical and geographical features. Based on the International Bathymetric Chart of the Arctic Ocean (IBCAO), Version 3.0 (Jakobsson *et al.*, 2012).





The first extensive study of Arctic Ocean oceanography was carried out by Fridtjof Nansen during the expedition with the ship *Fram*, which was frozen into the ice and drifted across Eurasian Basin from the New Siberian Islands to Fram Strait ([Figure 3.2](#); Nansen, 1902). During that expedition, soundings made to 3.5–4 km depth revealed that the Arctic Ocean was a deep-sea area (Nansen, 1904). Until about 1950, it was believed that the Arctic Ocean consisted of one large deep basin (Sverdrup, 1950). The existence of the Lomonosov Ridge separating the Amerasian and Eurasian basins was inferred from oceanographic measurements made during the aircraft-based "Ski Jump" project in the early 1950s (Worthington, 1953). Soviet scientists had already mapped the ridge in 1948, but the resultant map (prepared by Gakkel) was classified, and the findings were published in the open literature by Burkanov (1954). Since the 1930s, there have been extensive investigations of the Arctic Ocean from ice-drift stations, aircraft, submarines, and ice-breaking vessels. Pioneering contributions to the oceanographic studies were made by Zubov (1944), Timofeyev (1960), Coachman and Barnes (1961, 1962, 1963), Nikiforov and Shpaikher (1980), Aagaard (1981, 1989, Aagaard *et al.*, 1981, 1985), Rudels *et al.* (1991, 1996, 1999, 2004), Rudels and Friedrich (2000), and many others.

### 3.3.2 Five vertical water layers and general circulation pattern

In general, the Arctic Ocean consists of five vertical layers of waters or water masses (Coachman and Barnes, 1961; Nikiforov and Shpaikher, 1980; Rudels *et al.*, 1991, 2004; see [Figure 3.3](#)):

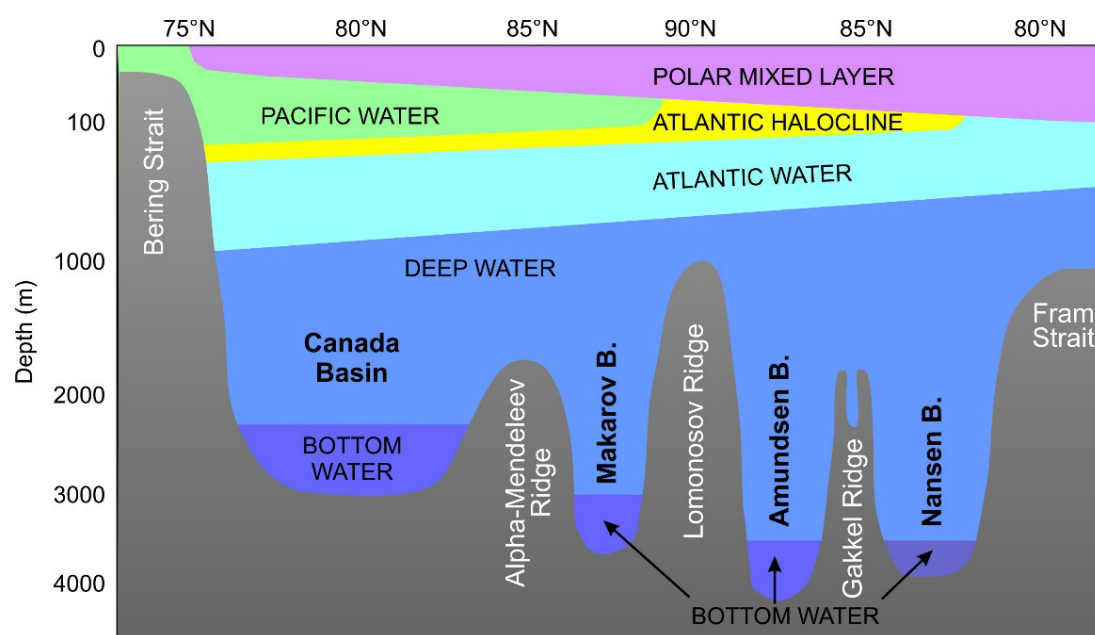


Figure 3.3. Cross section through water masses from the Kara Sea to the Beaufort Sea, crossing the Nansen and Amundsen basins on the Eurasian side, and Lomonosov Ridge, and Makarov and Canada basins on the American side. Note that the depth scale is roughly logarithmic down to about 1000 m, expanding the upper layers. The change in thickness and slope of the interfaces of water masses are exaggerated.

- A surface layer, about 50 m thick, of low-salinity water that is seasonally modified by ice formation and melting. It is referred to as the upper polar mixed layer.
- A gradient layer (halocline), with a strong increase in salinity and density between the surface layer and Atlantic water below, located typically at about 50–200 m depth. Pacific water from Bering Strait contributes to the gradient layer in Amerasian Basin.
- A thick layer of relatively warm (temperature > 0°C) Atlantic water, located below the halocline and down to about 1000 m.

- A deep-water layer of relatively uniform character (temperature between  $-0.7$  and  $-1.0^{\circ}\text{C}$  and salinity of 34.91–34.96) filling the deep basins below the Atlantic layer.
- A bottom-water layer with hydrographic characteristics close to those in the deep water in Eurasian Basin, but distinctly saltier (ca. 34.94–34.96) and warmer (about  $-0.42$  to  $-0.45^{\circ}\text{C}$ ) than the deep water in the Canada Basin (Rudels, 1986).

Sections 3.3.3–3.3.6 provide more information on each of the five layers, starting with the intermediate Atlantic water layer because it sets the stage with strong influence both upwards to the surface layer and downward to the deeper layers.

The circulation in the Arctic Ocean is characterized by through-flow of Atlantic water from the North Atlantic via the Norwegian Sea through Fram Strait and Barents Sea, and of Pacific water through Bering Strait and Chukchi Sea (Coachman and Barnes, 1961, 1963; Aagaard *et al.*, 1985; Aagaard, 1989). The ratio of these two inflows is roughly 5:1 (on the order of 5 Sv Atlantic water and 1 Sv Pacific water). Pacific water has a lower salinity and density than Atlantic water (salinity around 31–33 vs. nearly 35 respectively) and is present mainly in the upper and mid-halocline layer in Canada Basin. It exits the Arctic Ocean mainly through the Canadian Arctic Archipelago into Baffin Bay (Jones *et al.*, 2003; Rudels *et al.*, 2004; McLaughlin *et al.*, 2005). Atlantic water flows into the Arctic Ocean via two main branches (Barents Sea and Fram Strait) and circulates anticlockwise as a set of boundary currents along the slopes of the Arctic Ocean basins, with branches splitting off along Gakkel, Lomonsov, and Mandeleev ridges ([Figure 3.4](#); Timofeyev, 1960; Aagaard, 1989; Rudels *et al.*, 1999, 2000, 2004). The branches of Atlantic water that flow through the various basins come together again off northern Greenland and Morris Jessup Rise in the western end of Eurasian Basin, and continue south through Fram Strait as part of the East Greenland Current (Rudels *et al.*, 1999). Surface circulation is partly decoupled from the deeper circulation of Atlantic water, and is characterized by two prominent features: (i) the Transpolar Drift that flows from the Siberian shelf across the basins via the North Pole towards Fram Strait; and (ii) to its right (relative to the transport direction), the large Beaufort Gyre that spins clockwise (anticyclonic) in Canada Basin.

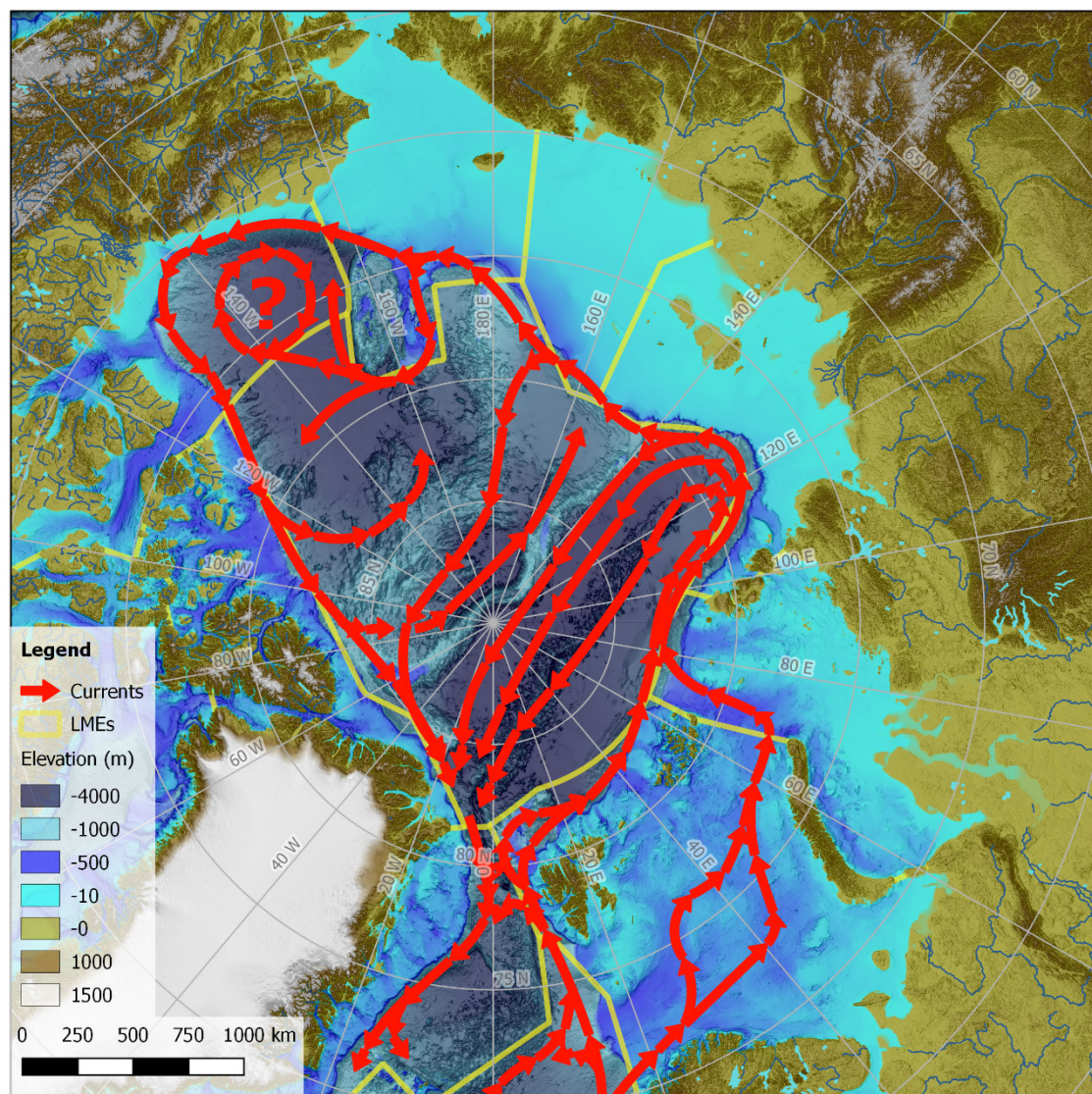
Atlantic water spreads around the entire Arctic Ocean, including Canada Basin, as a nearly 1-km thick layer with a core of maximum temperature (typically  $0.5$ – $2^{\circ}\text{C}$ ) at about 250–400 m depth (Rudels *et al.*, 2004). The deep waters of the basins originate from Atlantic water that was modified (slight increase in density) through entrainment of dense shelf waters, which were formed by cooling and brine rejection from ice formation, and then sank down along the continental slopes of the Eurasian Basin (Aagaard *et al.*, 1985; Jones *et al.*, 1995; Swift *et al.*, 1997; Rudels *et al.*, 1999; Ivanov and Golovin, 2007; Ivanov *et al.*, 2015a, 2015b). Atlantic water also forms the cold halocline layer between the surface and Atlantic layers in Eurasian Basin, and underlies the Pacific water in the lowest part of the halocline in Canada Basin (Aagaard *et al.*, 1981; Rudels *et al.*, 1996, 2004; Woodgate *et al.*, 2001). The cold halocline has a particularly significant role as an insulating layer between the warmer Atlantic layer below and the surface layer of cold polar water.

### 3.3.3 The intermediate Atlantic water layer and the Arctic Circumpolar Boundary Current

Atlantic water flows into the Arctic Mediterranean Sea from the North Atlantic over the ridge between Scotland and Iceland on both sides of the Faroe Isles (Orvik and Niiler, 2002; Orvik and Skagseth, 2003). This water flows north as the Norwegian Atlantic Current along the eastern margin of the Norwegian Sea (Polyakov *et al.*, 2005; Skagseth *et al.*, 2008). At the western entrance to the Barents Sea, the current splits into two branches, one branch flowing into the Barents Sea and another flowing north as the West Spitsbergen Current (WSC; Mosby, 1962; Aagaard *et al.*, 1987). The WSC then splits into a core branch and an offshore branch, the latter



of which recirculates in Fram Strait and flows south along the continental shelf break off Greenland, together with the East Greenland Current (Bourke *et al.*, 1988; Strass *et al.*, 1993; Beszczynska-Møller *et al.*, 2012; Hattermann *et al.*, 2016; Håvik *et al.*, 2017). The remaining water of the WSC turns right at the northwestern corner of Svalbard and continues east into Nansen Basin, splitting into three branches across and around Yermak Plateau (Svalbard, Yermak Pass, and Yermak Plateau branches; Cokelet *et al.*, 2008; Koenig *et al.*, 2017; Meyer *et al.*, 2017; Kolås and Fer, 2018). The three branches come together again north of Svalbard and continue east as a slope current along the northern Barents Sea shelf (Gascard *et al.*, 1995; Meincke *et al.*, 1997; Rudels *et al.*, 1999; Pérez-Hernández *et al.*, 2017, 2019). This flow is then called the Fram Strait branch of the Arctic Circumpolar Boundary Current (referred to hereafter as the boundary current; [Figure 3.4](#)).



**Figure 3.4.** Circulation of relatively warm ( $>0^{\circ}\text{C}$ ) Atlantic water flowing at intermediate depth (between approximately 200 and 800 m) as a cyclonic (anticlockwise) boundary current along the slopes and basin margins – the Arctic Circumpolar Boundary Current. The current is diverted into branches by the Lomonosov Ridge, Alpha-Mendeleev Ridge, and Chukchi Plateau. Based on Rudels *et al.* (1994, 2011). The anticyclonic (clockwise) circulation of Atlantic water, similar to the Beaufort Gyre in the upper layer, is tentative (indicated by "?") based on Nishino (2002) and McLaughlin *et al.* (2009).



The branch of Atlantic water that flows into the Barents Sea further diverges into branches south and north of the Central Bank. These branches continue through the deeper regions of the Barents Sea towards the northeastern area, where they exit through the opening between Novaya Zemlya and Franz Josef Land (Loeng *et al.*, 1997; Schauer *et al.*, 2002a; Lien *et al.*, 2013; Smedsrud *et al.*, 2013). This water flows out into Nansen Basin through St Anna Trough in the northern Kara Sea, and constitutes the Barents Sea branch of the boundary current (Schauer *et al.*, 1997; Rudels *et al.*, 1999, 2000).

Atlantic waters of the Fram Strait and Barents Sea branches are cooled and modified through ice formation, ice melt, and mixing *en route* to Nansen Basin. The temperature of the Fram Strait branch is typically 2–3°C, with a core salinity of about 35, while the Barents Sea branch is generally colder and slightly less saline (Quadfasel *et al.*, 1991, 1993; Schauer *et al.*, 1997; Rudels *et al.*, 1999, 2000, 2004; Pérez-Hernández *et al.*, 2017, 2019). Some of the Fram Strait branch water flows into deeper parts of the northern Barents Sea shelf (through Franz-Victoria Trench and partly in from St Anna Trough to the east) where it is further cooled and modified before it re-enters Nansen Basin mainly through St Anna Trough (Mosby, 1938; Hanzlick and Aagaard, 1980; Pfirman *et al.*, 1994; Steele *et al.*, 1995; Matishov *et al.*, 2009; Lind and Ingvaldsen, 2012). Barents Sea branch water is modified by various processes in the Barents Sea, such as heat loss to the atmosphere in ice-free areas, and brine injection from ice formation over shallow bank areas (Schauer *et al.*, 2002a; Gammelsrød *et al.*, 2009; Smedsrud *et al.*, 2010, 2013; Årthun *et al.*, 2011; Lien *et al.*, 2017; Skagseth *et al.*, 2020). The hydrographical properties and density of the boundary current source waters are not constant, but vary, according to the season and their origin, as they progress from the Norwegian Sea into Nansen Basin. The mean boundary current speed at the slope of the northern Barents Sea was found to be 10–15 cm s<sup>-1</sup> during a two-month measurement period in July–September 1980 (Aagaard, 1989), which was confirmed by a two-year measurement series at a mooring at 31°E during 2004–2006 (Ivanov *et al.*, 2009). A year-long mooring array at about 30°E gave a mean speed of ca. 15 cm s<sup>-1</sup> in the core of the boundary current, located at 300–700 m depth (Pérez-Hernández *et al.*, 2019).

The waters of the Fram Strait and Barents Sea branches meet at the exit from St Anna Trough in the northern Kara Sea. The Barents Sea branch occurs as a broad and deep wedge (200 km wide and located in the 200–1300 m depth interval) that detaches the Fram Strait branch from the slope and pushes it into the interior of Nansen Basin (Schauer *et al.*, 1997; Rudels *et al.*, 2000). A frontal structure separates the two branches as they flow east, with interleaving of waters occurring according to differences in density structures. This interleaving is associated with mixing, which takes place where the current branches flow into the western Laptev Sea along the steep slope off Severnaya Zemlya (Schauer *et al.*, 1997; Rudels *et al.*, 2000). Despite mixing, the two branches of the boundary current retain their identity and can be traced as they circulate around the Arctic Ocean. The Barents Sea branch keeps to the right along the peripheral slopes and predominates in the Canada Basin, while parts of the Fram Strait branch are deflected by the ridges and recirculate in the Eurasian and Makarov basins (Rudels *et al.*, 2004).

A major crossroad for the boundary current is at Lomonosov Ridge, where one part is deflected north along the slope of the ridge in Amundsen Basin, while the rest continues across the base of Lomonosov Ridge into Makarov Basin (Aagaard, 1989; Rudels *et al.*, 1999; Woodgate *et al.*, 2001). Current measurements have shown a largely barotropic current structure, flowing eastward along the slope off Laptev Sea at a mean speed of 3–6 cm s<sup>-1</sup> (Woodgate *et al.*, 2001). After they split at the base of Lomonosov Ridge, the two branches flow along the bathymetry with mean speeds around 2 cm s<sup>-1</sup>. The highest speeds were generally measured in the top part of the boundary current, and decreased with increasing depth. Current records taken over a year from summer 1995 to 1996, showed eddy features with episodic current speeds of up to 20–40 cm s<sup>-1</sup>. The eddies were mainly anticyclonic and included cold core eddies in the upper part of the boundary current (100–300 m) and warm core eddies extending deeper to about

1000 m (Woodgate *et al.*, 2001). Recent two-year measurements (2013–2015) at a cluster of six moorings in Laptev Sea (along 126°E) revealed substantial weakening of the eastward current speed with increasing water depth, from 11 cm s<sup>-1</sup> at the shallowest mooring on the upper slope (270 m depth) to 0.5 cm s<sup>-1</sup> at a mooring over 3400 m depth in Amundsen Basin (Baumann *et al.*, 2018; Pnyushkov *et al.*, 2018).

The boundary current branch that is deflected northward is steered by Lomonosov Ridge and continues along Amundsen Basin towards the western end and Fram Strait (Rudels *et al.*, 1994). There may be an additional deflection of some water by the deeper Gakkel Ridge, which steers water westward in the northern Nansen Basin (Quadfasel *et al.*, 1993; Rudels *et al.*, 1994; Schauer *et al.*, 2002b). A considerable part of the boundary current (perhaps about half) recirculates in the Eurasian Basin and exits through Fram Strait after a relatively short residence time of about 10 years. Recirculation in Eurasian Basin is predominated by water from the Fram Strait branch of the boundary current (Rudels *et al.*, 1999, 2004).

Water that crosses Lomonosov Ridge into the Amerasian Basin continues east, steered by the bathymetry. Mendeleev Ridge appears to be another crossroad where a branch of the boundary current is deflected north to recirculate in Makarov Basin (Rudels *et al.*, 1994, 2004; Swift *et al.*, 1997). The remaining, and probably the main part of the boundary current, flows across Mendeleev Ridge, from where it has been shown to flow south and around the Chukchi Abyssal Plain located between Mendeleev Ridge and Chukchi Rise (Woodgate *et al.*, 2007). The boundary current continues tightly locked to the complex topography around Chukchi Rise and Northwind Ridge. There is an active zone with interleaving and mixing with old basin water in the region between Mendeleev Ridge and Northwind Ridge (characterized by large zigzags in hydrographic properties; Woodgate *et al.*, 2007). The narrow Northwind Abyssal Plain (located between Chukchi Rise and Northwind Ridge) appears to have a stagnant and semi-trapped "relic" water column, with low ventilation from mixing of waters progressing from the north (Woodgate *et al.*, 2007). The boundary current in this Chukchi Borderland region contains waters from both the Fram Strait and Barents Sea branches, which progresses through the region in 1–2 years (assuming an average current speed of 2 cm s<sup>-1</sup>; Woodgate *et al.*, 2001, 2007).

The boundary current continues along the slope of Canada Basin in the southern Beaufort Sea, where the Atlantic water has been found to be mainly constituted of the Barents Sea branch (Rudels *et al.*, 2004). It appears that the Fram Strait branch, as the outer part of the boundary current, is diverted into the interior of the northern Canada Basin by Chukchi Plateau, while the Barents Sea branch continues along the slope of the southern Canada Basin (Rudels *et al.*, 2004). Tracer measurements suggest that one part of the boundary current splits while spreading into the interior (Smith *et al.*, 1999; Smethie *et al.*, 2000). Rudels *et al.* (2004) interpreted profiles presented by McLaughlin *et al.* (2004; their Type II water) as showing the presence of Barents Sea branch water underlying the Pacific water of the upper and middle halocline in the southern Canada Basin east of Chukchi Plateau. Circulation in this area can be complex, with input of Pacific water via Chukchi Sea through the Herald and Barrow canyons, associated with the formation of eddies that spread out in the southern Canada Basin (Manley and Hunkins, 1985; D'Asaro, 1988a, 1988b; Aagaard, 1989; Weingartner *et al.*, 1998, 2005a; Muench *et al.*, 2000; Pickart *et al.*, 2005). The boundary current has been measured as a topographically fixed slope current along the upper Beaufort slope (as the Beaufort Undercurrent running east in the opposite direction to the surface flow of the Beaufort Gyre; Aagaard, 1984, 1989).

The main features of the circulation in the Amerasian Basin have been depicted as two large-scale circulation cells in the Makarov and Canada basins (Rudels *et al.*, 1994; McLaughlin *et al.*, 2002). In the Canada Basin, in addition to the boundary current which flows anticlockwise along the southern margin, there may be an anticyclonic circulation of Atlantic water in the basin interior, underlying the Beaufort Gyre which spins around anticyclonically in the upper water

layers. Anticyclonic circulation was suggested from analysis of early data (Worthington, 1953, 1959; Timofeyev, 1957; Coachman and Barnes, 1963; Newton and Coachman, 1974). Nishino (2002) found evidence of a transbasin westward flow from a diagnostic analysis of the climatological density field, driven by buoyancy and eddy forcing. The branch of the boundary current which is diverted north by Chukchi Plateau spreads into the interior as thermohaline intrusions, which operate in an anticyclonic direction due to the influence of the Beaufort Gyre (McLaughlin *et al.*, 2009). In Makarov Basin, hydrographic observations suggest a return flow toward the Siberian side along Lomonosov Ridge (Swift *et al.*, 1997). Atlantic water from the boundary current returning from the Canada Basin is characterized by increased nutrient concentrations, particularly of silicate, resulting from admixture of some water of Pacific origin (Rudels *et al.*, 1994, 1999; Jones *et al.*, 1995; McLaughlin *et al.*, 2002).

The branches of the boundary current flowing through the various basins come together north of Greenland where they line up parallel with the continental slope according to their densities, with the lowest density water closest to the shelf; Rudels *et al.*, 2004). The reunited boundary current exits through the western Fram Strait along Greenland, where it becomes part of the East Greenland Current, along with recirculating Atlantic water deflected from the WSC (Rudels *et al.*, 1999, 2004; Beszczynska-Møller *et al.*, 2011; Håvik *et al.*, 2017).

The core of the boundary current loses heat, and its temperature decreases, as it circulates in the various branches in the Arctic Ocean (Coachman and Barnes, 1963; Rudels *et al.*, 1999, 2004). The temperature of the Fram Strait branch is 2.5–3°C as it enters the slope north of Svalbard (Pérez-Hernández *et al.*, 2017, 2019), while the Barents Sea branch may have a temperature of 0–1°C (Schauer *et al.*, 2002b). The maximum temperature of Atlantic water from the boundary current is about 1–1.5°C in Amundsen Basin, about 0.5–1°C in the eastern Makarov Basin, and about 0.3–0.5°C in the southern Canada Basin (Treshnikov, 1985; Melling, 1998; Morison *et al.*, 1998; McLaughlin *et al.*, 2002, 2004; Rudels *et al.*, 2004; Polyakov *et al.*, 2004, 2011, 2013). When the boundary current approaches the exit through Fram Strait, the maximum temperature is around 1°C, reflecting the mixture of warmer water recirculating through Eurasian Basin and colder water returning from Canada Basin (Rudels *et al.*, 1999, 2004).

### 3.3.4 The upper polar mixed layer

The upper polar mixed layer is a low-salinity and low-density buoyant layer of water that floats on top of the halocline. It is formed mainly of Atlantic water flowing east over the Eurasian shelves, which receives freshwater input from ice melt and river water from the large Siberian rivers (including Ob, Yenisei, and Lena) and the Yukon and Mackenzie rivers on the American side. The upper polar mixed layer supports the drifting polar pack ice and is seasonally modified by the cycle of ice formation and ice melt (Coachman and Barnes, 1962; Aagaard and Carmack, 1989; Rudels *et al.*, 1996). The circulation of the upper polar mixed layer follows, in broad terms, that of ice drift, and is partly decoupled from the circulation of Atlantic water deeper down below the halocline. Surface water flows as part of the Transpolar Drift across the CAO from the region of the East Siberian and Laptev seas towards the exit through Fram Strait. It also circulates clockwise as part of the Beaufort Gyre in Canada Basin before being entrained into the Transpolar Drift (Figure 3.5; Proshutinsky and Johnson, 1997). In addition, there is an anticlockwise (cyclonic) circulation feature in the Laptev Sea and some anticlockwise circulation in the East Siberian Sea near Wrangel Island (Hibler, 1989).

The salinity of the polar mixed layer shows a decreasing trend from the Fram Strait area and the western Nansen Basin, across the central part of the Arctic Ocean, to the southern Beaufort Sea (Figure 3.6). It changes from 34 to 34.5 in Nansen Basin north of Svalbard, to around 32 in the North Pole region over Lomonosov Ridge, and to about 30 or less in the Canada Basin (Coachman and Barnes, 1962; Rudels *et al.*, 1996; Morison *et al.*, 1998; McLaughlin *et al.*, 2004).



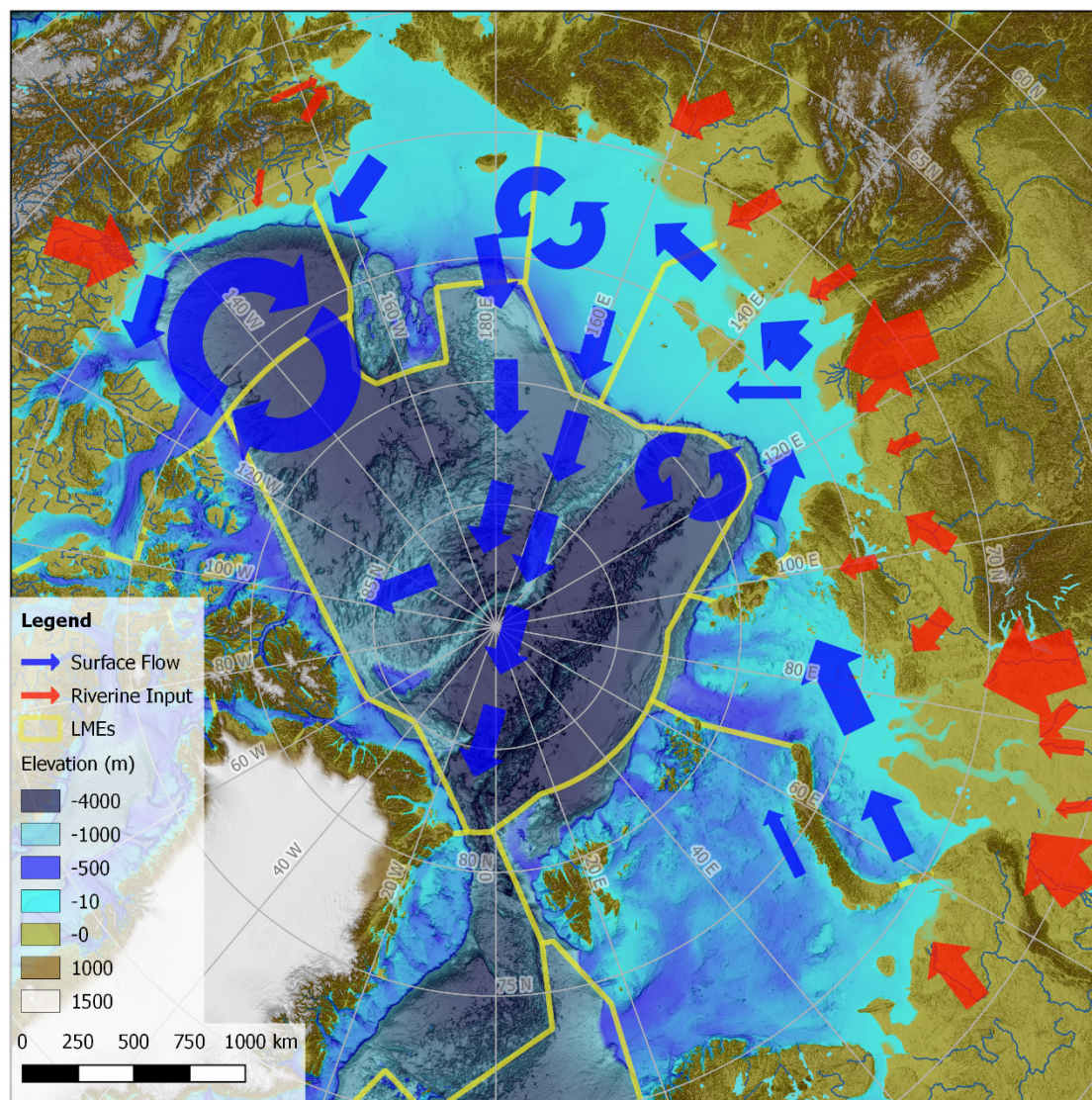


Figure 3.5. Schematic circulation of the surface water layer in the CAO showing the Transpolar Drift, the anticyclonic Beaufort Gyre, and the cyclonic circulation features in Laptev and East Siberian seas. Also shown are surface circulation on the shelves, including the waters from the Norwegian Coastal Current and outflow from the White Sea, through Kara Gate and Kara Sea, and waters from the Alaska Coastal Current carrying freshwater discharge from the Yukon River. Rivers discharging into coastal waters of the shelves surrounding the CAO are shown with red arrows. Arrow width indicates annual river discharge in three categories: smaller rivers ( $< 50 \text{ km}^3$ ), large rivers ( $50\text{--}150 \text{ km}^3$ ), and very large rivers ( $> 300 \text{ km}^3$ ). The rivers are, in sequence from west to east (with annual discharge in  $\text{km}^3$  given in parentheses): Kara Sea – Ob (411), Nadym (18), Pur (33), Taz (45), Yenisei (635), Pyasina (71), Nizhnyaya Taymyra (34); Laptev Sea – Khatanga (87), Anabar (18), Olenek (39), Lena (553), Yana (35); East Siberian Sea – Indigirka (55), Kolyma (124); Chukchi Sea – Amguema (9), Kobuk (9), Noatak (15); Beaufort Sea – Colville (9), McKenzie (313).

The polar mixed layer is seasonally dynamic. In summer, it consists of a low-salinity meltwater layer with near-freezing temperature. This layer is homogenized by ice formation and brine rejection in winter, and forms a mixed layer at freezing temperature extending down to the top of the permanent pycnocline (see [Section 3.3.5](#)). The thickness of the polar mixed layer is generally inversely related to surface salinity, ranging from 100 m or more in the western Nansen Basin to about 30 m in the Canada Basin (Rudels *et al.*, 1996). Seasonal ice melt in the Nansen, Amundsen, and Makarov basins has been estimated to be 0.5–1.5 m, with the highest values in the waters over the Gakkel and Lomonsov ridges (Rudels *et al.*, 1996). Input of freshwater from rivers in the Eurasian Basin takes place mainly in Laptev Sea, where waters



from the large rivers Ob and Yenisey, along with freshwater from the Norwegian Coastal Current and the White and Pechora seas, flow off-the-shelf and spread as a thin layer over the adjacent basins (Figure 3.5). Some of this river water flows east, along with water from Lena River, into the Amerasian Basin. Mackenzie River is a major freshwater source with input into Canada Basin, as is water from the Yukon River, which flows north as part of the Alaskan Coastal Current into the southern Beaufort Sea (Weingartner *et al.*, 2005b). The input of freshwater from rivers has a strong seasonality, with a peak flow associated with snow melt in spring and early summer. As a result of the strong seasonality in ice and river discharge, the salinity of the polar mixed layer can change markedly between summer and winter, by 2 units, as observed from Russian ice-drift stations (Coachman and Barnes, 1962; Gorshkov, 1980).

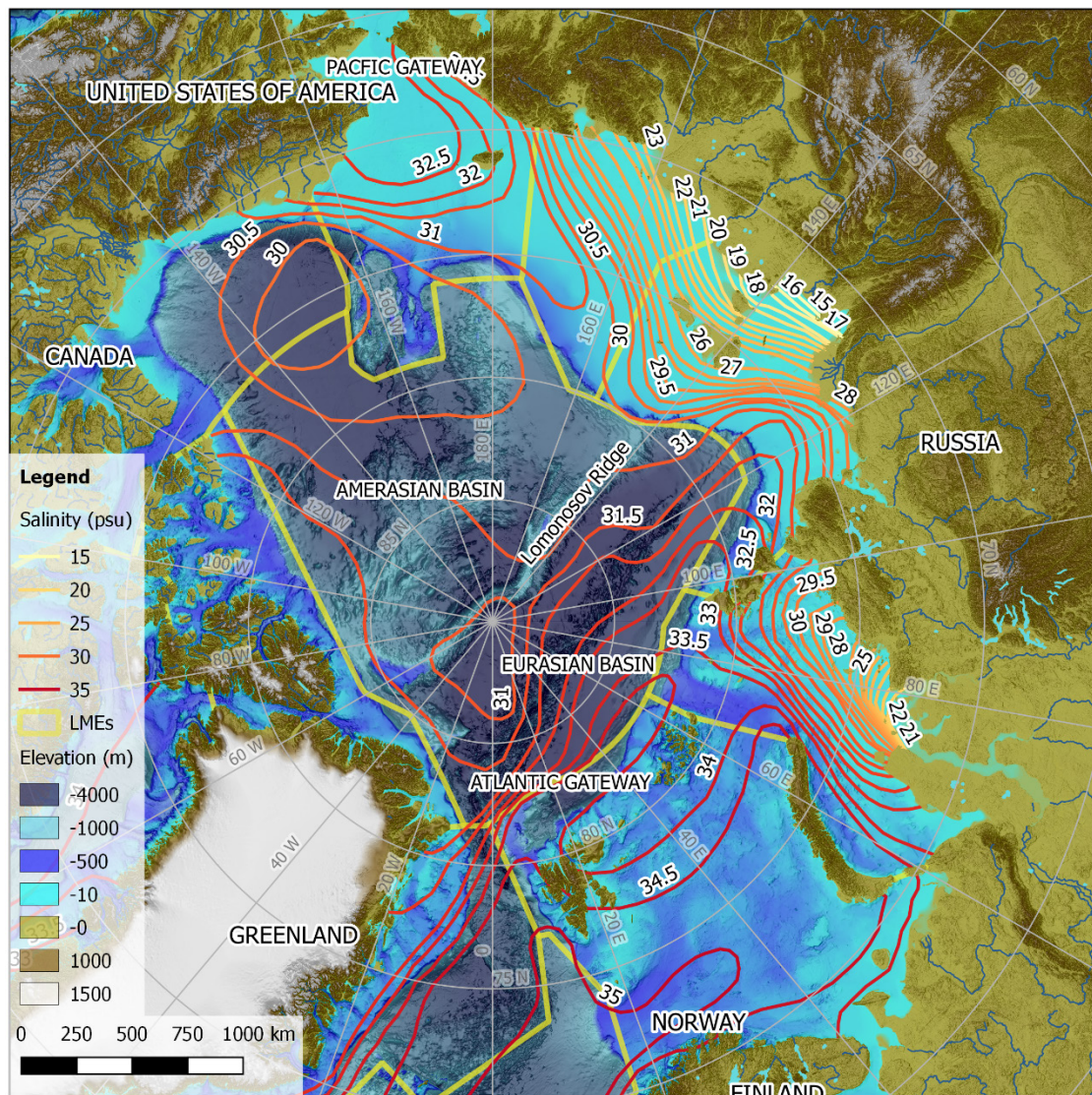


Figure 3.6. Surface layer salinity in the Arctic Ocean in winter. Based on Gorshkov (1980).

Total river discharge to the Arctic Ocean is about  $3200 \text{ km}^3 \text{ year}^{-1}$ , representing a flux of about 0.1 Sv ( $100\,000 \text{ m}^3 \text{ s}^{-1}$ ; Serreze *et al.*, 2006; Dickson *et al.*, 2007; Magritsky *et al.*, 2018). This is an annual average and represents a freshwater amount of about 0.35 m if distributed evenly over the nearly 10 million  $\text{km}^2$  area of the Arctic Ocean (Aagaard and Carmack, 1989; Serreze *et al.*, 2006). The contribution of freshwater from rivers can locally be much larger, reflecting the flow patterns and residence times of the surface layer in different areas. Freshwater from the

Mackenzie River contributed up to 8 m of an inventory in the upper 40-m surface layer in Canada Basin (Macdonald *et al.*, 2002).

The flow of Pacific water through Bering Strait is another major source of freshwater input to the Arctic, due to its lower salinity, and contributes an annual amount of about 2500 km<sup>3</sup> of freshwater (relative to the mean salinity of the Arctic Ocean of 34.8; Woodgate and Aagaard, 2005; Serreze *et al.*, 2006). Pacific water is found mainly in the halocline layer (see [Section 3.3.5](#)). The amount of freshwater in the Arctic Ocean (for the upper polar mixed and halocline layers combined, relative to a salinity of 34.8) ranges from around 5 m in the Nansen and Amundsen basins, to around 10 m in Makarov Basin, and around 15–18 m in the Canada Basin (Serreze *et al.*, 2006; Proshutinsky *et al.*, 2009). This represents a total amount of freshwater of about 84 000 km<sup>3</sup>, of which sea ice constituted around 10% (about 10 000 km<sup>3</sup>, based on ice conditions in 1979–2001; Serreze *et al.*, 2006).

The upper polar mixed layer from a wide area feeds into the Transpolar Drift. About an equal amount of freshwater leaves the Arctic Ocean as low-salinity water and sea ice through Fram Strait (2400 and 2300 km<sup>3</sup> year<sup>-1</sup>; Vinje *et al.*, 1998; Meredith *et al.*, 2001; Serreze *et al.*, 2006; Jones *et al.*, 2008). Most of the freshwater from the Pacific inflow in the halocline layer exits from the Arctic Ocean through the Canadian Arctic Archipelago (Melling, 2000; Prinsenbergh and Hamilton, 2005; Dickson *et al.*, 2007).

### 3.3.5 The halocline layer

#### 3.3.5.1 Cold halocline

The halocline is a special feature in the Arctic Ocean separating the upper polar mixed layer ([Section 3.3.4](#)) from the intermediate Atlantic water layer beneath ([Section 3.3.3](#)). For much of the area, the halocline differs from a regular pycnocline by having separate gradients for salinity and temperature and is called a cold halocline ([Figure 3.7](#)). If physical mixing occurred between the cold, low-salinity, upper polar mixed layer above and the warmer and saltier Atlantic water layer below, it would result in corresponding gradients in salinity and temperature. The fact that the gradients are separate suggests that the mechanisms involved in generating and maintaining the halocline include the advection of cold water that results from ice formation and brine rejection over adjacent shelves and then spreads along density isopycnals between the upper and intermediate layers (Nansen, 1902; Treshnikov, 1959; Coachman and Barnes, 1962; Treshnikov and Baranov, 1976; Aagaard *et al.*, 1981, 1985; Melling and Lewis, 1982; Steele *et al.*, 1995; Rudels *et al.*, 1996, 2004). This would explain the low (near freezing) temperature in a zone of increasing salinity, which is why it is termed cold halocline.

The halocline structure in the Eurasian basins differs from that in the Amerasian Basin, where Pacific water interleaves in the upper and middle part of the halocline. The halocline is typically located between around 50 to 200–250 m depth (Rudels *et al.*, 2004). In the western Nansen Basin, the inflowing Atlantic water in the Fram Strait branch causes melting of sea ice and formation of a two-layer system, with less-saline surface water overlying warmer Atlantic water. Ice formation during winter causes homogenization and a deepening of the cold upper layer, extending down to 100 m depth or more (Rudels *et al.*, 1996, 2004). This deep winter mixed layer is possible due to the relatively high surface salinity in the western Nansen Basin. With ice melt and freshening of the surface layer the next summer, and as the water is being overlain by fresher water from Siberian rivers farther east in the Laptev Sea, the pycnocline at the base of the winter mixed layer is gradually transformed into a halocline structure (Rudels *et al.*, 1996, 2004). The halocline structure differs in some respects between the Fram Strait and Barents Sea branches of Atlantic water (Rudels *et al.*, 2004). Temperature is lower and nearer to the freezing point for the Fram Strait branch halocline, with a sharp bend in a temperature–salinity plot at



salinity values around 34.2–34.4. The Barents Sea branch halocline is slightly warmer, and the bend in the temperature–salinity plot is more gradual. These features allowed Rudels *et al.* (2004) to trace waters from the two branches as they circulated around the basins of the Arctic Ocean. They found that Atlantic water, mainly from the Barents Sea branch, formed the lower halocline in Canada Basin.

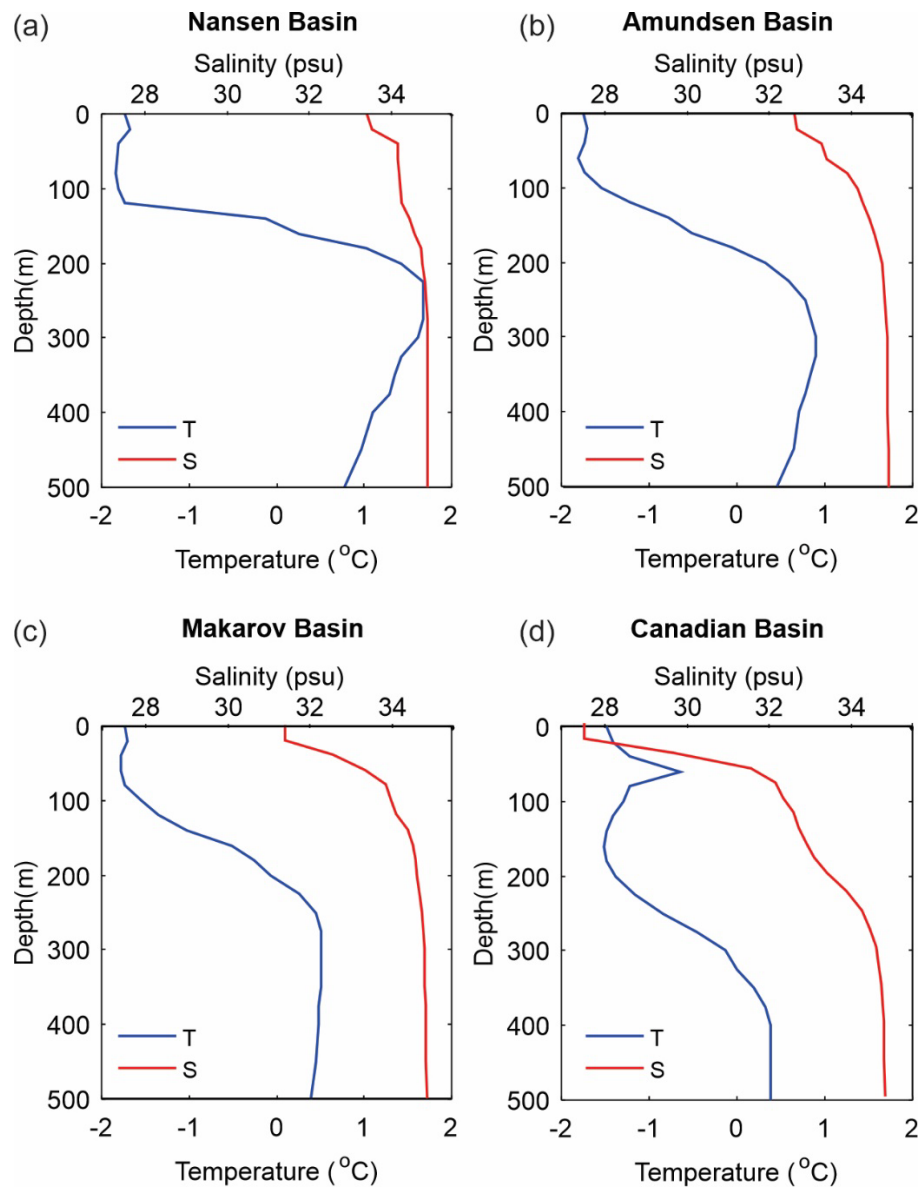


Figure 3.7. Vertical profiles of temperature and salinity in the Nansen (a), Amundsen (b), Makarov (c), and Canada (d) basins between the surface and 500 m. The profiles show the upper polar mixed layer, the halocline layer, and the upper part of the Atlantic water layer, with the core of maximum temperature at about 250 m (Nansen Basin) to 450 m (Canada Basin). The cold halocline is a thin layer in the upper 50 m in the Nansen Basin profile, while it is a thicker layer at about 50–100 m in Amundsen and Makarov basins. In Canada Basin, the maximum temperature at about 60 m reveals the layer of Pacific summer water overlying Pacific winter water, with a temperature minimum at about 150 m depth. Below this, between about 200 and 300 m, there is a pynocline layer of Atlantic origin above the Atlantic water layer. Based on Rudels *et al.* (2004), their Figure 1.

In Canada Basin, the halocline consists of three parts: the upper- (salinity  $\approx 31\text{--}32$ ), mid- (salinity  $\approx 33.1$ ), and lower- (salinity  $\approx 34.2$ ) halocline (Coachman and Barnes, 1961; Kinney *et al.*, 1970; Aagaard *et al.*, 1981; Jones and Anderson, 1986; McLaughlin *et al.*, 2004). The upper- and mid-halocline waters are derived from the Pacific Ocean, while the lower halocline water is made up of Atlantic water modified by shelf water from the Eurasian side. Pacific water that flows north through Bering Strait and Chukchi Sea has a salinity (31–33) and density that is intermediate to those of the upper polar mixed and Atlantic layers, and becomes interleaved in the upper and mid halocline in the Canada Basin, above the Atlantic water of the lower halocline (Figure 3.7, panel d).

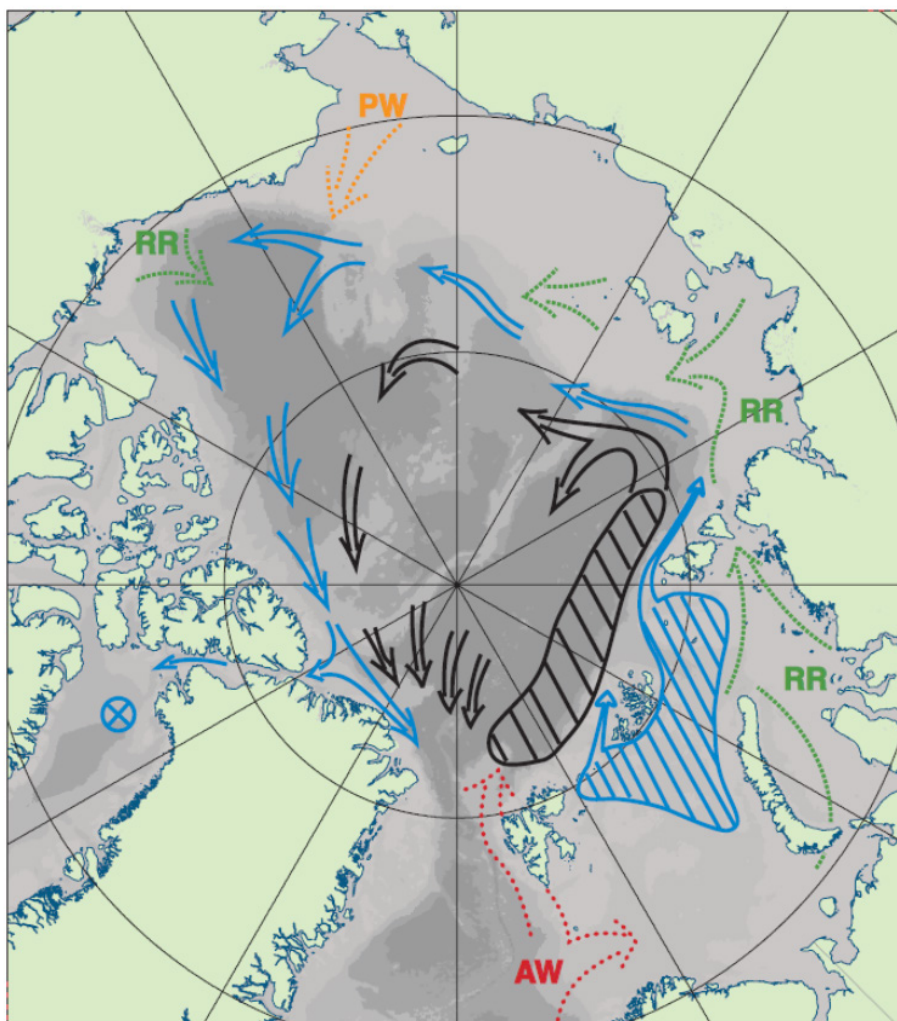


Figure 3.8. Formation areas and spread of halocline waters associated with the Fram Strait branch of Atlantic water in the Nansen Basin (black hatched area and arrows) and with the Barents Sea branch in the northern Barents and Kara seas (blue hatched area and arrows). AW – Atlantic water, RR – river run-off. From Rudels *et al.* (2004).

### 3.3.5.2 Pacific water

Pacific water originating from the Bering Sea shows a pronounced seasonal variation in properties as well as in transit time through the Chukchi Sea, where it is modified by cooling, formation of ice, and melting of ice (Weingartner *et al.*, 1998, 2005a; Winsor and Chapman, 2002; Woodgate *et al.*, 2005a, 2005b). It is common to recognize two types of Pacific water: Pacific summer water and Pacific winter water (Coachman and Barnes, 1961; Kinney *et al.*, 1970; Aagaard *et al.*, 1981; Jones and Anderson, 1986; McLaughlin *et al.*, 2004). Bering Strait transport

is comprised of three water masses in summer and autumn: Anadyr Water (AnaW;  $S > 32.5$ ,  $T = -1.0$ – $-1.5^{\circ}\text{C}$ ) in the west, Bering Shelf Water (BSW;  $S = 31.8$ – $32.5$ ,  $T = 0$ – $4^{\circ}\text{C}$ ) in the centre, and Alaskan Coastal Water (ACW;  $S < 31.8$ ,  $T > 4^{\circ}\text{C}$ ) near the Alaskan coast (Coachman *et al.*, 1975; Coachman, 1987; Grebmeier *et al.*, 1988). As the AnaW and BSW are usually not distinct in the Chukchi Sea, the combined water mass is called the Bering Shelf–AnaW (BSAW). The ACW becomes less important during winter, due to lower river discharge. In addition to water-mass properties, there is a clear seasonal pattern in the transport of water through Bering Strait, with stronger flow in summer and reduced flow in winter (Coachman, 1993; Woodgate *et al.*, 2005b). This is due to a prevalence of northerly winds in winter that act as a brake to reduce the northern flow of water (which is generally driven by a pressure head caused by the higher water level in the North Pacific than in the Arctic Ocean and the North Atlantic; Coachman and Aagaard, 1966; Stigebrandt, 1984; Carmack and McLaughlin, 2011). There is large interannual variability in the Bering Strait transport, with typical minimum winter transports of 0.3–0.5 Sv and summer maximum transports of 1.0–1.5 Sv (Woodgate *et al.*, 2005b). The mean annual transport, which is determined based on mooring observations, has increased by about 40% from 2001 (0.7 Sv) to 2011 (1.1 Sv), associated with increases in heat and freshwater fluxes (Woodgate *et al.*, 2012, 2015).

The winter-transformed Pacific water is cold (at or near the freezing point), relatively saline, and becomes layered in the mid-portion of the halocline in Canada Basin (Coachman and Barnes, 1961; Aagaard *et al.*, 1981; McLaughlin *et al.*, 2004; Shimada *et al.*, 2005). Water that makes it across the Chukchi shelf during summer retains some of the heat, is less saline, and becomes layered in the upper part of the halocline below the upper polar mixed layer (Figure 3.7, panel d). In vertical profiles from Canada Basin, Pacific summer water is recognized as a temperature maximum at salinities between about 31 and 32, and varies in its location from around 40 to 90 m depth (McLaughlin *et al.*, 2004). Pacific winter water is recognized as a temperature minimum in the mid-portion of the halocline, at a salinity of about 33.1, and is located typically at 100–150 m depth (Aagaard *et al.*, 1981; McLaughlin *et al.*, 2004). Occasionally, cold hypersaline (salinity  $> 34$ ) dense water, formed in winter in polynya regions off the coast of Barrow, Alaska, can ventilate layers deeper than the mid-halocline (Weingartner *et al.*, 1998).

The structure and properties of the halocline in Canada Basin show considerable variation due to differences in the properties and spread of the Pacific summer and winter waters (Shimada *et al.*, 2001, 2005; McLaughlin *et al.*, 2004; Steele *et al.*, 2004). Summer waters flowing through the western and eastern Chukchi Sea differ, the former being BSAW (salinity  $> 32$ ) and the latter ACW (containing Yukon run-off, with salinity  $< 32$ ; Shimada *et al.*, 2001; Steele *et al.*, 2004). Pacific water exits from the Chukchi Sea through Herald Canyon (between Herald Island and Herald Shoal) and the Central Trough (between Herald and Hanna shoals) into the Chukchi Borderland region, where it can spread in complex patterns (McLaughlin *et al.*, 2004; Shimada *et al.*, 2005). Summer water in the upper halocline may enter partly into the Transpolar Drift and partly into the Beaufort Gyre (Steele *et al.*, 2004; Shimada *et al.*, 2005).

ACW exits through Barrow Canyon and flows east along the shelf break as a coastal undercurrent (Steele *et al.*, 2004). Mooring observations in Barrow Canyon have been carried out since the late 1990s (Itoh *et al.*, 2013; Williams *et al.*, 2014), and the data indicate a significant increase in ACW temperature during the 2000s (from  $\sim 4^{\circ}\text{C}$  to  $8^{\circ}\text{C}$ ). In winter, cold and saline dense water is formed off the coast of Barrow, Alaska, where coastal polynyas appear (Weingartner *et al.*, 1998). Recently, Hirano *et al.* (2016) suggested that the Barrow coastal polynya, previously considered to be a latent heat polynya, is a wind-driven, hybrid latent and sensible heat polynya, with sea-ice divergence and upwelling of warm and saline Atlantic water caused by the same northeasterly winds. Time-series of ice-draft data, which were obtained from a moored ice-profiling sonar off Pt. Barrow, show seasonal growth of sea-ice draft, occasionally interrupted by coastal polynya (Fukamachi *et al.*, 2017). Recently, it was found that,

in addition to the Barrow Canyon through-flow and the coastal undercurrent, westward jets along the Chukchi shelf break are identified with a subsurface warm-water transport during winter toward the Chukchi Borderland (Watanabe *et al.*, 2017).

Pacific water in the halocline is characterized by high nutrient content, especially for winter water and for silicate, which can reach concentrations of 35–50  $\mu\text{mol l}^{-1}$  in the temperature minimum at salinity 33.1 (Coachman and Barnes, 1961; Kinney *et al.*, 1970; Jones and Anderson, 1986; Salmon and McRoy, 1994; McLaughlin *et al.*, 1996, 2002, 2004). Nitrate and inorganic phosphate are also elevated in the Pacific water relative to concentrations in Atlantic water, with maximum values of 15–18  $\mu\text{mol l}^{-1}$  for nitrate, and about 2  $\mu\text{mol l}^{-1}$  for phosphate (McLaughlin *et al.*, 1996, 2002, 2004). The high silicate content, and high phosphate concentration relative to nitrate (low N/P ratio) are used as tracers to identify Pacific water and delineate its boundary to Atlantic halocline water (Jones and Anderson, 1986, 1990; Wilson and Wallace, 1990; Jones *et al.*, 1998; Salmon and McRoy, 1994). Pacific halocline water used to extend into Makarov Basin, with a frontal boundary to Atlantic water located over Lomonosov Ridge. However, in the early 1990s, there was a shift in the position of the Atlantic–Pacific boundary farther east to Mendeleev Ridge, caused by an increased flow of Atlantic water in the boundary current along the Eurasian slope (Anderson *et al.*, 1994; McLaughlin *et al.*, 1996, 2002, 2004; Carmack *et al.*, 1997; Swift *et al.*, 1997; Morison *et al.*, 1998).

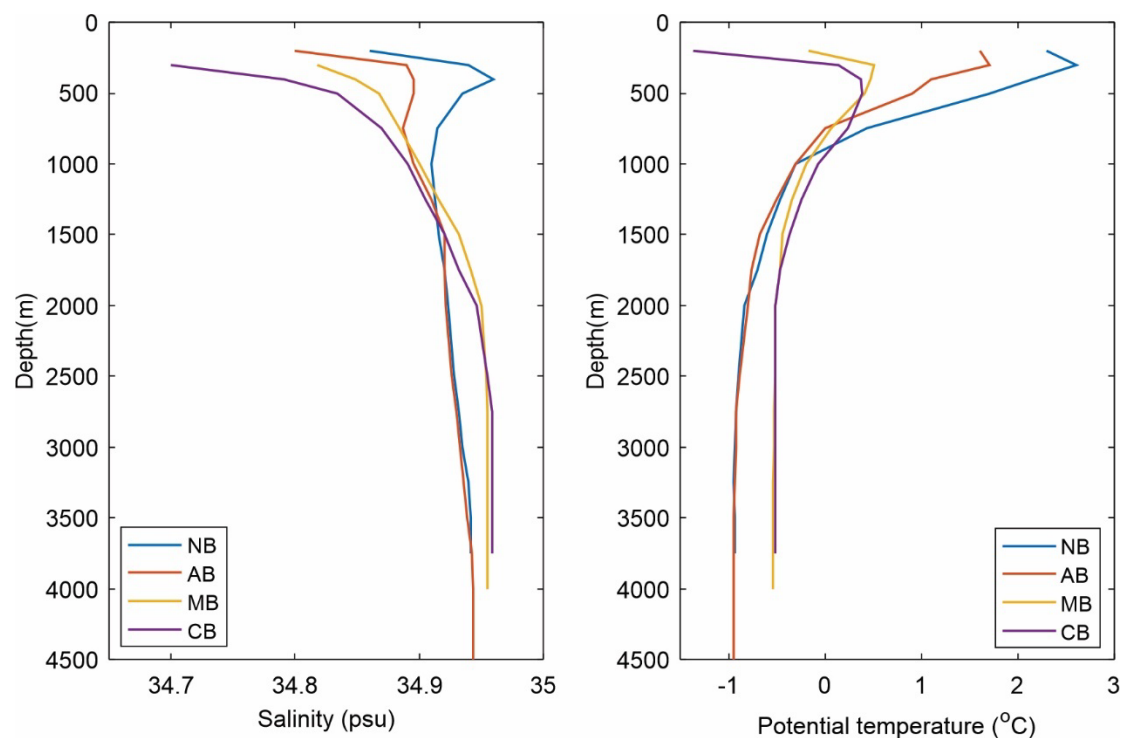
### 3.3.5.3 Roles of the halocline

The halocline layer plays an important role in regulating heat transport between the warmer intermediate Atlantic layer and the cold upper polar mixed layer. The cold Atlantic halocline (as well as the cold Pacific winter water in the mid-halocline in Canada Basin) insulates the Atlantic layer, absorbing the low heat flux through the strong density gradient and shielding the upper layer with sea ice from warming and ice melting (Aagaard *et al.*, 1981; Steele *et al.*, 1995; Steele and Boyd, 1998). The maintenance of the cold halocline appears to be dependent on advection, which transports cold water at intermediate salinities and acts as a wedge or layer between warm Atlantic and cold polar mixed layers (Steele and Boyd, 1998). The cold halocline retreated from Amundsen Basin in the early 1990s, reflecting a shift to the east in the flow of river water from the Kara and Laptev seas that lead to more winter convection and a weakening and disappearance of the true cold halocline layer (Steele and Boyd, 1998; Johnson and Polyakov, 2001).

In Canada Basin the situation is different, in that the warm Pacific summer water occupies the upper halocline below the polar mixed layer (Shimada *et al.*, 2001, 2005; McLaughlin *et al.*, 2002, 2004). Homogenization of the polar mixed layer, through ice formation and brine rejection in winter, can result in convection reaching the summer water below, bringing up heat that leads to ice melt and slower and decreased new ice formation. This may, in turn, shift the seasonal balance between ice formation and ice melt, which is thought to be one of the mechanisms behind the pronounced reduction in sea ice cover in Canada Basin that started in the late 1990s (Shimada *et al.*, 2006). The spread of summer water is influenced by atmospheric circulation, and wind-driven circulation of sea ice and the upper water layer (Steele *et al.*, 2004). In autumn, when there is much open water, anticyclonic winter circulation becomes more effective, leading to a larger spread of summer water into the central part of the basin (Shimada *et al.*, 2006). In addition to the inflow of Pacific summer water from Chukchi Sea, there is also seasonal heating of the upper layer in Canada Basin, which leads to heat accumulation in the layer below the surface meltwater layer throughout summer (Perovich *et al.*, 2007a, 2007b, 2008). This is an albedo-related positive feedback mechanism that contributes to delayed and decreased sea ice formation during winter (Perovich *et al.*, 2007a; Steele *et al.*, 2008; Jackson *et al.*, 2010).

### 3.3.6 Deep and bottom waters

Below the intermediate Atlantic layer, there is a large volume of deep and bottom waters that extend from around 1000 m depth to the bottom of the basins. There is no sharp boundary between the Atlantic and deeper layer, but rather a gradual transition to temperatures  $< 0^{\circ}\text{C}$  and a salinity minimum around 34.9 in the Eurasian Basin. The salinity of deep water increases slightly with depth (to about 34.93 in Eurasian Basin and 34.95 in the Canada Basin, where the salinity is somewhat higher; [Figure 3.9](#); Aagaard *et al.*, 1985; Jones *et al.*, 1995; Swift *et al.*, 1997). The basins show different vertical trends in temperature. In the Eurasian Basin temperature decreases with increasing depth [to nearly  $-1^{\circ}\text{C}$  ( $-0.96^{\circ}\text{C}$ ) in Amundsen Basin; Jones *et al.*, 1995], while, in Canada Basin it slightly increases (Aagaard *et al.*, 1985; Woodgate *et al.*, 2001; Timmermans *et al.*, 2003). These gradients and differences between the two main basins of the Arctic Ocean are slight and require high precision measurements to document. However, they are significant in reflecting and revealing the processes that contribute to the formation, circulation, and exchange of the deep waters (Aagaard *et al.*, 1985; Aagaard, 1989; Jones *et al.*, 1995; Swift *et al.*, 1997; Rudels *et al.*, 1999; Rudels, 2012, 2015).



**Figure 3.9.** Vertical profiles of potential temperature (right panel) and salinity (left panel) of deep and bottom waters in the four main basins of the CAO. NB – Nansen Basin, AB – Amundsen Basin, MB – Makarov Basin, CB – Canada Basin. The deep water extends below the Atlantic layer (technically defined by temperature  $> 0^{\circ}\text{C}$ ), with slightly increasing salinity and decreasing temperature with increasing depth in NB and AB. Note the crossover with higher salinity and temperature of the Atlantic layer and lower salinity and temperature of the deep and bottom waters in the two Eurasian basins, when compared to the Amerasian basins. Based on Rudels (2012; his Figures 10 and 16).

The bottom water can be distinguished from the deep water as a homogenous layer (isothermal and isohaline) about 400 and 800 m thick in the Nansen and Amundsen basins, and 600 and 1200 m thick in the Makarov and Canada basins, respectively.

Lomonosov Ridge separates the two main basins and restricts exchange of waters between them. In fact, the temperature difference between the two basins originally led to the postulation of the existence of the ridge (Worthington, 1953). While much of the ridge is about 1000 m deep, there are deeper gaps (down to nearly 2000 m) that provide some exchange of waters between



the Amundsen and Makarov basins (Aagaard *et al.*, 1985; Jones *et al.*, 1995; Woodgate *et al.*, 2001; Bjørk *et al.*, 2007; Rudels, 2012, 2015). Some of the cold and saline water from the Barents Sea branch may be dense enough to sink under the Atlantic boundary current and contribute to the deep water of the Eurasian Basin (Jones *et al.*, 1995; Schauer *et al.*, 1997; Rudels *et al.*, 1999; Rudels, 2012). It is also thought that plumes of dense water, stemming from ice formation and brine rejection on the northern Barents and Kara shelves and sinking down the slopes, contribute to the deep-water formation (Aagaard *et al.*, 1985; Jones *et al.*, 1995). Inflow of deep water from the Norwegian Sea through Fram Strait has been considered a third source of deep water in Eurasian Basin, but observations (from the RV Oden cruise in 1991) suggested that its importance was relatively low (Jones *et al.*, 1995).

Deep water in the Amerasian Basin stems from the Eurasian Basin, and there appears to be two main mechanisms involved in its formation: (i) plumes of dense shelf water (from the Chukchi and East Siberian seas) sinking through the Atlantic layer boundary current, and (ii) water flowing through the deep passages of Lomonosov Ridge (Aagaard *et al.*, 1995; Jones *et al.*, 1995; Swift *et al.*, 1997; Woodgate *et al.*, 2001). Silicate concentrations are higher in the deep water in the Amerasian Basin than in the Eurasian Basin (12–14 vs. 10–12  $\mu\text{mol l}^{-1}$ ), which is thought to reflect plumes of water with high silicate content and salinity sinking into the intermediate boundary layer and spreading into the deep basin water by diffusion, mixing, and lateral injection (Aagaard *et al.*, 1985; Jones *et al.*, 1995; Swift *et al.*, 1997). Water from Amundsen Basin flowing through deep passages in Lomonosov Ridge would sink in Makarov Basin if it was slightly denser than the resident water there. Waters on each side of the ridge have slight differences in temperature and salinity, with the water in Amundsen Basin being colder and less saline. Due to differential effects of temperature and salinity on the compressibility of seawater (with cold water being more compressible), water from Amundsen Basin would become relatively denser under pressure, which would increase its sinking and mixing into Makarov Basin water (Aagaard and Carmack, 1989).

Deep waters of the Arctic Ocean are distinguished as an upper layer (upper polar deep water) and deeper layers according to density and hydrographic criteria (Canadian Basin and Eurasian Basin deep water and bottom water; Rudels *et al.*, 1999). The upper layer of the deep water exchanges relatively unrestricted between basins through gaps in Lomonosov Ridge, whereas the deep and bottom waters of Canada Basin are relatively isolated. The lower 1 km of bottom water in Makarov Basin is homogenous, overlain by another 1 km of nearly homogenous deep water. Canada Basin bottom water has had a very long residence time, having existed without ventilation since the beginning of the Little Ice Age around 500 years ago (Macdonald *et al.*, 1993; Aagaard and Carmack, 1994).

### 3.3.7 Residence time of waters

The mean residence time (or mean turnover time) for freshwater in the Arctic Ocean is around 14 years (Aagaard and Carmack, 1989; Bauch *et al.*, 1995; Dickson *et al.*, 2007). The total freshwater reservoir (relative to salinity 34.9) is about 85 000 km<sup>3</sup> (representing a mean height of nearly 10 m of freshwater), while the total annual freshwater input by rivers and Pacific water is about 5700 km<sup>3</sup> (Serreze *et al.*, 2006). This gives a turnover time (volume/input) of about 15 years. Freshwater from Siberian rivers was found to have residence times of 2–4 years on the shelves (mean 3.5 years) before being advected out into the basin (Schlosser *et al.*, 1994). Using various tracers (halocarbons, tritium, and oxygen isotopes), the mean age of the surface layer in Eurasian Basin was suggested to be 7–8 years, while the residence time of freshwater in the halocline layer was found to be 10–14 years (Wallace *et al.*, 1992; Bauch *et al.*, 1995).

The average residence time of the Atlantic layer water in the Arctic Ocean is roughly 25–40 years, based on comparison of the volume of the 200–1000 m layer (about 4 million km<sup>3</sup>)



with the flux of Atlantic water (3–5 Sv or  $0.9\text{--}1.6 \times 10^5 \text{ km}^3 \text{ year}^{-1}$ ). The age of the Atlantic layer water in Nansen Basin was estimated to be 10–20 years based on tracers (Wallace *et al.*, 1992), probably reflecting the shorter circulation time here compared to in Amerasian Basin.

The age of the water increases with depth. Residence times for bottom water of the Eurasian Basin have been estimated at around 200–250 years (Schlosser *et al.*, 1997), while the deep water of Amerasian Basin is even older, estimated at around 500 years (Macdonald *et al.*, 1993; Schlosser *et al.*, 1997). The very low rate of ventilation of Amerasian Basin has been related to climate variation. The shift from a warmer to a colder climate with the onset of the Little Ice Age, around 500 years ago, was probably associated with more summer ice and less dense water formation from brine excretion on the surrounding shelves, which resulted in a strong reduction in ventilation of the deep water (Aagaard and Carmack, 1994).

### 3.3.8 Sea ice conditions

Sea ice is a very important component of the CAO ecosystem ([Figure 3.10](#); Melnikov, 1997; Eamer *et al.*, 2013). The entire Arctic Ocean is ice covered in winter, except for smaller areas of polynyas and leads that are mostly located in the periphery, over the shelves that surround the Arctic Ocean basins. During summer, sea ice generally melts and disappears from the surrounding shelves, but remains in most of the CAO area. Maximum ice cover is generally reached in March or April, while minimum ice cover is found in September ([Figure 3.11](#)). The seasonal change in sea ice extent for the whole Arctic, including the surrounding Subarctic seas, used to oscillate in the 1980s from a winter maximum of about 14 million  $\text{km}^2$  to a summer minimum of 5–6 million  $\text{km}^2$  (Parkinson *et al.*, 1999). In recent years, there has been a significant reduction in the summer extent of sea ice in the Arctic Ocean ([Section 3.4.3](#)).



Figure 3.10. Drifting sea ice pack of multiyear ice in the CAO north of Greenland. Photo: Pauline Snoeijs-Leijonmalm.



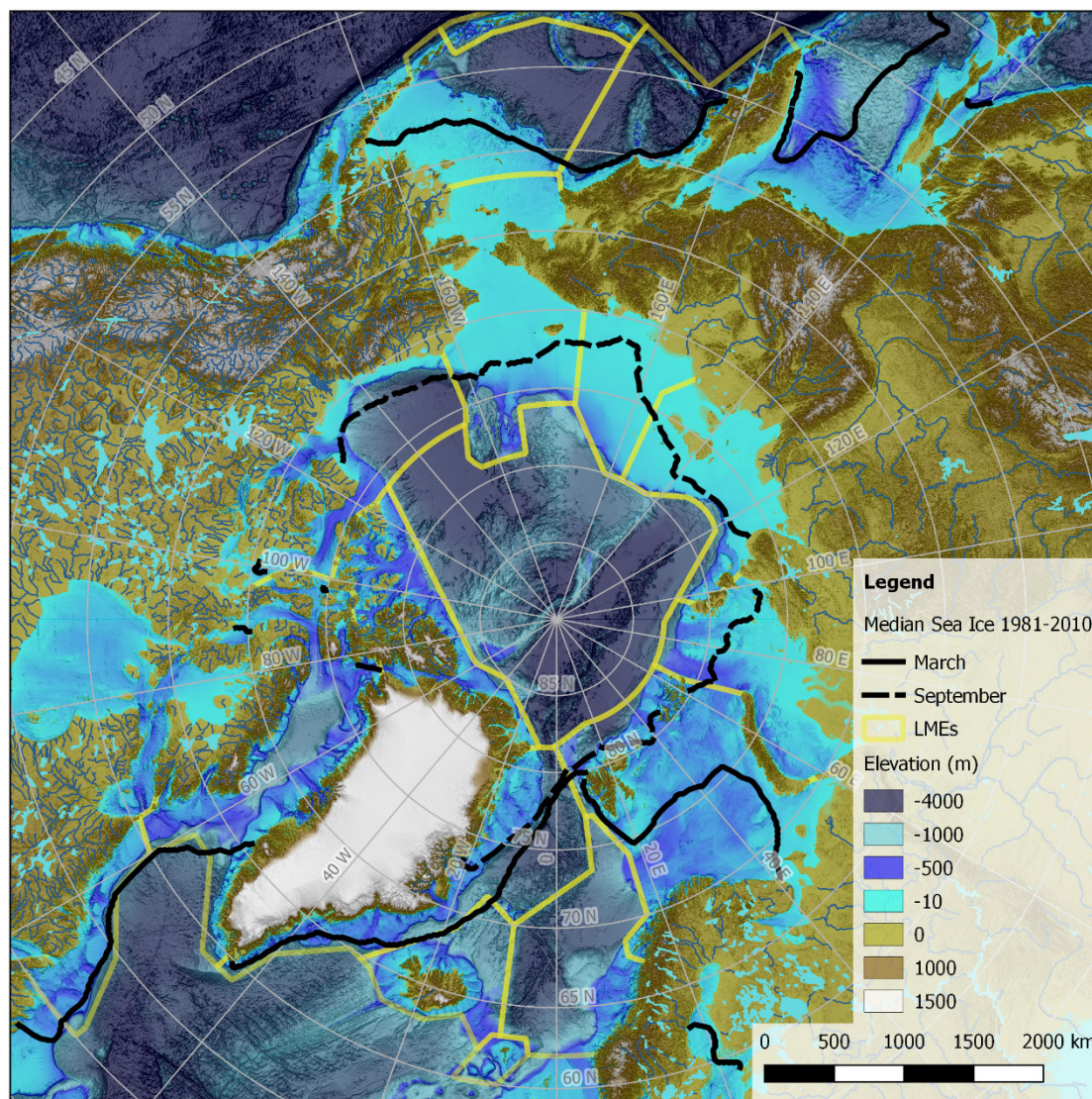


Figure 3.11. Sea ice distribution in the CAO and surrounding shelves at maximum extent in winter (March) and minimum extent in summer (September). Median sea ice boundaries for 1981–2010. Data from the National Snow and Ice Data Center (NSIDC), Boulder, Colorado, USA.

Sea ice accumulates in the CAO as multiyear or perennial ice, while new annual ice forms each winter over the shelves and the peripheral parts of the basins that have open water by the end of summer. The annual ice grows to a thickness of around 2 m in the high Arctic, while the thickness of the perennial ice is typically 3–4 m (Wadhams *et al.*, 1992; Melling, 2002; Laxon *et al.*, 2003; Rothrock *et al.*, 2003). Sea ice drifts in two broad patterns in the Arctic Ocean: in a clockwise manner in the Beaufort Gyre in Canada Basin, and as the Transpolar Drift from the East Siberian and Laptev seas across the CAO towards Fram Strait (Sokolov, 1962; Proshutinsky and Johnson, 1997; Rigor *et al.*, 2002). Transit time for sea ice is around 2–3 years in the Transpolar Drift, while the transit time (and age) of perennial ice can be 5–6 years or more for ice in the Beaufort Gyre (Rigor *et al.*, 2002). The heaviest ice conditions are found on the Canadian side of the Arctic Ocean (north of the Queen Elisabeth Islands) where the average draft is 4–7 m, consisting of heavily deformed ice with ridges and keels generated by pressure and shear from the movement of ice in the Beaufort Gyre (Bourke and Garret, 1987).

Sea ice exits the Arctic Ocean with the Transpolar Drift through Fram Strait. The amount of ice leaving annually has been estimated to be about 2500 km<sup>3</sup> (Vinje *et al.*, 1998; Vinje, 2001; Serreze

*et al.*, 2006). This amount is equivalent to an area of around 1.1 million km<sup>2</sup> of sea ice, with a mean ice thickness of 2.7 m (Vinje *et al.*, 1998).

## 3.4 Variation and change

### 3.4.1 Meteorology of the Central Arctic

The basic concepts of Arctic meteorology, such as the polar vortex and annual cycle of the Arctic heat budget, have been qualitatively known for decades. However, the advent of satellite data, the Arctic buoy programme (since 1979), and the computer power necessary for spatial analyses, have provided a more quantitative overview. The CAO region is characterized by (i) a large annual cycle of solar forcing, (ii) the impact of global warming and loss of sea ice, and (iii) interannual internal variability of weather events tied to two large-scale weather patterns, the Arctic Oscillation (AO) and the Arctic Dipole (AD). For more basic information on the Arctic climate and climate change, see e.g. ACIA (2005), McBean *et al.* (2005), Walsh (2008), Walsh *et al.* (2011), AMAP (2017), and Meredith *et al.* (2019).

The main control of Arctic climate comes from the tilt of the rotation axis of the earth, that causes a transition from absence of sun in winter to 24-h presence in summer. Although the height of the Arctic sun above the horizon is low during summer, its 24-hour presence gives a large daily average of solar heating from May through July, reaching into the Subarctic latitudes.

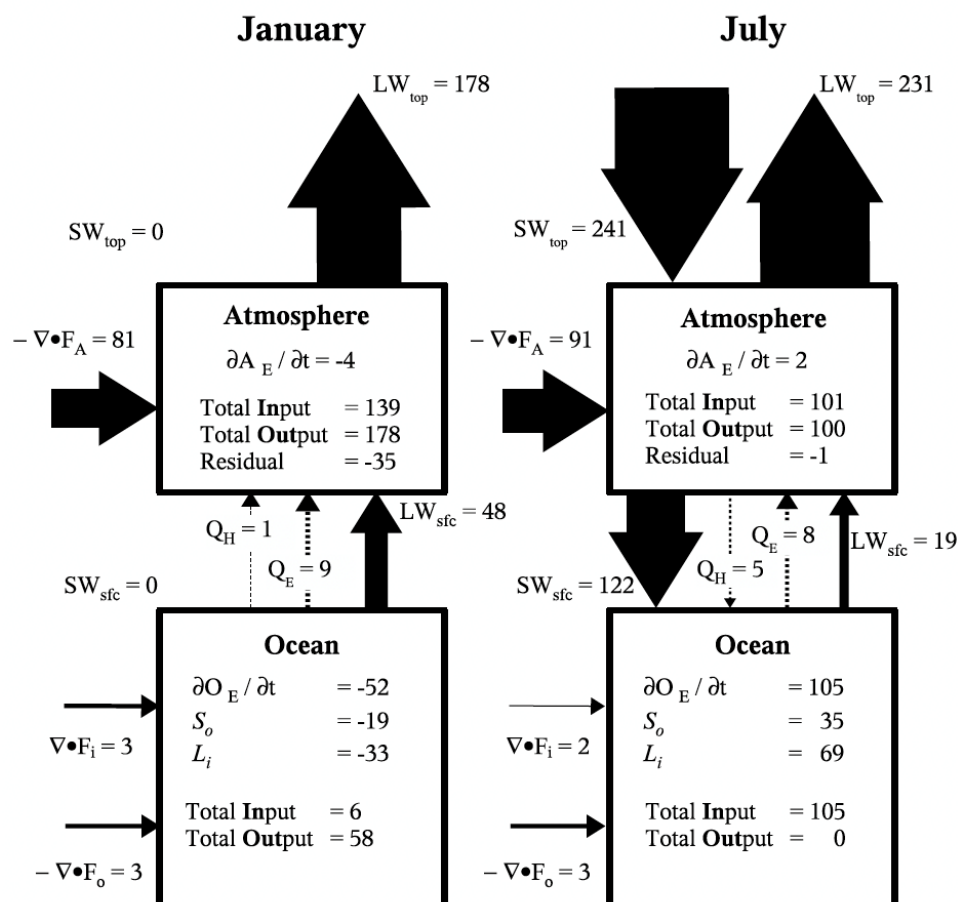


Figure 3.12. Schematic of Arctic energy budget for January and July after Serreze *et al.* (2007a; reproduced with permission). Units are W m<sup>-2</sup>.



The second controlling feature is the presence of sea ice. As a consequence of the white nature of sea ice, it has a large albedo and reflects more sunlight than open ocean water, which allows solar absorption. Another physical impact of sea ice is its low heat conductivity. Although Arctic sea temperatures are limited to the freezing point ( $-2^{\circ}\text{C}$ ), winter near-surface air temperatures are in the range of  $-15$  to  $-30^{\circ}\text{C}$  due to the insulating properties of sea ice. Some ocean heat flux does get through, leading to warmer winters in the central Arctic when compared to land areas of Antarctica (which are also colder because of the much higher elevation). The central Arctic heat budget for the atmosphere and ocean during winter and summer is summarized in [Figure 3.12](#), where the width of the arrows is proportional to the size of the heat transport. Although the data for the figure are from before Arctic Amplification warming (see [Section 3.4.4](#)), the relative importance of the fluxes represents the seasonal cycle. In July, the solar input to the Arctic atmosphere is nearly balanced by the loss by long-wave radiation to space. About half of the solar input reaches the ocean. In both winter and summer, heat is provided to the Arctic from mid-latitudes as part of the overall earth heat budget.

### 3.4.2 Two circulation regimes

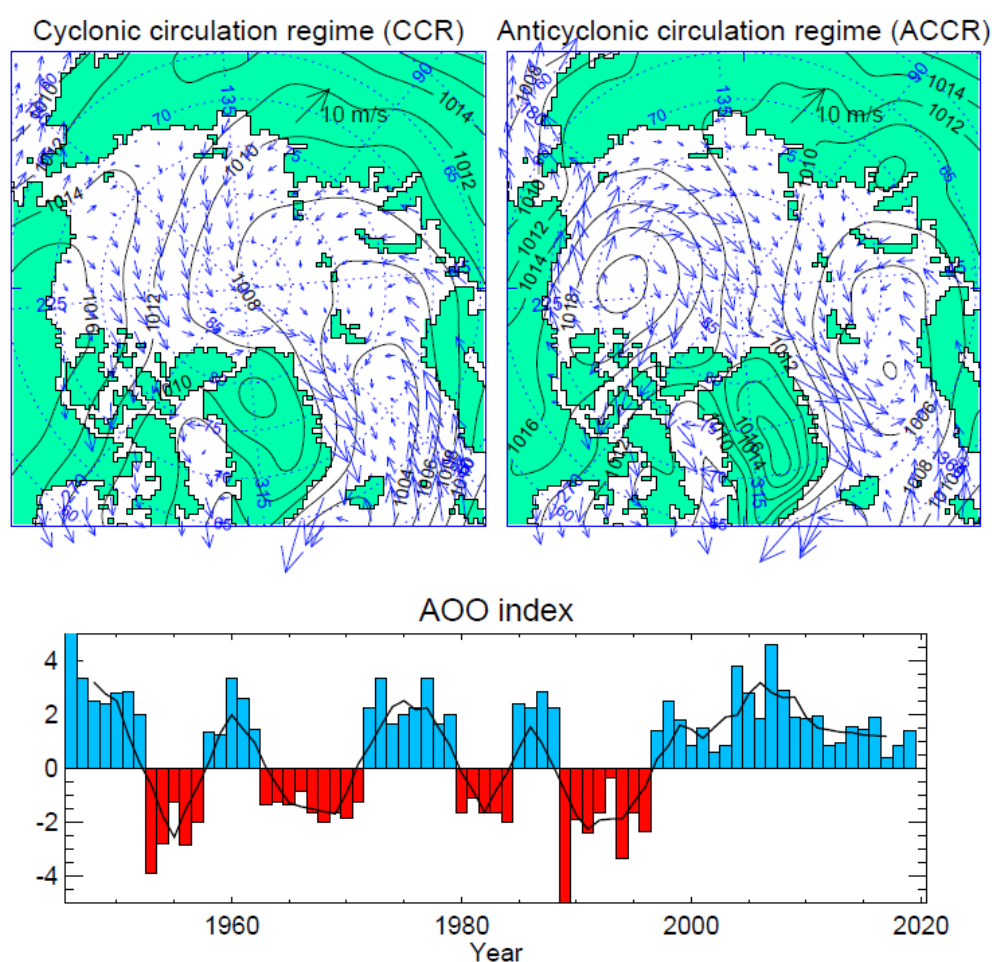


Figure 3.13. Two circulation regimes of sea ice and surface water in the CAO: (upper right panel) an anticyclonic regime where the high air pressure system over Canada Basin and the Beaufort Gyre are well developed, and (upper left panel) a cyclonic regime where the Beaufort Gyre is suppressed by strong activity from the Iceland Low in the Atlantic sector. The Arctic Ocean Oscillation (AOO) index (lower panel) reflects the two regimes (it is calculated from the sea surface slope generated by the circulation dynamics). The AOO index has been fluctuating between these two modes since 1948, with a period of quasi-oscillation of about 10–15 years, but with a persistent positive (anticyclonic) mode for the last 23 years. Based, with permission, on Proshutinsky *et al.* (2015) with updates; downloaded from <https://www.whoi.edu/page.do?pid=66578>

Two circulation regimes have been described for ice drift and transport in the upper polar mixed layer, related to the atmospheric pressure systems over the Arctic region ([Figure 3.13](#); Proshutinsky and Johnson, 1997; Polyakov *et al.*, 1999; Proshutinsky *et al.*, 2002). In winter, there is typically a prominent polar high pressure situated north of Canada that drives an anticyclonic (clockwise) atmospheric circulation over the CAO. This leads to a strengthened anticyclonic flow of the Beaufort Gyre. The anticyclonic pattern alternates with a situation where the polar high over the Beaufort Sea is weakened and the Siberian High is strengthened, leading to a shift to cyclonic (against the clock) circulation over the CAO and a contraction and weakening of the Beaufort Gyre. Using data for 1946–1993, Proshutinsky and Johnson (1997) showed that the anticyclonic and cyclonic flow patterns oscillated with a periodicity of 10–15 years, and each pattern persisted for 5–7 years (Proshutinsky *et al.*, 2015). The contraction of the Beaufort Gyre in the cyclonic circulation mode is associated with an expansion of a cyclonic gyre in the Laptev Sea and a shift of the Transpolar Drift toward the centre of the Arctic Ocean (through the North Pole region; Sokolov, 1962; Proshutinsky and Johnson, 1997). It is also associated with an eastward shift in the trajectory of freshwater from the Siberian rivers, from the Laptev Sea into the East Siberian Sea (Steele and Boyd, 1998; Anderson *et al.*, 2004; Peterson *et al.*, 2006).

The shift in the atmospheric pressure situation over the Arctic Ocean is related to the shifting strength of the Iceland Low as part of the North Atlantic Oscillation (NAO) index (Dickson *et al.*, 2000). A high NAO index situation with a well-developed Iceland Low leads to a trajectory for the low pressures into the western Russian Arctic, resulting in a weakening and push-back of the Polar High associated with the cyclonic circulation pattern (Proshutinsky and Johnson, 1997).

### 3.4.3 Decline in sea ice – the “Great Melt”

Arctic Ocean sea-ice conditions change with the circulation pattern, being more extensive and heavier during the anticyclonic circulation regime than during the cyclonic regime (Proshutinsky and Johnson, 1997; Polyakov *et al.*, 1999; Proshutinsky *et al.*, 1999). Modelling results and observations suggest that the ice thickness in the CAO can vary by about 1 m between the two regimes (from 2–3 to 3–4 m in the cyclonic and anticyclonic regimes, respectively), with a corresponding change in sea ice volume of about 20% (Polyakov *et al.*, 1999; Proshutinsky *et al.*, 1999).

The seasonal change in ice extent (including open drift ice) between maximum ice in winter (March) and minimum in summer (September) is around 30%, while the seasonal change in ice area (excluding open water) is about 50–60%. This pattern reflects, that about half of the ice-free area is caused by leads and openings in the ice, while the other half is a consequence of ice melt in the marginal ice zone (Polyakov *et al.*, 1999). The range in seasonal variation in ice thickness is about 0.5–1 m in the ice-covered part of the Arctic Ocean (Polyakov *et al.*, 1999; Kwok, 2018). With less ice, there is more melting, due to the higher heat absorption by open water than by ice, which has an albedo effect (Curry *et al.*, 1995; Polyakov *et al.*, 1999). This is a positive feedback mechanism, whereby warming and a reduction in ice leads to accelerated melting of the remaining ice (Polyakov *et al.*, 1999; Maslanik *et al.*, 2007).

There has been a substantial decrease in sea-ice extent and area during the last three decades (e.g. Serreze *et al.*, 2007b; Perovich and Richter-Menge, 2009; Perovich *et al.*, 2019). This has been associated with a decline in the fraction and age of the thick perennial pack ice, and a shift to more newly formed first-year ice (Johannessen *et al.*, 1999; Comiso, 2002; Belchansky *et al.*, 2004; Maslanik *et al.*, 2007; Nghiem *et al.*, 2007; Stroeve *et al.*, 2007; Kwok and Untersteiner, 2011; Meier *et al.*, 2014). From 1980 to 2005, the summer minimum ice cover (extent) in September decreased by about 20% from about 8 to around 6 million km<sup>2</sup> (Maslanik *et al.*, 2007). In 2007, the sea ice extent dropped by another 20–25% to a record low of 4.2 million km<sup>2</sup> (Comiso *et al.*, 2008; Stroeve

*et al.*, 2008). The declining trend in summer ice continued with another record low of 3.4 million km<sup>2</sup> in 2012 (Figure 3.14), driven in part by a summer storm in August that accelerated ice melt (Parkinson and Comiso, 2013). The 2012 minimum is still the record low (as of early 2020). Minimum sea ice extent fluctuated after 2012, with lows of about 4.1 million km<sup>2</sup> in 2016 and 2019 (Perovich *et al.*, 2019). The minimum summer sea-ice extent is on a declining trend, with the 2012 value being exceptionally low relative to the trend (Figure 3.15). While the pronounced decline in sea ice in recent decades has occurred in the era of satellite records, historical sea-ice observations dating back to 1850 show that this decline is unprecedented for the whole observation period (Walsh *et al.*, 2017).

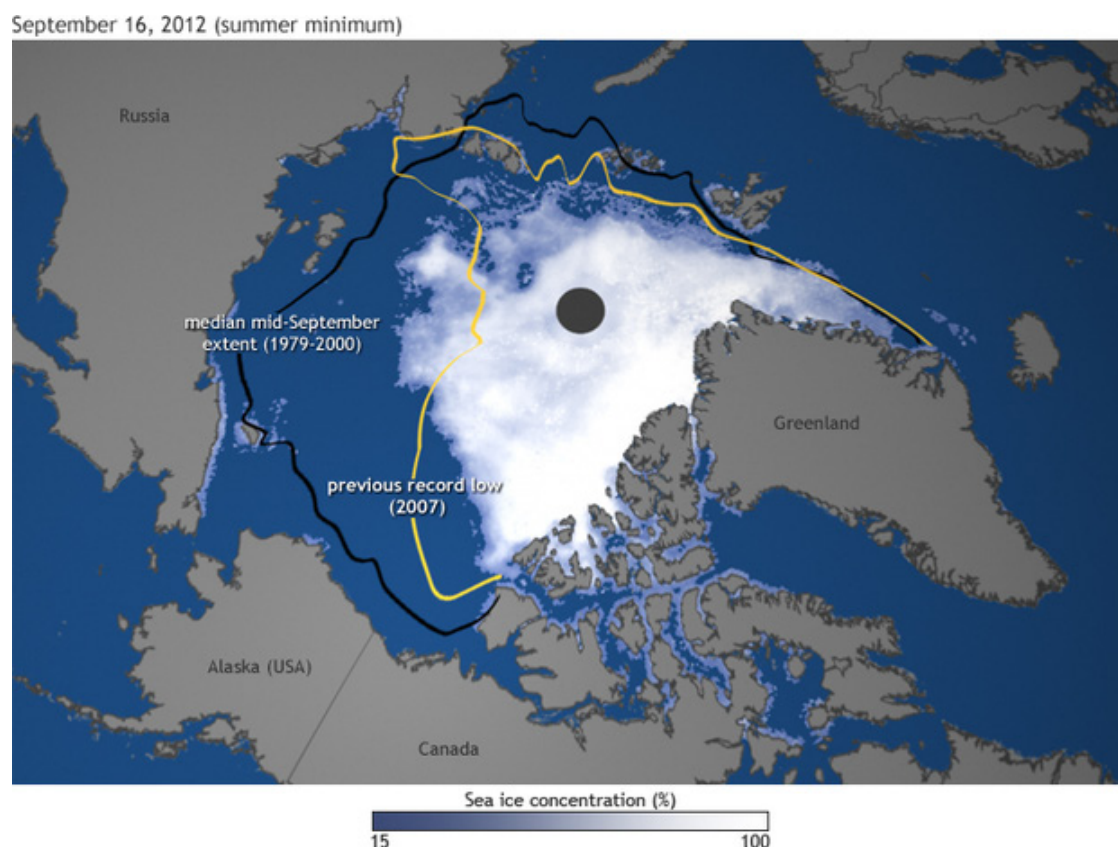


Figure 3.14. The record low minimum sea ice extent in September 2012. The yellow line shows the second lowest ice extent (until 2019) in 2007, while the black line shows the climatological median sea ice extent in September for 1979–2000. From NOAA (<https://www.climate.gov/news-features/featured-images/arctic-sea-ice-2012-record-low-was-18-smaller-previous-record-nearly>), based on data from National Snow and Ice Data Center. See Perovich *et al.* (2019).

Older ice types have largely disappeared, and remaining multiyear ice is now mostly young (2–3 years; Maslanik *et al.*, 2007, 2011; Perovich and Richter-Menge, 2009; Carmack *et al.*, 2015). Older ice (> 4 years) used to be a dominant ice type in the 1980s (about 35%), but is now down to only 1% of the ice cover (Kwok, 2018; Perovich *et al.*, 2019). Seasonal sea ice (< 1 year) is now dominant, and has made up about 70% of the ice cover since 2007 (Perovich *et al.*, 2019). The loss of perennial ice and the shift to seasonal ice has been associated with a marked decline in the thickness and volume of summer sea ice in the Arctic Ocean (Rothrock *et al.*, 2008; Perovich and Richter-Menge, 2009; Kwok and Untersteiner, 2011). The thickness of summer ice in the CAO has declined from about 2.5–3 m around 1980 to about 1.5 m in the most recent years (Kwok, 2018). The volume of multiyear ice in winter dropped by 40% between 2005 and 2008 (Kwok *et al.*, 2009). Compared to the previous situation when perennial sea ice dominated,



summer sea ice volume has decreased to about a quarter. This very substantial loss has been made up, roughly equally, by reductions in ice area and ice thickness.

A continued loss of sea ice is likely, and model predictions suggest that an ice-free Arctic Ocean in summer could be reached within the next 30 years under the influence of global climate change (Wang and Overland, 2009; Notz and Stroeve, 2016, 2018). Less and thinner sea ice, and, correspondingly, more open water, are associated with the potential for further rapid loss of summer sea ice (Maslanik *et al.*, 2007; Ivanov *et al.*, 2016, 2019). A summer ice-free CAO could have a substantial effect on global climate, with an estimated additional heating equivalent to an advancement of global warming by 25 years (Pistone *et al.*, 2019). The projected future loss in sea ice depends on how effectively the Paris agreement is implemented (Jahn, 2018; Sigmond *et al.*, 2018). In addition to the positive feedback effect on ice melt from reduced albedo, there are also thermodynamic contributions from the heat content of underlying waters (Carmack *et al.*, 2015). An intensified flow and spreading of Pacific summer water may have played a role in the recent events of extensive melting and low summer ice cover in Canada Basin (Shimada *et al.*, 2006; Ikeda, 2009). Seasonal heating of the upper layer in Canada Basin may also constitute an albedo-related positive feedback mechanism that contributes to delayed freezing and reduced sea-ice formation during the following winter (Perovich *et al.*, 2007b; Steele *et al.*, 2008; Jackson *et al.*, 2010). The retreat of the cold halocline from the Eurasian Basin may have had a similar effect on the energy flux and mass balance of sea ice (Steele and Boyd, 1998; Bjørk *et al.*, 2002). Mechanisms involving ocean heat may have contributed to the spatial pattern, with the largest losses of summer sea ice in the areas north of Russia and Alaska (Stroeve *et al.*, 2012; Onarheim *et al.*, 2018).

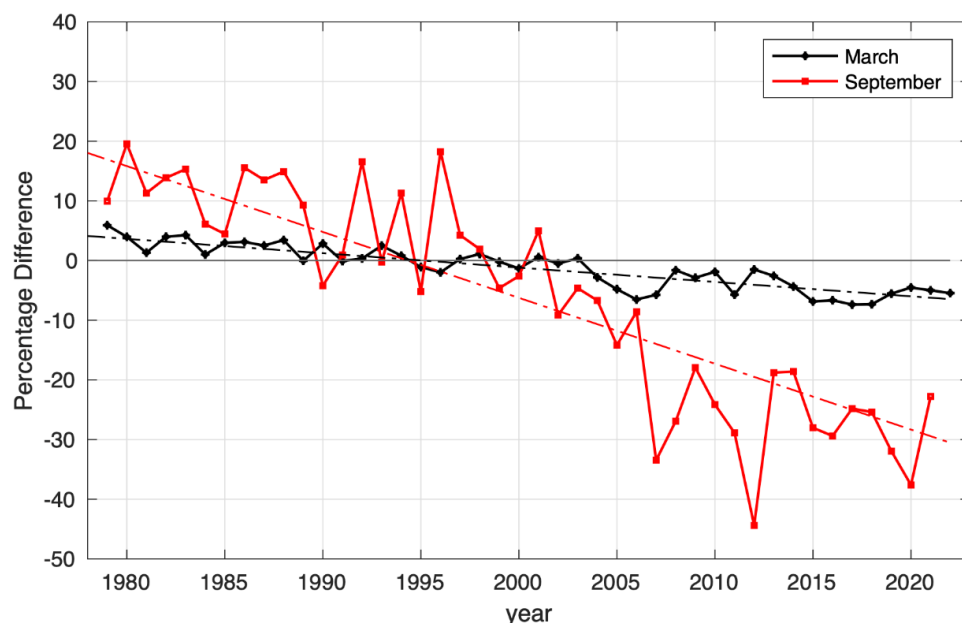


Figure 3.15. Declining trends (shown by dashed lines) in annual maximum (March) and minimum (September) sea ice extent (area with sea ice concentration at 15% or more including open water area in a grid box with ice) from 1979 to 2022 (the satellite era). The values are anomalies (solid line with markers) expressed as the difference (in %) in ice extent each year relative to the mean values for the period 1981–2010. Sea ice extent data are obtained from the National Snow and Ice Data Center (NSIDC), Boulder, Colorado, USA (<https://nsidc.org/data/G02135/versions/3>). Figure is updated from Perovich *et al.* (2019).

There has been sea-ice loss in the entire Arctic region in all months of the year (Meier *et al.*, 2014; Barber *et al.*, 2015). A broad pattern observed has been that loss of summer ice has been dominant for the central areas including the CAO, whereas loss of winter ice has been the

strongest signal for the peripheral parts of the Arctic (Onarheim *et al.*, 2018). There is a functional connection between the seasons, in that little summer ice leads to more warming and delayed ice formation the following winter. Associated with the loss in ice, there has been an increase in the duration of the open-water period in seasonally ice-covered waters (Stroeve *et al.*, 2014a; Barber *et al.*, 2015; Carmack *et al.*, 2015). It is worth noting that associated with the loss in sea ice, there has been an increase in the amount of ice produced in a given winter (Kwok, 2018). This is because thin ice grows faster than thick ice (due to the insulating effect of ice itself, which reduces the heat flux from the water to the atmosphere). The loss in sea ice volume is, therefore, lower for winter than for summer, with average annual loss rates of 287 and 513 km<sup>3</sup> for winter and summer, respectively, calculated over a 15-year period with satellite altimetry data (Kwok, 2018). By comparison, annual ice formation during winter for the Arctic Ocean has been 12 500 km<sup>3</sup> on average for the last 10 years (Perovich *et al.*, 2019).

In the years after 2010, the gradual decay of the ice cover around the Arctic Ocean may have reached a point where changing conditions at the sea surface have started to notably affect physical processes in the underlying ocean waters. The first signs of oceanic response to the shifted energy balance at the ocean–air interface have emerged, as expected, in the transition zones between boreal and Arctic domains. Arctic warming hot spots, whose origins can likely be directly linked with the Arctic sea-ice decline, were recently reported in the Chukchi–Beaufort seas (Timmermans *et al.*, 2018) and in the Barents Sea (Lind *et al.*, 2018).

### 3.4.4 Arctic amplification

Arctic amplification is the term used to refer to the fact that the Arctic is warming 2–3 times faster than the rest of the globe, driven, to large extent, by loss of sea ice. The change in Arctic sea-ice over the last two decades is a bellwether for global climate change. [Figure 3.16](#) shows the loss of multiyear sea ice in the Arctic based on satellite observations (Kwok, 2018). The shift from old to young and thin sea ice is dramatic for such a relatively short period. Sea-ice loss has occurred in both winter and summer, and is unique in scale for records dating back to 1901 (Schweiger *et al.*, 2019). Arctic warming has interrupted sea ice formation and the transpolar sea ice drift (Krumpen *et al.*, 2019). While the extent of summer sea ice has decreased over the last two decades, a startling development in recent years is the lower sea-ice concentrations (sea-ice area) within the summer ice pack itself. Lower sea-ice concentration (more open water) implies a greater area for the solar absorption of heat. If the decrease in sea-ice concentrations and the thinning of sea-ice continues, might summer sea-ice disappear completely in a near future late summer (Pistone *et al.*, 2019)? Recent model studies suggest this might happen by 2050 (SIMIP Community, 2020), but other studies suggest much earlier (Wang and Overland, 2012). There has also been a delay in autumn freeze-up by two months in the Chukchi and Barents seas, the regions shown in black in [Figure 3.16](#) for 2017.

Central Arctic annual temperatures have been increasing, as corroborated by multiple datasets and reanalysis products (Labe, 2020). Since the early 1900s, it has risen more than +2.5°C, compared to the global average of +1.1°C. Recent winter averages of air temperature increase are higher. [Figure 3.17](#) shows regional hot spots of > 4°C warming for the last five years, relative to the end of the 20th century. Multiple sources are proposed for Arctic Amplification, with shifts in albedo and the trapping of heat in the atmosphere (Lapse-rate and Planck feedbacks) as being the most important (Pithan and Mauritsen, 2014). A recent study emphasized an increasing role for atmospheric transport from the Subarctic (Kapsch *et al.*, 2019). Increases in winter air temperatures ([Figure 3.17](#)) are related to reduced ice formation and thinner sea ice.

The phenomenon of Arctic Amplification will continue into the future. [Figure 3.18](#) shows projections for the global mean, and annual and winter Arctic mean temperatures for a range of greenhouse gases increases. The blue scenario [representative concentration pathway (RCP)

4.5 ( $\text{W m}^{-2}$ )] is a projection for a global increase in average air temperature of  $\sim 2^{\circ}\text{C}$  by the end of the century, with extensive, but reasonable, mitigation of greenhouse gases. The red scenario (RCP 8.5) is the extreme case, without extra mitigation measures ("business as usual"). Note that all scenarios show a continued Arctic temperature increase to more than  $2^{\circ}\text{C}$  by 2050 based on projections relative to current conditions.

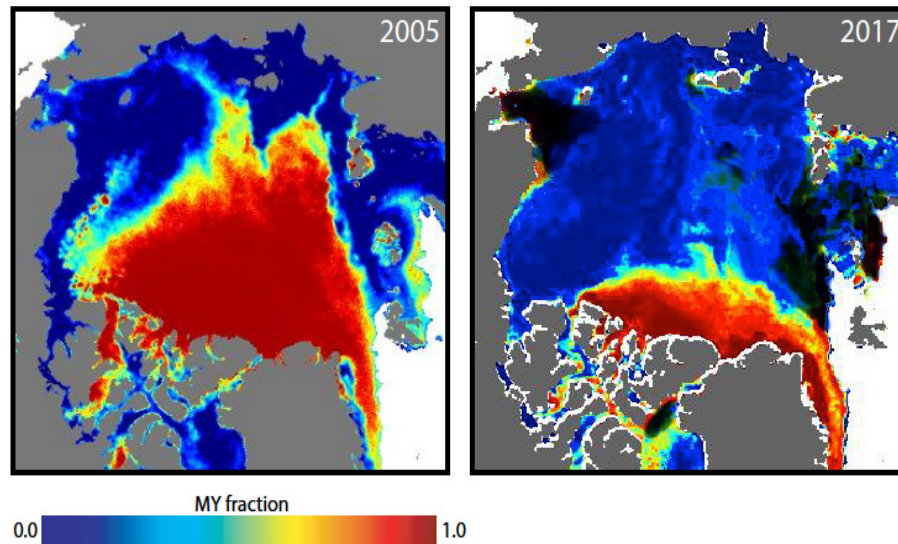


Figure 3.16. Decadal decline in January multiyear Arctic sea-ice coverage from the QuikSCAT (1999–2009) and ASCAT (2009–2018) satellite-based scatterometers. Old multiyear sea ice (red) is tracked through its lower salinity. Multiyear sea ice now covers less than one-third of the Arctic Ocean, and seasonally formed sea ice (blue) has become the dominant ice type. After Kwok (2018).

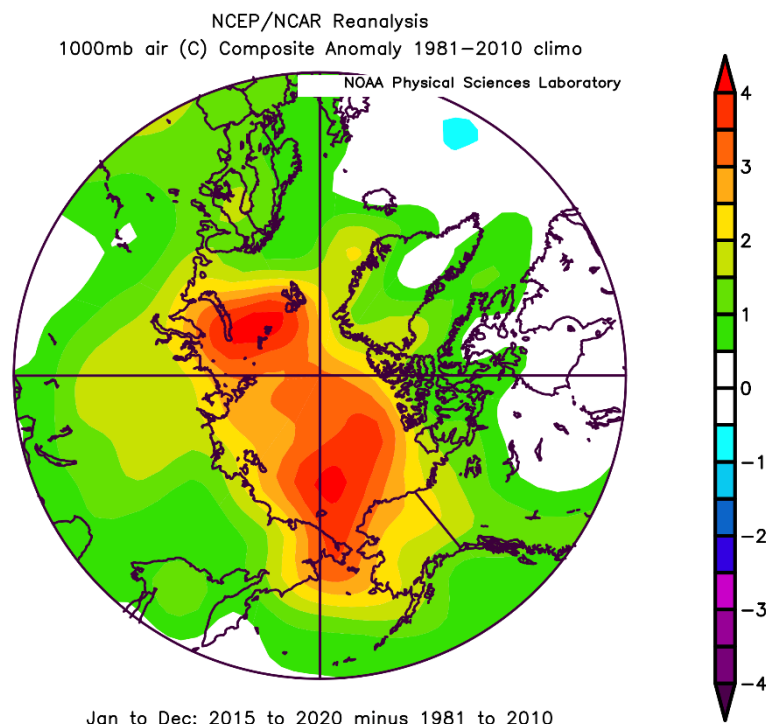
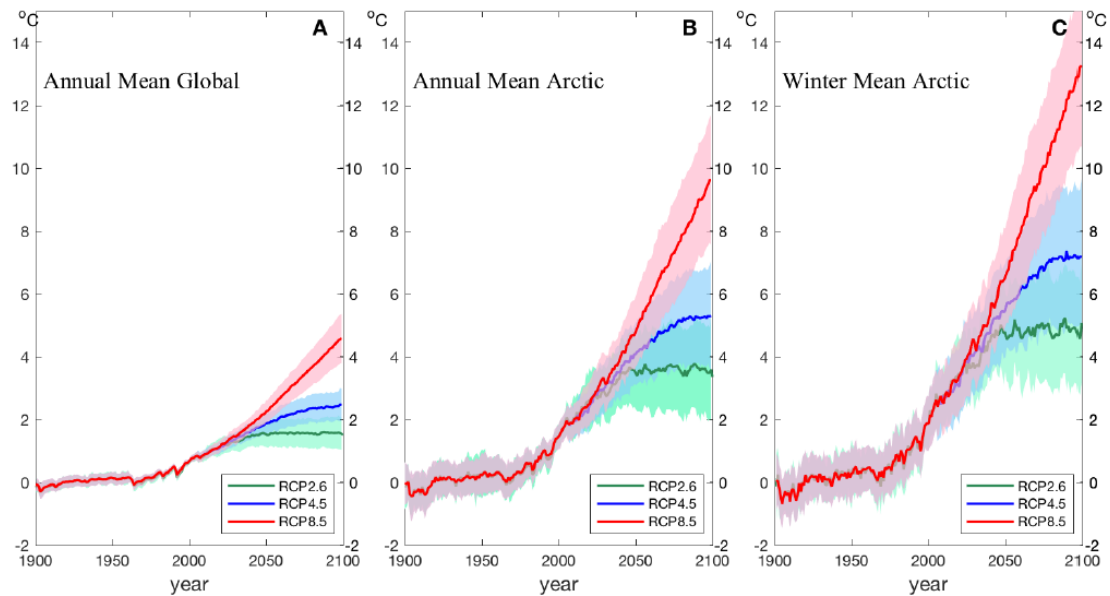
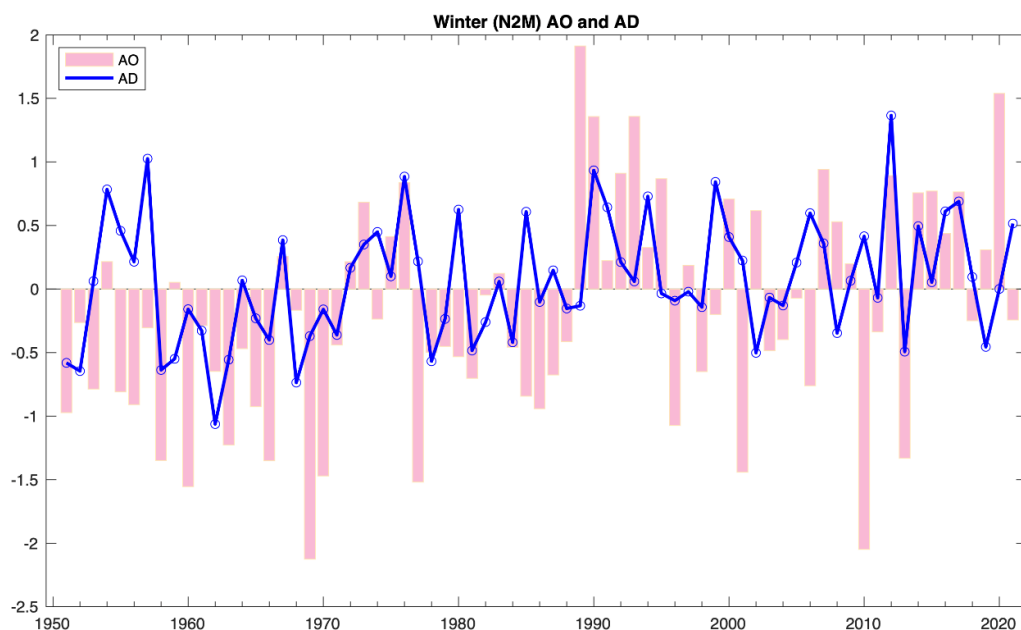


Figure 3.17. Winter air-temperature anomalies for 2016–2020, relative to 1981–2000. From NOAA/ESRL.



**Figure 3.18.** Projections of global mean temperature (A), and annual (B) and winter (C) Arctic mean temperatures based on CMIP5 simulations under the RCP 2.6 (green), RCP 4.5 (blue), and RCP 8.5 (red) scenarios. The thick line shows the model ensemble mean, and the shadings indicate the spread of the model runs (Overland *et al.* 2019a).



**Figure 3.19.** The time-series of the Arctic Oscillation (AO) and Arctic Dipole (AD) weather patterns averaged for the five winter months November–March. The AO and AD is computed as the first and second principal component, using sea level pressure between 70 and 90°N for 1948–2019 based on the NCEP–NCAR reanalysis.

Several papers, but especially Overland *et al.* (2019b), show that overall temperature increases since 1990, and associated features such as sea-ice loss, represent a separate physical forcing of the Arctic to the month-to-month and year-to-year variability of the wind pattern, as represented by the Arctic Oscillation (AO) and Arctic Dipole (AD; [Figure 3.19](#)). The positive phase of the AO represents a strong west-to-east wind vortex, while a negative AO allows for a more wavy north-south orientation of the windfield, carrying extra heat both north and south. For example, winters during the early 1990s had a strong positive AO, while multiple individual

years since 2000 had a more wavy wind pattern where cold Arctic air reached further into the Subarctic. Some winters can be dominated by a second pattern, the AD, with high pressure on the North American side of the Arctic and low pressure on the Eurasian side, giving strong winds over the central Arctic and promoting the exit of sea ice through Fram Strait. The AD was present for several winters in the last decade.

The projections in [Figure 3.18](#) suggest that the central Arctic will see an additional continued annual warming to +2°C by mid-century, with greater increases in winter. Weather patterns such as the AO and AD will add year-to-year variability and regional differences.

### 3.4.5 Warm anomalies in the Arctic Ocean

The high positive NAO situation around 1990 led to an intensification of the transport of Atlantic water up along the eastern margin of the Norwegian Sea (Mork and Blindheim, 2000; Blindheim, 2004). This increased flux of warm water continued into the Arctic Ocean via the Fram Strait and Barents Sea branches, and was recorded as a warm anomaly as it progressed along the boundary current in Eurasian Basin (Quadfasel *et al.*, 1991; Carmack *et al.*, 1995, 1997; McLaughlin *et al.*, 1996; Swift *et al.*, 1997; Grotenfendt *et al.*, 1998; Morison *et al.*, 1998, 2000; Zhang *et al.*, 1998; Dickson *et al.*, 2000; Schauer *et al.*, 2002b; Gerdes *et al.*, 2003; Karcher *et al.*, 2003). The increased flow of Atlantic water was also evident in the Makarov and Canada basins, where the signal arrived 5–8 years later, reflecting the transport time of the Atlantic layer boundary current (Woodgate *et al.*, 2001; McLaughlin *et al.*, 2002, 2004; Shimada *et al.*, 2004). Part of the signal in Canada Basin manifested as a cooling and freshening of the Atlantic layer water, suggesting an increased flow and fraction of water proceeding from the Barents Sea branch (Melling, 1998; McLaughlin *et al.*, 2002, 2004; Woodgate *et al.*, 2007).

The increased flow and warming of the Fram Strait branch in the early 1990s and the eastward shift in freshwater input from Siberian rivers were associated with a retreat of the cold halocline layer from Amundsen Basin, across Lomonosov Ridge, and into Makarov Basin (Steele and Boyd, 1998; Rudels *et al.*, 2004). This shift likely had an effect on the energy flux and mass balance of sea ice in this part of the Arctic Ocean (Steele and Boyd, 1998; Bjørk *et al.*, 2002). After the warm pulse in the early 1990s, the cold halocline returned to Amundsen Basin in the late 1990s, although it was less pronounced than it was before the warm event (Bjørk *et al.*, 2002; Boyd *et al.*, 2002).

Another warming event took place in the early 2000s, recorded first in Fram Strait in 1999 and, subsequently, in Laptev Sea in 2004 (Schauer *et al.*, 2004; Polyakov *et al.*, 2005; Dmitrenko *et al.*, 2008, 2009). During this event, the Fram Strait branch was anomalously warm (with temperature >3°C in the western Nansen Basin), while the Barents Sea branch was found to be cooler (by 0.4°C), denser, and more ventilated (Dmitrenko *et al.*, 2009; Lind and Ingvaldsen, 2012). After the second warming event, Atlantic water temperature did not return to the climatic mean values typical for the second part of the 20th century, but remained higher than the 20th century average by about 0.5–0.75°C (Polyakov *et al.*, 2011).

### 3.4.6 Atlantification of the Eurasian Basin

Atlantification is a term used to describe the increased influence of warm Atlantic water in the Arctic (e.g. Polyakov *et al.*, 2017; Lind *et al.*, 2018). In the western Nansen Basin, eastward-moving warm Atlantic water meets the sea ice that is drifting out from the central basin. This collision results in the cooling and freshening of the upper part of the Atlantic water due to ice melt. Under the conditions which were typical for the second half of the 20th century, a restricted region north of Svalbard (the so-called Whalers Bay) remained ice-free in winter, as a consequence of a persistent sensible heat polynya maintained by the heat content of the



inflowing Atlantic water. In the current warming climate, with decreasing Arctic sea-ice cover, the share of seasonal ice has been increasing, while the ice itself has become thinner and more mobile and fragile. These changes on a pan-Arctic scale have invoked regional responses, which have included reduced sea-ice import to the marginal transition zones (seas) from the central basin (Ivanov *et al.*, 2016). In the western Nansen Basin, the earlier steady-state heat and salt balances in the upper polar mixed layer have shifted. Decreased ice melt, together with an increased heat and salt import with the Atlantic water inflow, have led to reduced vertical density stratification. This, in turn, has facilitated the development of a winter thermohaline convection along the pathway of Atlantic water (Ivanov *et al.*, 2018). Enhanced convection delivers additional heat and salt to the upper mixed layer, contributing to the accelerated sea-ice melt and/or reduced local ice formation. This is an example of a positive feedback loop associated with the connection between regional sea-ice decay and a change in the vertical thermohaline structure of the water column.

The strong seasonal cycle of temperature in the Atlantic water layer, with a maximum in early winter for the mid-part of the western Nansen Basin (Ivanov and Repina, 2018), additionally facilitates convection above the warm core of the Atlantic water. Satellite observations reveal the outcome of this chain of events, as an anomalously long duration of a low-ice concentration zone in the western Nansen Basin in mid-winter since 2012 (Ivanov *et al.*, 2018).

Recently acquired data show that signs of atlantification, previously identified only in the western Nansen Basin, are now also emerging in the eastern Nansen Basin (Polyakov *et al.*, 2017). The major driver for these changes is the joint effect of declining sea-ice volume and weakening of stratification in the layers overlaying intermediate Atlantic-origin water. Weaker stratification, shoaling of the upper boundary of the Atlantic water, and net loss in ice volume, facilitate deep winter ventilation in the eastern Nansen Basin. This ventilation has resulted in enhanced upward heat fluxes from the Atlantic water, which lead to additional melting in the ice cover.

### 3.4.7 Recent changes in Canada Basin

In Canada Basin, the recent loss of sea ice, and the more fragmented and mobile sea ice conditions, could enhance the Beaufort Gyre circulation (Shimada *et al.*, 2006; Yang, 2009), which has shown a persistent anticyclonic circulation regime since 1997 (Figure 3.13; Proshutinsky *et al.*, 2011, 2015). The enhanced Beaufort Gyre would accumulate more freshwater within the gyre (Proshutinsky *et al.*, 2009), which might cause a deepening of the nutricline, with possible negative effects on primary production (PP; McLaughlin and Carmack, 2010; Nishino *et al.*, 2011a; Coupel *et al.*, 2015). However, in this region, eddies could have a larger role than previously thought in supplying nutrients laterally and maintaining phytoplankton production (Nishino *et al.*, 2011b, 2018; Aguilar-Islas *et al.*, 2013; Watanabe *et al.*, 2014; Yun *et al.*, 2015). The enhancement of the Beaufort Gyre may, in turn, shift the Atlantic–Pacific boundary toward the eastern Arctic Ocean. In fact, Pacific summer water, or its modified water by winter cooling, were again found in Makarov Basin in the 2000s (Nishino *et al.*, 2013). The recent delay in autumn freeze-up in the East Siberian Sea resulted in the formation of a large-volume water mass through cooling and convection. The spreading of this water mass into Makarov Basin caused shoaling of the nutricline, which might have increased primary productivity (Nishino *et al.*, 2013). Thus, the hydrographic and biogeochemical responses to sea-ice loss could be quite different between the Alaskan and Siberian sides of the region.

## 4 Algae and primary production

*Hein Rune Skjoldal, Bodil Bluhm, Hauke Flores, Toru Hirawake, Haakon Hop, and Cecilie von Quillfeldt*

### 4.1 Introduction

The plants that provide the energy basis for the CAO ecosystem are microscopically small algae that live either suspended in the water as phytoplankton or attached to or in sea ice as ice algae. These two compartments are composed of the same taxonomic groups of algae, dependent on the geographical area, with considerable overlap in species composition (Poulin *et al.*, 2011; Bluhm *et al.*, 2017a, 2017b; Hardge *et al.*, 2017a, 2017b; Lovejoy *et al.*, 2017; Hop *et al.*, 2020). When sea ice forms in autumn, it may get inoculated with algae from the water column, where ice-algae species can survive the ice-free period, although commonly in low density. Inoculation may occur with algal cells from sediments in shallow waters. In spring, with the return of light after the polar night, the algae that start to grow on the underside of or inside the ice can be a mixture of specialized ice algae and generalists that can live both associated with sea ice and free in the water column. When ice melts in summer, ice algae may get sloughed from the ice into the water where they can constitute a part of the phytoplankton community, but often they become part of the vertical flux of material which sinks out from the upper water layer (Morata *et al.*, 2011; Wassmann and Reigstad, 2011; Lalande *et al.*, 2014, 2019; Wiedmann *et al.*, 2020). An increase in under-ice blooms of phytoplankton due to changes in ice conditions has been observed (Arrigo *et al.*, 2012; Assmy *et al.*, 2017).

Knowledge of Arctic biodiversity is increasing as a result of improved sampling techniques, advanced microscopic and molecular methods, electronic databases and gene libraries, and increased international cooperation (Daniëls *et al.*, 2013), as well as increased sampling in the central basins (e.g. Melnikov, 1997; Katsuki *et al.*, 2009; Joo *et al.*, 2012; Tonkes, 2012; Hardge *et al.*, 2017a).

Specialized ice algae are, in a sense, benthic life forms that have come to use the "inverted seabed" that is the floating sea ice in the Arctic (Melnikov, 1997). Benthic micro- and macroalgae do not play a role, or only a very small role, in the energy flow and carbon (C) cycle of the CAO. Apart from shallow coastal areas, or banks on the surrounding Arctic shelves, the CAO water is too deep to support growth of benthic algae. Large macroalgae, like kelp, grow in the Arctic on hard substrates. They are generally deeper than the upper 5 m of the sublittoral zone, which is influenced by sea ice and ice scour (Dunton *et al.*, 1982; Dunton and Dayton, 1995). The growth of macroalgae has become shallower with the reduction in coastal sea ice (Krause-Jensen and Duarte, 2014). Some of these plants may be transported by ice and currents into the CAO, but it is assumed that this process plays a very small role as a C source compared to local production by ice algae and phytoplankton.

The primary production (PP) by phytoplankton and ice algae is the food and energy source for zooplankton and ice fauna, and the basis of the foodweb that supports fish, birds, and marine mammals. PP is low in this ecosystem, as a consequence of low light, due to the high-latitude location of the CAO (literally at the top of the world) and the presence of sea ice, and the strong stratification of the water masses, which limits the supply of nutrients to the upper euphotic zone. Very important questions are how low the rate or level of PP is, and what changes in PP may occur in response to the substantial reduction in CAO sea ice.

This report describes the small algae that compose the CAO phytoplankton and ice algae ([Section 4.2](#)), limiting factors for algal growth and PP, notably light and nutrients ([Section 4.3](#)), and information on biomass of phytoplankton and ice algae ([Section 4.4](#)). [Section 4.5](#) then provides a review of the available information on rates of PP and assesses the overall level of PP in the CAO and how this is affected by the ongoing climate change.

## 4.2 Species composition

### 4.2.1 Phytoplankton

Phytoplankton growth takes place mainly in the upper polar mixed layer of the CAO, although PP can extend down into the halocline layer. The upper layer stratifies in summer as a consequence of ice melt and input of freshwater from rivers, and salinity can be very low in the water beneath melting sea ice. Physiologically, this is a demanding zone for phytoplankton growth, and requires adaptation to these extreme conditions.

Diatoms and flagellates are dominant components of phytoplankton in the CAO ([Figure 4.1](#)), and more generally in Arctic marine waters (Sakshaug, 2004; Poulin *et al.*, 2011; Hardge *et al.*, 2017a, 2017b; Lovejoy *et al.*, 2017). Melnikov (1997) listed about 200 species of phytoplankton based on a review of literature and his own studies until the 1980s. Most of the species known at that point were diatoms (163 species), with about equal proportions of centric and pennate forms. Dominant genera included *Chaetoceros*, *Coscinodiscus*, *Rhizosolenia*, and *Thalassiosira* among the centric diatoms, and *Navicula* and *Nitzschia* among the pennate diatoms (Melnikov, 1997). Later, Poulin *et al.* (2011) reported 1874 phytoplankton taxa from ice-covered Arctic waters, with dominance of diatoms (57%) and dinoflagellates (23%). An updated compilation by Lovejoy *et al.* (2017) produced an even higher value of 2241 taxa. Poulin *et al.* (2011) listed eight centric diatoms (including *Chaetoceros furcillatus*, *Thalassiosira gravida*, and *T. nordenskioeldii*) and six pennate diatoms (including *Cylindrotheca closterium* and *Fragilariopsis oceanica*) as the most frequently reported species for the pan-Arctic region. The composition of phytoplankton varies seasonally in Arctic waters (von Quillfeldt, 2000; Lovejoy *et al.*, 2002; Ratkova and Wassmann, 2002; Sukhanova *et al.*, 2009).

Phytoplankton taxonomy is evolving, and there is still insufficient knowledge of species composition and diversity in the Arctic. The majority of identified species are relatively large (> 20 µm), while much less is known about species of small phytoplankton in the size range of pico- and nanoplankton (Poulin *et al.*, 2011; Lovejoy *et al.*, 2017).

Booth and Horner (1997) studied the composition of phytoplankton (and ice algae) in a transpolar section across the Arctic Ocean. They identified 49 diatom species and 12 dinoflagellate taxa, but unidentified flagellates made up a large proportion of total phytoplankton cell numbers. Picoplankton (cells < 2 µm in size) contributed an average of 93% of total cell numbers, and about a third of the estimated biomass. Flagellates > 5 µm in size contributed another third of the biomass, while diatoms made up much of the rest (26%; Booth and Horner, 1997). Another study in the North Pole region found that diatoms and a range of flagellates belonging to the groups of cryptophytes, haptophytes, chlorophytes, chrysophytes, and dinoflagellates, contributed to the protist biomass in the upper mixed layer (Olli *et al.*, 2007). Diatoms were represented with 71 observed taxa and dinoflagellates with 68 taxa. This study also found a dominance of relatively small and often unidentified flagellates (Olli *et al.*, 2007).

Fujiwara *et al.* (2014) studied the community structure of surface waters in the western Arctic Ocean based on pigments analysis. They reported that haptophytes dominated in the warmer water in 2008, whereas prasinophytes dominated in the colder water in 2009 and 2010. This interannual difference might be attributed to a change in the timing of sea-ice retreat. A study

in the Eurasian Basin using gene sequencing fingerprinting in summer 2012 found a dominance of chlorophytes in the picoplankton fraction, with the prasinophyte *Micromonas pusilla* as an important species (Metfies *et al.*, 2016). This species has been found to be abundant in Arctic waters (Thronsdén and Kristiansen, 1991; Not *et al.*, 2005; Lovejoy *et al.*, 2007; Vader *et al.*, 2015). Many studies now suggest that small algae in the picoplankton fraction are an important component of the CAO phytoplankton (Booth and Horner, 1997; Sherr *et al.*, 2003; Metfies *et al.*, 2016). The proportion of picoplankton to total phytoplankton was found to increase with the freshening of the surface layer in Canada Basin between 2004 and 2008 (Li *et al.*, 2009).

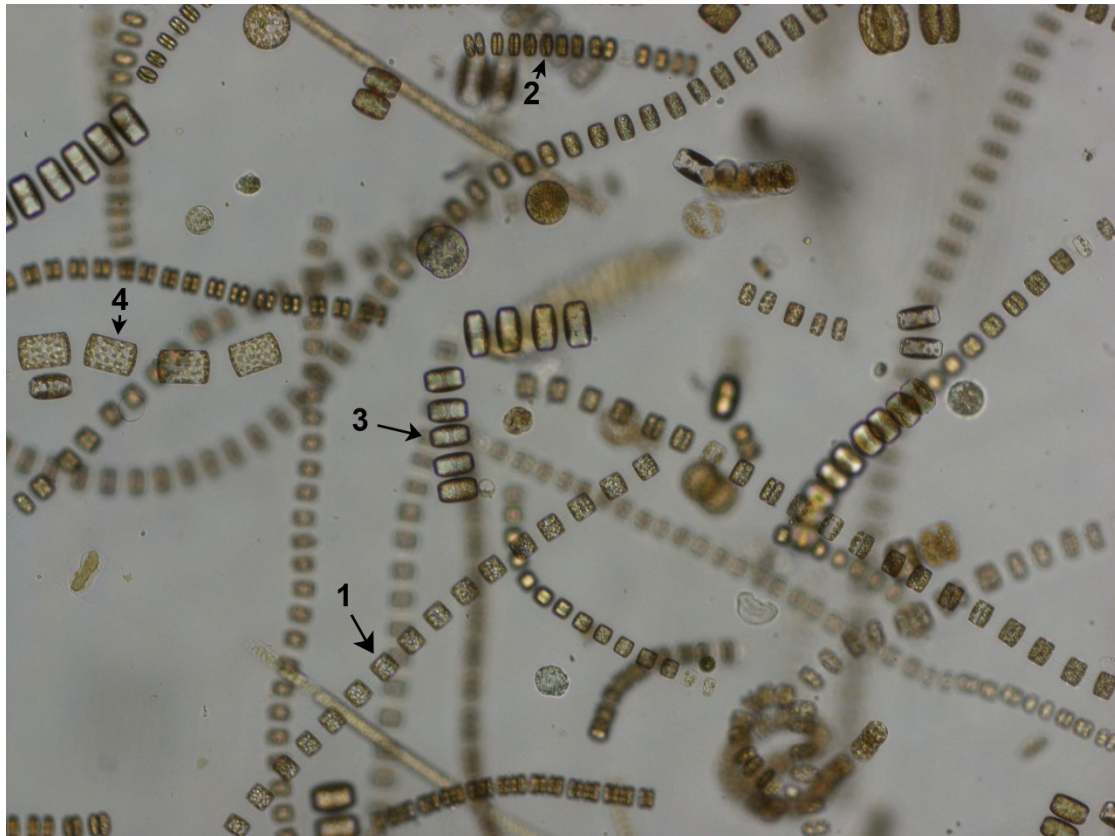


Figure 4.1. Microscope photo of Arctic spring bloom phytoplankton, showing dominance of chain-forming centric diatoms. Species include *Thalssiosira antarctica* var. *borealis* (1), *T. hyalina* (2), *Porosira glacialis* (3), and *Shionodiscus bioculatus* (4). Photo: Philipp Assmy, Norwegian Polar Institute.

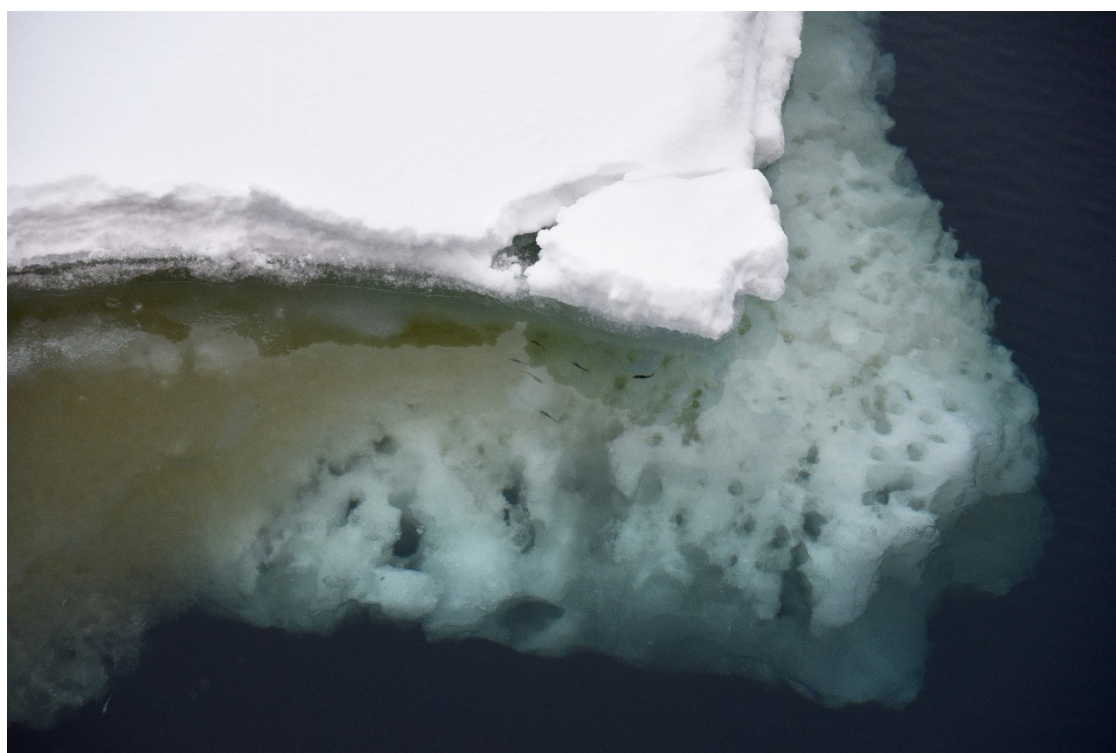
#### 4.2.2 Ice algae

In addition to phytoplankton that live suspended in the water, there is also an important fraction of algae that live in or are attached to the ice. Ice algae were observed during early expeditions to the Arctic during the 19th century. Nansen (1897) and Gran (1904) provided detailed descriptions of ice-algae communities based on year-round observations during the Fram expedition across the Arctic Ocean. Ice algae may grow as thin layers, mats, or filaments on the underside of the ice (Figure 4.2), within the ice matrix itself, and on the upper surface of the ice (Horner *et al.*, 1992; Melnikov, 1997; von Quillfeldt *et al.*, 2009; Bluhm *et al.*, 2017a, 2017b). Ice algae are physiologically adapted to the extreme environment, which has large changes in salinity due to melting and freezing. They are largely made up of the same groups of species as the phytoplankton, with diatoms and various flagellates dominating (Poulin *et al.*, 2011; Bluhm *et al.*, 2017b; Hop *et al.*, 2020).

In their review, Poulin *et al.* (2011) recognized 1027 sea ice (or sympagic) taxa of unicellular eukaryotes, which includes ice algae and also some heterotrophic forms. Bluhm *et al.* (2017b)



showed that an increased effort raises this number, which is now at almost 1300 taxa. Out of the 2106 total taxa in the inventory by Poulin *et al.* (2011), 1874 and 1027 taxa were recorded in the phytoplankton and as ice-associated taxa, respectively. From this it can be inferred that most species are recorded as both phytoplankton and sympagic. While most species are found in both environments, there are generally differences in species numerical abundance and dominance. This reflects the fact that many ice algae are specialists, adapted to living on or in ice with a benthic lifestyle. Diatoms make up an even larger fraction of the known sea ice algae (71%) than of phytoplankton, with a dominance of pennate species (52–77%; Poulin *et al.*, 2011). Important species among the pennate diatoms include the genera *Fragilariopsis*, *Navicula*, and *Nitzschia*, with *Nitzschia frigida* as the key species distributed widely in Arctic sea ice (Poulin *et al.*, 2011). The centric species *Melosira arctica* may grow as massive mats which can form long trailing curtains hanging down several meters from the underside of pack ice (Figure 4.3; Booth and Horner, 1997; Melnikov, 1997; Gradinger, 1999; Boetius *et al.*, 2013; Poulin *et al.*, 2014).



**Figure 4.2.** Layer of ice algae shown as brown coloration growing attached at the edge of an ice floe. The picture also shows small juvenile polar cod (*Boreogadus saida*). Photo: Pauline Snoeijs-Leijonmalm.

Ice algae tend to occur in characteristic communities at the bottom, in the interior, or at the surface of the ice (Horner *et al.*, 1988, 1992; Syvertsen, 1991). The different types of communities are characterized by specific species (von Quillfeldt, 1997; Gradinger, 1999; Melnikov *et al.*, 2002; von Quillfeldt *et al.*, 2003; Zheng *et al.*, 2011; Fernández-Méndez *et al.*, 2018; Melnikov, 2018; van Leeuwe *et al.*, 2018; Hop *et al.*, 2020). Irradiance is the most important factor in determining the abundance of ice algae. Snow depth, and ice thickness, structure, and age, control light in sea ice and, therefore, algal abundance (Gosselin *et al.*, 1997; Robineau *et al.*, 1997; Krembs *et al.*, 2002; Hop *et al.*, 2020).

Two types of bottom assemblages can be distinguished in sea ice: sub-ice and interstitial. The sub-ice assemblage consists of algae floating directly beneath the ice or attached to the underside of the ice, often to platelets and ice crystals protruding down into the water. This assemblage may form mats or strands that trail into the water column, and may reach

thicknesses of several tens of cm or even several meters, such as with *Melosira arctica* in pack ice (Figure 4.3; Melnikov and Bondarchuk, 1987; Melnikov, 1997; von Quillfeldt, 1997; Ambrose *et al.*, 2005; Boetius *et al.*, 2013). Such algal layers may be loose and easily disturbed by currents and ice movements. The interstitial assemblage is formed by algae in the water between the ice crystals and platelets, and it is more firmly integrated into the matrix of the ice. Pennate diatoms of genera *Navicula* and *Nitzschia* are common in this assemblage.



**Figure 4.3.** Strands of mucilaginous colonies of the centric diatom *Melosira arctica* hanging from the underside of an ice flow. Photo: Oliver Müller.

Two types of assemblages are also distinguished for the interior of the ice (Horner *et al.*, 1992): band and brine channel. The band assemblage occurs as a regular band in the ice, and may be formed by the accretion of new ice under a previously formed bottom-ice algal layer (Olsen *et al.*, 2017). The brine channel assemblage occurs in brine channels, cavities, and cracks in the ice. They are likely formed after some melting in spring when brine channels become connected to form a network within the ice. Algae may also occur more scattered throughout the ice.

Finally, pool and infiltration assemblages can be found on the surface of the ice. The pool assemblage consists of algae growing in ponds. The ponds may be formed by ice thawing, flooding by seawater, or a combination of the two processes. Infiltration assemblage occurs at the snow–ice interface when the lower part of the snow layer is flooded with seawater due to increased snow load relative to ice thickness (McMinn and Hegseth, 2004; Fernández-Méndez *et al.*, 2018; Hop *et al.*, 2020). This assemblage is commonly found in the Southern Ocean, but has recently been observed more frequently in the Arctic (Fernández-Méndez *et al.*, 2018).

Syvertsen (1991) suggested a latitudinal zonation pattern in the distribution of subice assemblages in the Arctic, based primarily on observations in Barents Sea. In spring, prior to ice melt, he observed a subice algal layer consisting mainly of actively growing planktonic species in the marginal ice zone. Farther north, in the first-year ice, this changed into a thicker layer of specialized subice algae, often dominated by *Nitzschia frigida*. This zone covered most of the Barents Sea ice in late spring and summer. Still farther north, in areas with multiyear ice, a specialized subice assemblage dominated by *Melosira arctica* was found. However, the pattern

may be more complex, as studies over nearly four decades have shown that the diversity of algae changes with the location and presence of multiyear sea ice (Hop *et al.*, 2020).

### 4.3 Limiting factors for algal growth

Photosynthesis and algae growth require light and nutrients. Both of these factors can strongly limit PP by phytoplankton and ice algae in the Arctic Ocean (Sakshaug, 2004; Popova *et al.*, 2010, 2012; Tremblay *et al.*, 2015). The CAO is located between about 75–80°N and the North Pole. The high latitude location, and the presence of sea ice, limit incoming light to the sea surface and the underside of sea ice. Concentrations of inorganic nutrients, specifically nitrate and phosphate, are generally low in the upper polar mixed layer (Codispoti *et al.*, 2013). This is a consequence of the strong salinity and density stratification, which restricts upward transport of nutrients by mixing from deeper layers.

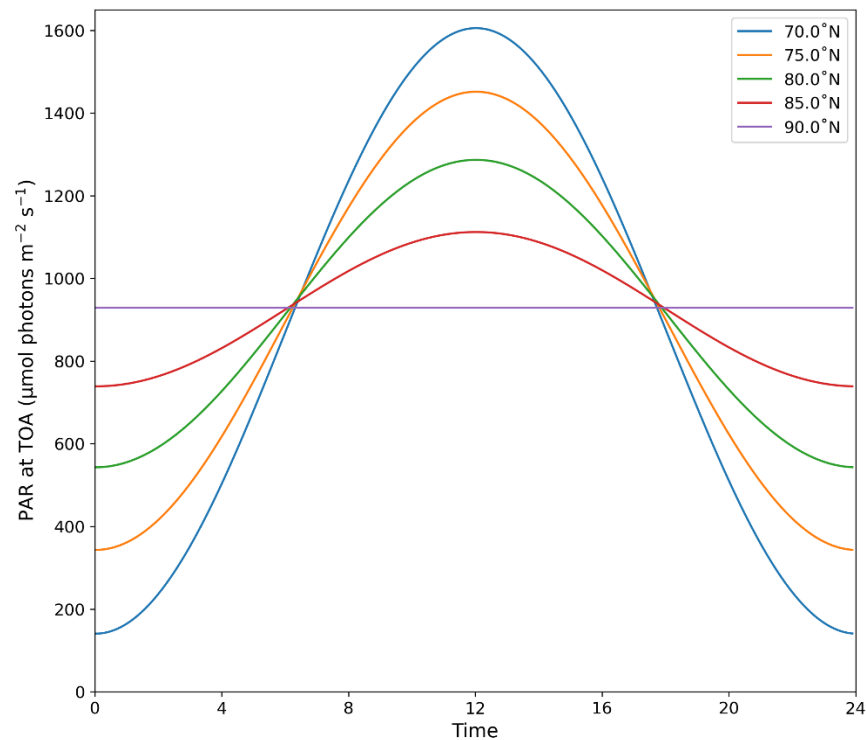
The limitation by light and nutrients interact, and their relative roles can vary seasonally and with depth. Generally, for the boreal and Arctic regions, light is limiting in spring before nutrients become depleted, and in summer in the lower part of the euphotic zone where concentrations of nutrients are increasing in the nutricline. Conditions in the CAO are extreme, and the system there may be generally light-limited (Codispoti *et al.*, 2013). Low light leads to low production and slow utilization of nutrients, which may, therefore, not be seasonally depleted. This pattern is possibly seen in some parts of Eurasian Basin. In contrast, nutrient levels in the Beaufort Gyre region in Canada Basin are very low even in winter, and nutrient limitation is likely to be important even if the level of production is very low (Codispoti *et al.*, 2013). More incoming light in the southern parts of the CAO, where there is seasonal ice cover and open water in summer, combined with low initial nutrient concentrations due to strong stratification, makes it more likely that nutrients become depleted and limit algal growth in summer.

#### 4.3.1 Light conditions

##### 4.3.1.1 Irradiance

Photosynthetically active radiation (PAR) is in the visible part of the light spectrum, and is defined as total radiation in the 400–700 nm spectral interval (Sakshaug *et al.*, 1997, 2009). Light of this type is termed irradiance (denoted  $E$ ). It is the integrated radiance over vertical directions, and is expressed as incoming light per unit of surface area and unit of time, either in units of energy ( $\text{W m}^{-2}$ ) or quanta ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  or  $\text{mol m}^{-2} \text{d}^{-1}$ ; Sakshaug *et al.*, 1997). PAR represents about 40–45% of the total solar radiation at sea level.

The high latitude position of the CAO (at the top of the world) means that the sun's trajectory is flat relative to the rotating earth (Sakshaug *et al.*, 2009). Therefore, the transition between polar night, when the sun is below the horizon, and polar day, with midnight sun, is gradual and prolonged. The sun angle at mid-day is low even in midsummer (34° at 80°N and 23.5° at the North Pole), leading to a reduced amount of light per unit area relative to zenith radiation (called cosine effect; Sakshaug *et al.*, 2009; see [Figure 4.4](#)). This is compensated by long days with midnight sun. Therefore, when integrated over a 24-hour period, the incoming light per unit area may be equally high as in lower latitudes ([Figure 4.5](#); about  $60 \text{ mol m}^{-2} \text{d}^{-1}$ ; Sakshaug *et al.*, 2009). Light reaching the sea surface at noon under ideal clear sky conditions is about  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  at the North Pole, compared to about  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  at 60°N and  $2200 \mu\text{mol m}^{-2} \text{s}^{-1}$  under zenith sun (Sakshaug *et al.*, 2009).



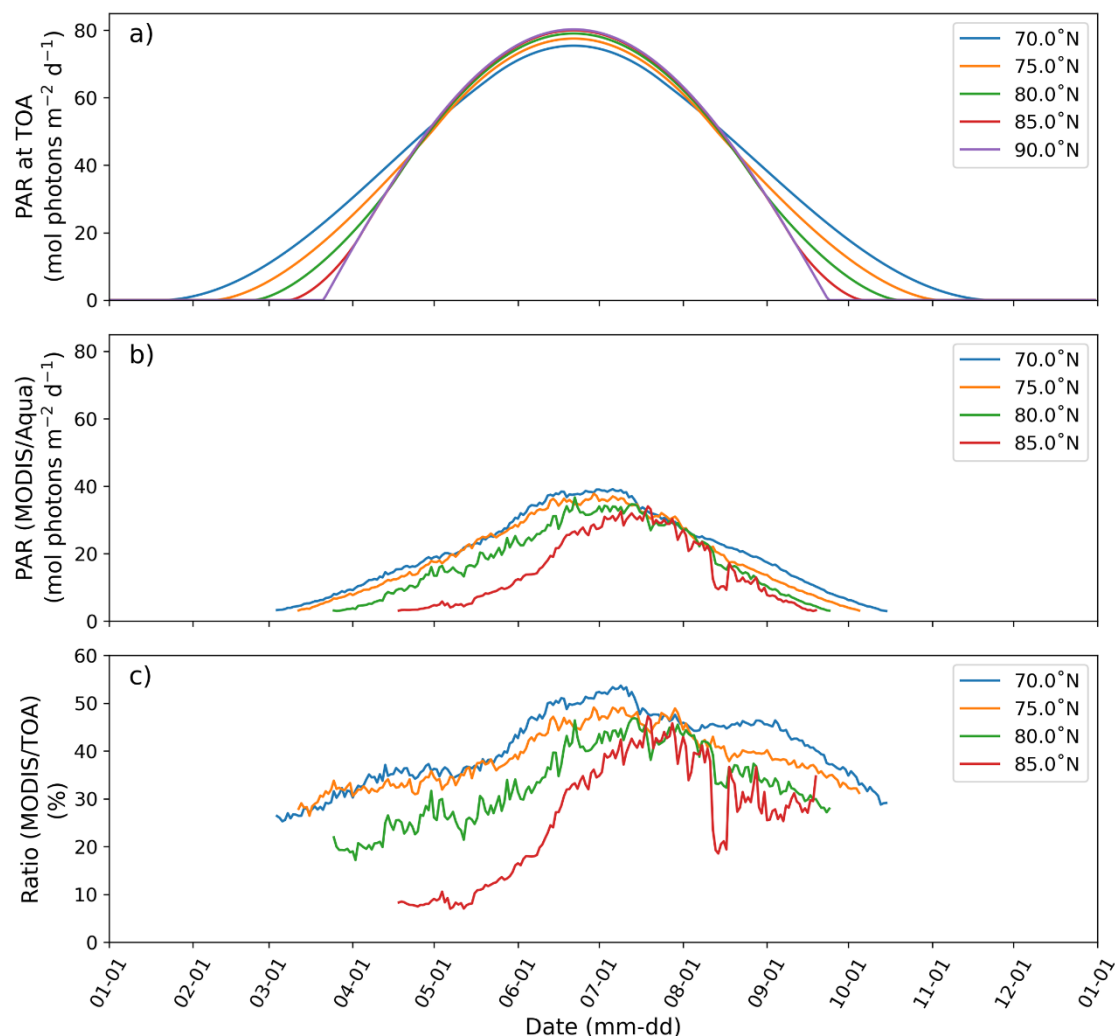
**Figure 4.4. Irradiance (PAR) at the top of the atmosphere during the 24-hour day–night cycle at midsummer for latitudes of 70, 75, 80, 85, and 90°N.**

There are three factors which contribute to the substantial reduction in the amount of light that reaches the subsurface water layer in the Arctic Ocean: reflectance, clouds, and sea ice (including snow cover). Some of the incident light is reflected back to the atmosphere by the sea surface. The fraction that is reflected increases strongly at low sun elevation, from around 10% reflectance at 20° elevation to near 100% reflection from a calm sea when the sun is at the horizon (Sakshaug *et al.*, 2009). Waves and choppy seas reduce reflectance (and increase transmission into the sea) to about 30–40% reflectance with the sun at the horizon, by what is known as wave focusing. The low sun angle leads to reduced subsurface irradiance, perhaps by the order of a third of the incident light to the sea surface, particularly in the early and late stages of the polar day between the spring and autumn equinoxes. The long twilight periods between polar night and polar day also shorten the productive season, when there is sufficient light for algal growth, to a maximum of about four months.

#### 4.3.1.2 Clouds

Clouds and fog can substantially reduce the amount of light that reaches the sea surface, commonly by 60–70% (Sakshaug *et al.*, 2009). Clouds and fog prevail in the Arctic Ocean, and there are very few days with clear skies in areas where there are leads and open water. Clouds are, by themselves, a complex issue, with different types of clouds depending on the interactions between the atmosphere, ocean, and land masses. Eastman and Warren (2010) recognized nine types in their analysis of Arctic clouds, with five low, three middle, and one high cloud types. The Arctic is generally cloudy, but with a strong seasonal signal of more clouds in summer than in winter for the high Arctic Ocean, including the CAO (Vowinkel, 1962; Walsh and Chapman, 1998; Intrieri *et al.*, 2002; Walsh, 2008). In their synthesis based on observations of clouds from ships and drifting stations (1954–2008), Eastman and Warren (2010) found that the total cloud cover increased from 50–60% in winter to 80–85% in summer, with a marked upward shift from April to May (and back again from September to October) driven by low stratiform clouds (Figure 4.6).





**Figure 4.5.** Seasonal changes in daily irradiance (PAR, 400–700 nm) reaching (a) the top of the atmosphere (TOA) and (b) the sea surface for latitudes of 70, 75, 80, 85, and 90°N. Irradiance at the TOA was calculated from solar zenith angle as a function of latitude and Julian day (Frouin *et al.*, 2003) and solar spectral irradiance (Thuillier *et al.*, 2003). Irradiance at the surface are estimates of PAR from MODIS/Aqua remote sensing, using MODIS daily L3 SMI (Standard Mapped Image) data for 2003–2019, calculated as mean values for a band of  $\pm 2.5^\circ$  around each target latitude. Note that MODIS only provides data where there is open water, and that there are no data for the North Pole at 90°N. (c) MODIS PAR as percentage of irradiance at TOA.

Clouds have a dual effect on light conditions for phytoplankton growth, directly, by reducing PAR, and indirectly, by affecting sea ice conditions. Clouds in the Arctic generally have a warming effect in all seasons except summer, due to emission of longwave radiation from clouds (Vavrus, 2004; Shupe and Intrieri, 2004; Eastman and Warren, 2010). In summer, the warming effect from longwave radiation is countered by a cooling effect due to scattering of shortwave radiation, which may have an overriding effect when the sunlight is at its maximum. Cloud feedback is the mechanism whereby more clouds give more warming and less sea ice, which, in turn, means more open water and more clouds.

Eastman and Warren (2010), through their observational time-series, found increasing trends in total and low (stratus) cloud cover for the CAO, with higher cloudiness during autumn in recent low-ice years compared to previous years with more ice. This implied that cloud cover increased in response to the increased extent of open water. Bélanger *et al.* (2013) estimated incident PAR to investigate effect of cloudiness on PP, and they revealed that PAR had significantly decreased

due to increased cloudiness over the entire Arctic and Subarctic seas (except a part of the CAO) over the 1998–2010 period.

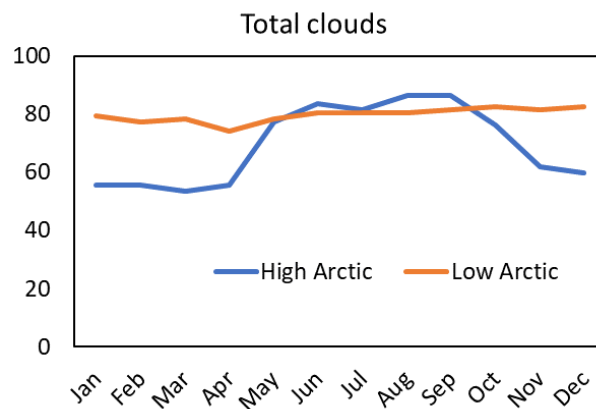


Figure 4.6. Seasonal cycles of total cloud cover (%) in the maritime Arctic, spatially averaged for the High Arctic (CAO and adjacent shelf seas) and Low Arctic (Bering Sea, Chukchi Sea, Nordic seas, and Barents Sea) zones. Data obtained from Eastman and Warren (2010, their Figure 5B).

#### 4.3.1.3 Albedo and melting snow and ice

Snow-covered sea ice has pronounced effects on the under-ice light climate, which can be complex with regard to optical properties (Perovich *et al.*, 1998; Mundy *et al.*, 2005). Snow has a strong albedo effect, reflecting 80 to nearly 100% of the light at low sun angle (Melnikov, 1997; Sakshaug *et al.*, 2009). Snow-covered sea ice in late winter, when light is returning after the polar night, reflects most of the irradiance. As snow starts to melt, the albedo decreases in a pattern that depends on the type of ice and formation of melt ponds on the ice surface (Figure 4.7; Perovich and Polashenski, 2012). Melting typically starts around late May to early June, when air temperature reaches about 0°C. As snow melts away, and melt ponds form on the ice surface (Figure 4.8), the albedo decreases to a level of about 0.4–0.5 (40–50% reflectance). Bare ice without snow has an albedo of 0.7, compared to 0.85 for snow-covered sea ice (Perovich *et al.*, 2007b). With seasonal ice, the albedo decreases further as melting progresses, to about 0.2, before the ice melts away rapidly and the albedo drops to about 0.1 for open water (Perovich and Polashenski, 2012). With multiyear sea ice (MYI), the albedo drops to a minimum of about 0.4 in late summer, when melt ponds are most extensive (Perovich *et al.*, 2002, 2007b).

The seasonal progression of ice melt plays an important role for the growth of algae by affecting irradiance (PAR) for both ice algae and phytoplankton, and by determining the habitat for ice algae. The decrease in albedo leads to an increase in PAR and accelerated melting which, in turn, leads to a further increase in PAR. Since the growing season is short at the high latitude location of the CAO, timing is important, and even small shifts can have large implications for algae growth and total PP. The melt season in the CAO is only about three months (June–August), with considerable interannual variability (Markus *et al.*, 2009; Stroeve *et al.*, 2014a). Snow depth and levelness of the sea ice influence the pattern and trajectory of melt. Deep snow delays the onset of melt through the albedo effect. Multiyear ice with more variable surface relief (more hummocked) may experience earlier melt in patches of thinner snow, but overall slower melt due to less extensive coverage of melt ponds, when compared to first-year ice (FYI) with flatter topography (Webster *et al.*, 2015). The pond fraction (in relation to the total surface area) may reach 0.3–0.4 for MYI, while it can be > 0.7 for FYI (Fetterer and Untersteiner, 1998; Perovich *et al.*, 2002, Polashenski *et al.*, 2012). As melting progress, the albedo may temporally increase due to pond drainage through channels in the ice (Perovich and Polashenski, 2012).

In association with warming and the loss of sea ice, the melt season length has increased in recent decades by about 3.5 days per decade, or about 10 days for 1979–2013 (Markus *et al.*, 2009; Stroeve *et al.*, 2014a). The lengthening of the melt season has involved both an earlier onset of melt and a later freeze-up. Earlier melt reflects the substantial change in ice type from MYI to FYI. While it is expected that precipitation will increase in the Arctic as a whole due to global warming, observations suggest that precipitation and snow depth have declined for the CAO (Warren *et al.*, 1999; Eastman and Warren, 2010). This can be one factor leading to an earlier melt. Earlier melt and less sea ice extent lead to more heating of the upper ocean layer, which, in turn, contribute to a later freeze up.

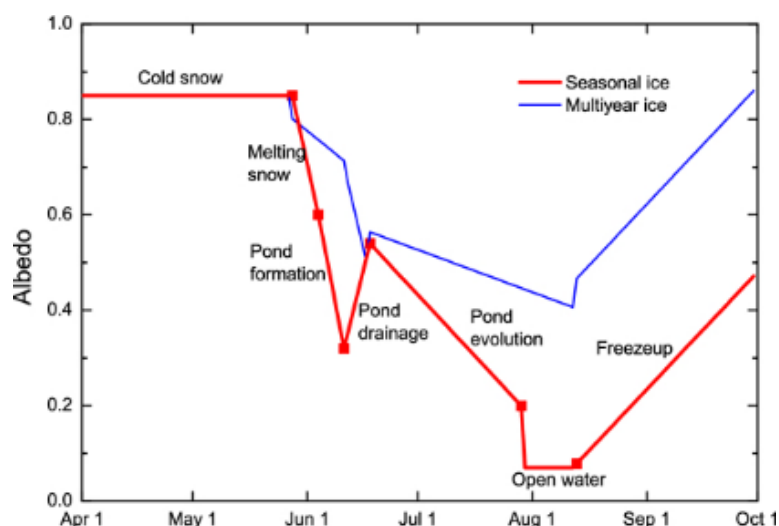


Figure 4.7. Seasonal change in albedo from late winter to autumn for multiyear and seasonal sea ice. Schematic summary with seven phases of melting of snow and ice recognized, based on measurements made in fast ice near Barrow, Alaska (Perovich and Polashenski, 2012) and in drifting pack ice in the Canada Basin (Perovich *et al.*, 2007b). Figure reproduced, with permission, from Perovich and Polashenski (2012).

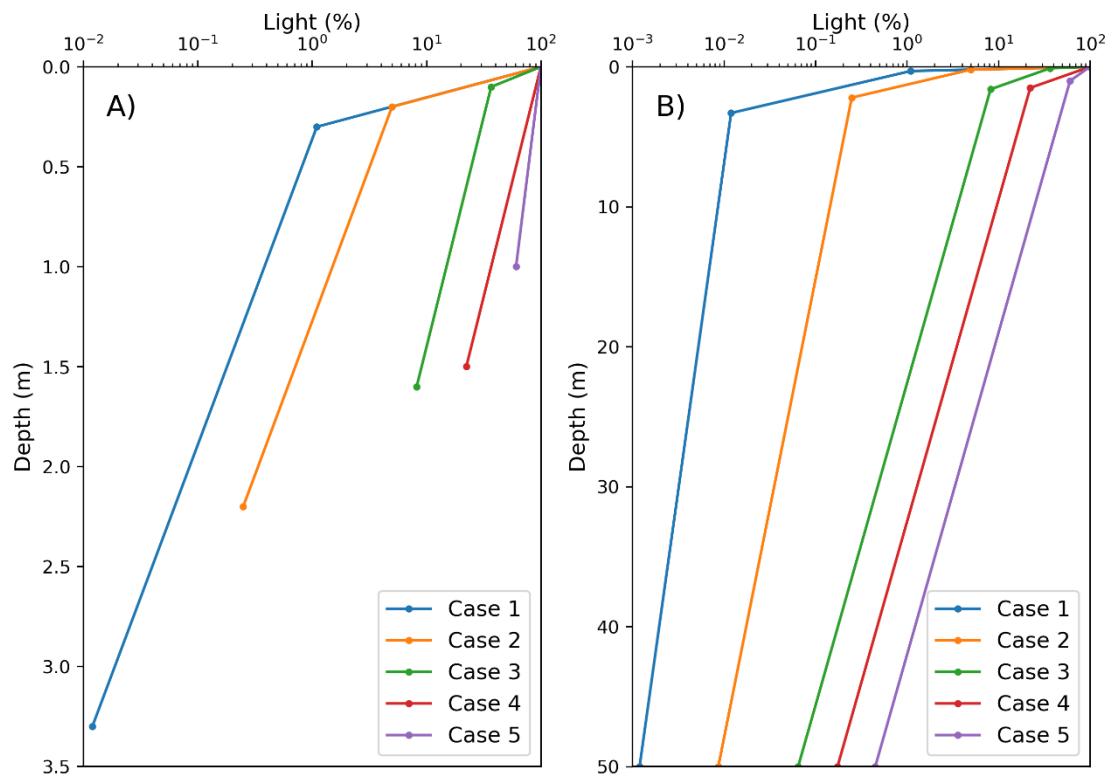


Figure 4.8. Photographs of sea ice with cold snow in late winter (left panel) and with melting snow and melt ponds in early summer (right panel). Photos: Pauline Snoeijs-Leijonmalm.

#### 4.3.1.4 Light transmission through snow and ice

The optical properties of snow and ice are known in general terms (Grenfell and Maykut, 1977; Untersteiner, 1986; Perovich, 1996; Perovich *et al.*, 1998), and there has been renewed interest in studies of light absorption and transmission through sea ice in recent years due to the need to understand the melting processes in more detail (e.g. Perovich, 2005; Wang *et al.*, 2014; Light *et al.*, 2015; Lu *et al.*, 2018). One reason for this interest is the fact that it takes only a small shift in

the overall energy balance for the Arctic Ocean (by  $1 \text{ W m}^{-2}$ ) to explain the large loss in sea ice (Kwok and Untersteiner, 2011).



**Figure 4.9.** Hypothetical cases of light transmission through snow and sea ice in various stages of seasonal melting based on reported light transmission coefficients. Left panel: Light transmission (% of surface irradiance) through snow and ice of various thickness (depth scale) for five cases - Case 1: 30 cm of snow on top of 3 m sea ice, with  $k$  values of 15 and  $1.5 \text{ m}^{-1}$  for snow and ice, respectively; Case 2: 20 cm of snow and 2 m ice, with same  $k$  values as in case 1; Case 3: 10 cm of snow and 1.5 m ice, with  $k$  values of 10 and  $1.0 \text{ m}^{-1}$ , respectively; Case 4: no snow and 1.5 m ice,  $k$  of  $1.0 \text{ m}^{-1}$ ; Case 5: no snow and 1.0 m ice,  $k$  of  $0.5 \text{ m}^{-1}$ . Right panel: Light transmission through snow and ice and the upper 50 m of the water column for the same five cases as in the left panel. Diffuse attenuation absorption coefficient ( $k$ ) for seawater is  $0.05 \text{ m}^{-1}$  in Case 1,  $0.07 \text{ m}^{-1}$  in Case 2, and  $0.1 \text{ m}^{-1}$  in Cases 3–5.

Transmission of light through snow is low due to high extinction, with coefficients of  $10\text{--}15 \text{ m}^{-1}$  found for snow cover in the Arctic Ocean (Grenfell and Maykut, 1977). This means only about 10% of light passes through a 5-cm snow layer and  $<1\%$  passes through a 40-cm thick layer (Melnikov, 1997). Sea ice itself is much more transparent than snow, but the transparency depends on the structure of ice, and is reduced by e.g. bubbles and tubular configurations. Untersteiner (1961) determined the broadband extinction coefficient for MYI at  $1.5 \text{ m}^{-1}$ . Similar values of around  $1\text{--}1.5 \text{ m}^{-1}$  were found by Grenfell and Maykut (1977) for the interior (below the upper 20 cm) of both white MYI and blue FYI. However, they found much higher extinction coefficients ( $> 3 \text{ m}^{-1}$ ) for the surface granular layer (upper 5–10 cm) of the ice. Katlein *et al.* (2015) found values of  $1.4\text{--}2.2 \text{ m}^{-1}$  for ice in the northern Fram Strait at about  $82^\circ\text{N}$ . The ice was a mixture of deformed and undeformed FYI and MYI, with a granular surface layer and melt ponds. Considerably lower values were found by Light *et al.* (2008) for MYI at the SHEBA site in the Canada Basin, with average extinction coefficients of  $0.8 \text{ m}^{-1}$  for bare ice and  $0.6 \text{ m}^{-1}$  for ponded ice. The effect of such differences in extinction coefficient ( $k$ ) is large. At  $k = 0.5 \text{ m}^{-1}$ , 37% of light would be transmitted through 2 m sea ice, while it decreases to 5% at  $k = 1.5 \text{ m}^{-1}$  (Figure 4.9). Thus, Katlein *et al.* (2015), in their study, found light transmittance of 2–10% with a modal value of 3–4%.



Empirical data from the northern Barents Sea have shown that 0.2–5% of surface light was transmitted through snow-covered sea ice, varying in thickness from 1 to 3 m, and from annual to multiannual ice (Sakshaug *et al.*, 2009). This was found to be in general agreement with calculations by Maykut and Grenfell (1975). Measurements at the NP-23 ice-drift station in summer 1977 showed transmission of about 0.5% of surface irradiance through snow-covered multiannual ice, increasing to a maximum of 9% in September when all the snow and about 1 m of ice had melted from the surface (Melnikov, 1979, 1997).

Sunlight which reaches the surface of sea ice is either reflected (albedo), absorbed, or transmitted through the ice. This partitioning of solar radiation has been examined in several recent studies of melting sea ice in the Arctic Ocean. Lu *et al.* (2018) summarized previous studies (in their Table 1), including Nicolaus *et al.* (2012), Hudson *et al.* (2013), and Light *et al.* (2015). These field studies found that 7–39% of incident solar energy is transmitted through the sea ice, while 46–73% is absorbed, and 15–34% is reflected. Lu *et al.* (2018) obtained similar results with a radiative transfer model, estimating that about 20% of the light was transmitted through 1 m sea ice and a melt pond 0.3 m deep. Most of the absorption was calculated to take place in the melt pond, and not in the ice itself. Other studies have found higher light transmission (40–70%) below shallower (0.1 m) melt ponds (Ehn *et al.*, 2011). This suggests that melt ponds play an important role in the absorption of heat and in the melt of sea ice (Fetterer and Untersteiner, 1998; Liu *et al.*, 2015; Webster *et al.*, 2015). Katlein *et al.* (2019) described the seasonal evolution of light transmission by combining several datasets for spatially varying sea ice conditions from spring to autumn in the CAO.

#### 4.3.1.5 Subsurface light (PAR) under ice in open water

Incoming solar radiation to the atmosphere can be calculated for any location and is well known. The CAO is located broadly north of 75–80°N, and the seasonal variation in light is very pronounced between polar night and polar day (Figure 4.5). Light follows a sinusoid curve, which can be approximated as a broad peak with high light intensity (2/3 or more of maximum light at summer solstice) of about three-month duration (early May to early August) bracketed by periods of about three weeks with steep ascending or descending light intensity (10% of maximum light or less; from mid-April to early May, and from early to late August). There is some light before and after these periods (e.g. from spring equinox around 20 March and until autumn equinox around 23 September), but light intensity is low. Based on incoming light from solar radiation, and not accounting for the absorption by snow and ice, the length of the growing season for algae in the CAO is about 4–5 months, being about one month shorter at the North Pole than at 75°N.

Incoming light to the surface has been measured from ice stations in the CAO. Pautzke (1979) presented a composite seasonal pattern of PAR irradiance based on measurements at ice stations AIDJEX (around 75°N) and T-3 (around 85°N) in the Amerasian Basin. Extensive and detailed light measurements were done at the SHEBA (Surface Heat Budget of the Arctic Ocean) ice-drift station in 1998 (Perovich *et al.*, 1999). The seasonal curve for incident solar radiation from 1 March to 1 October showed a maximum daily average radiation of about 300 W m<sup>-2</sup> around midsummer (Perovich and Polashenski, 2012). The seasonality of incoming solar radiation was described for the area of the Transpolar Drift between the North Pole and Fram Strait (80–90°N) from the frozen-in schooner Tara in 2007 (Nicolaus *et al.*, 2010) and from buoy deployments at the Russian Barneo ice camp in 2012 and 2013 (Wang *et al.*, 2014, 2016).

Solar irradiance, as PAR, is about 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at noon at the North Pole, with a daily average of about 900  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the CAO between 75–80°N and the North Pole (Sakshaug *et al.*, 2009; Leu *et al.*, 2015). For the broader peak of high light during the three months around midsummer, the average daily irradiance reaching the atmosphere is 600–900  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . With a reduction of 2/3 due to clouds, the irradiance reaching the ice (or sea) surface would be

around 200–300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Higher values were recorded in the drift area between the North Pole and Fram Strait, with daily average incident PAR of 400–600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  reaching the ice surface for the months May–July (Wang *et al.*, 2014, 2016). This reflected relatively light cloud conditions, with a fully overcast sky only about half the time (Wang *et al.*, 2016). Nicolaus *et al.* (2010) reported the results from the Tara expedition in units of energy, with an average of 109  $\text{J m}^{-2} \text{s}^{-1}$  for a four-month period from the end of April to late August. There is no exact conversion from units of energy to photons since this depends on wavelength, and the spectral composition of PAR varies. However, using an average factor of 4.27  $\text{mmol J}^{-1}$  (Lu *et al.*, 2018) gives 465  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , which is similar to the results of Wang *et al.* (2014, 2016).

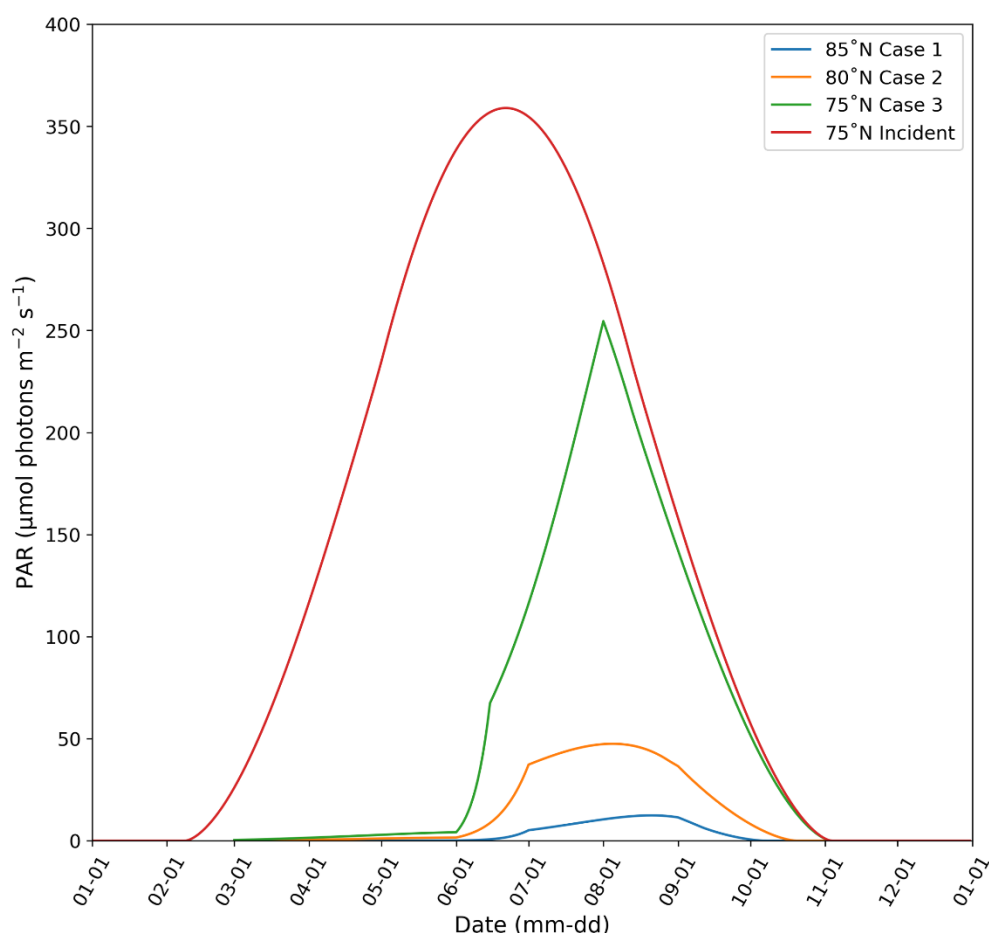
During the Arctic Ocean Section cruise in 1994, an incident irradiance of about 50–250  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was recorded at latitudes of 80–90°N (Gosselin *et al.*, 1997). These recordings were made in August when irradiance is generally decreasing.

Due to the strong absorption in snow, very little light is transmitted through snow-covered ice in the CAO before the onset of snow melt (Figure 4.10). Melt typically starts in late May in the southern fringes of the CAO, and about a month later in the central part near the North Pole. Therefore, broadly, the first half of the seasonal PAR, up to about midsummer, is not available for algae growth. The effective growing season is correspondingly shortened to about 2–2.5 months. With the onset of melt, the transparency of ice increases and more light reaches the undersurface of the ice. Lower albedo also contributes to the increase in light conditions. In the high-light solar period (May–July), when PAR irradiance to the atmosphere is 600–900  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , about 200–600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  reach the surface (as daily average values). Typical values for light transmission through melting sea ice is 5–20%, which give under-ice light values of 10–120  $\mu\text{mol m}^{-2} \text{s}^{-1}$  as a typical range for the second half of the high-light period in the CAO (basically from midsummer through July into early August). In open water, in leads, or where sea ice melts completely, subsurface irradiance is higher, typically 100–400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (accounting for reflection due to the low sun angle).

Measurements of light in ice-covered waters are in general agreement with the range expected from absorption by clouds and ice. During the Arctic Ocean Section cruise in 1994, subice irradiance was recorded as about 5–15% of the surface irradiance, or roughly 5–30  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Gosselin *et al.*, 1997). Autonomous recordings from drifting ice from the North Pole towards Fram Strait gave mean daily average irradiance of 81  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in July (104  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the maximum irradiance at noon), with an average of 32  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the three-month period of June–August (Wang *et al.*, 2014). Nicolaus *et al.* (2010) found an average of 13  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for a four-month period (May–August) in the same area. Since there was little light transmission in May and the first half of June, this represents a mean of about 20  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the 2.5-month period from mid-June through August. The highest transmission in late June–early July was 32  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (daily maximum of 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), or about 6% of the PAR at the ice surface (Nicolaus *et al.*, 2012). Olli *et al.* (2007) measured higher values of 100–400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 1 m depth in the North Pole region. However, the measurements were made from the edge of an ice floe and, as the authors noted, were probably not representative for the light field under the ice.

One feature noted by Nicolaus *et al.* (2010) was a reduction in the under-ice irradiance (measured in the water 1.4 m below the ice) due to absorption by sea ice algae. This is in line with the notion in the literature that ice algae absorb light, thereby shading for, and limiting, the growth of phytoplankton in the water column under ice (Leu *et al.*, 2015). Thus, a sequence may occur where an ice algal bloom occurs first, followed by a phytoplankton bloom in the water column a month or two later, when the ice algal bloom culminates in the late stage of ice melt. This phenology appears to be a common pattern for areas with land-fast ice, where a layer of ice algae under a relatively level ice sheet can have a shading effect for phytoplankton growth. However, this might not be the case for drifting pack ice, where there are always leads

and openings in the ice. The leads and openings form windows where light can transmit into the water bypassing the sea ice. Thus, the light field under broken sea ice cover can be complex, with the amount of light increasing with depth in the upper meters under an ice floe as more light shines in from the sides (Frey *et al.*, 2011). Therefore, it is important to consider spatially integrated light fields rather than local measurements. This can be done by combining under-ice profiling platforms covering large distances and satellite measurements of large-scale ice coverage (Massicotte *et al.*, 2019; Matthes *et al.*, 2020).



**Figure 4.10.** Seasonal patterns of under-ice or subsurface water irradiance under various scenarios of sea ice conditions in the CAO. The incident light at 75°N reaching the surface of ice or water is the PAR at the top of the atmosphere reduced by 60% (factor 0.4) for extinction by the atmosphere. Cases 1–3 are incident light at the surface at 85, 80, and 75°N, respectively, reduced by absorption by snow and sea ice. Case 1 is a MYI scenario at 85°N with 20-cm snow that melts away during the month of June, and with 3-m thick ice that melts from 1 July to 2 m by 1 September. Case 2 is a scenario at 80°N with 15-cm snow that melts during June, and 2-m ice that melts to 1 m by 1 August, and further to 50% ice cover (1-m thick) by 1 September. Case 3 is a FYI scenario at 75°N with 10-cm snow that melts away between 1 and 15 June, and 1.5-m ice that melts away to 100% open water by 1 August. Extinction coefficients were set as 10 m<sup>-1</sup> for snow, and 1.5 or 1.0 m<sup>-1</sup> for ice. Albedo (reflectance) was set as 0.85 for snow, decreasing to 0.4 and 0.2 for MYI and thin FYI, respectively, and to 0.1 for open water (based on Perovich and Polashenski, 2012; see [Figure 4.7](#)).

In early spring, when there is still snow-covered ice and light transmission is of the order of 1% of surface irradiance, it would only take an extent of openings of this magnitude (in the order of 1%) to provide as much light for phytoplankton as for ice algae. The amount of subsurface light is broadly proportional to the fraction of the total area comprised by the openings (Arndt and Nicolaus, 2014). Phytoplankton in water under ice will, on average, receive light in proportion to the fraction of open water, and most of the light for photosynthesis may come

through cracks and leads in drifting pack ice. Therefore, phytoplankton may start to grow as early as, or even earlier than, ice algae in drifting pack ice, depending on the areal proportion of leads and openings as well as general ice conditions (Arrigo *et al.*, 2012; Assmy *et al.*, 2017).

To summarize, the transparency of sea ice varies strongly, with extinction coefficients from  $0.5 \text{ m}^{-1}$  to  $> 2 \text{ m}^{-1}$ . Very little light penetrates through snow-covered sea ice, and it is first when snow melts away that there is a substantial amount of light reaching the underside of the ice (Figure 4.10). This is typically 5–10%, but can be lower (1–5%) with granular surface ice and higher (10–40%) for transparent melting ice. With incident PAR of  $200\text{--}600 \mu\text{mol m}^{-2} \text{ s}^{-1}$  to the ice surface during the high-light period in summer, this corresponds to subsurface irradiance values of typically  $10\text{--}60 \mu\text{mol m}^{-2} \text{ s}^{-1}$  ( $2\text{--}30 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the low end of sea ice transparency and  $20\text{--}200 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the high end). In open water without ice, subsurface light may be  $100\text{--}300 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , assuming 50% reflectance due to low sun angle as a 24-h average. The range of values for subsurface underwater light is of relevance when considering the light dependence of photosynthesis and can indicate potential rates of PP and the degree of light limitation (see Section 4.5.6).

#### 4.3.1.6 Depth of euphotic zone

The depth of the euphotic zone, where positive net growth of phytoplankton can take place, is commonly defined as extending down to the depth with 1% light level relative to the incident light at the surface. Light is attenuated exponentially and with a spectral shift, since blue light penetrates deepest in clear ocean water (Sakshaug *et al.*, 2009). The 1% criterion has been established as a matter of convenience, since it is the absolute light level that counts for PP. The euphotic zone is the upper portion of the water column that supports net PP (NPP), and extends from the surface down to the compensation depth, where gross photosynthesis and respiration losses are equal. The 1% criterion has been empirically determined from studies at lower latitudes. If referenced to subsurface PAR, the depth of the euphotic zone in the Arctic Ocean would be considerably shallower than the 1% light level, roughly the 10% light level if subsurface PAR is 10% of surface PAR.

Chlorophyll (Chl) is a main absorbent of light, and light transmission is strongly dependent on phytoplankton biomass containing Chl. In the Barents Sea, the 1% light level varied from 17 to 50 m depth for chlorophyll *a* (Chl *a*) concentrations between  $0.6$  and  $9 \text{ mg m}^{-3}$  (Sakshaug *et al.*, 2009). The Chl *a* level is usually lower, and transparency higher, in large parts of the CAO. In the oligotrophic Canada Basin, with low Chl *a* concentrations (around  $0.1 \text{ mg m}^{-3}$ ), the euphotic zone extends to 50 m or deeper, as reflected by the deep position of the Chl *a* maximum (McLaughlin and Carmack, 2010; Yun *et al.*, 2012). Varela *et al.* (2013) recorded that the depth of the 0.1% light level varied from 65 to 159 m in Canada Basin. Using a large dataset of Chl *a* profiles (5206 stations), Ardyna *et al.* (2013) showed that the Chl *a* maximum was mainly located at or near the surface for the pre-bloom situation in late winter or early spring, and for high surface Chl *a* conditions during blooms in the open-water period, whereas deeper Chl *a* maxima occurred during the post-bloom period, when surface Chl *a* was low.

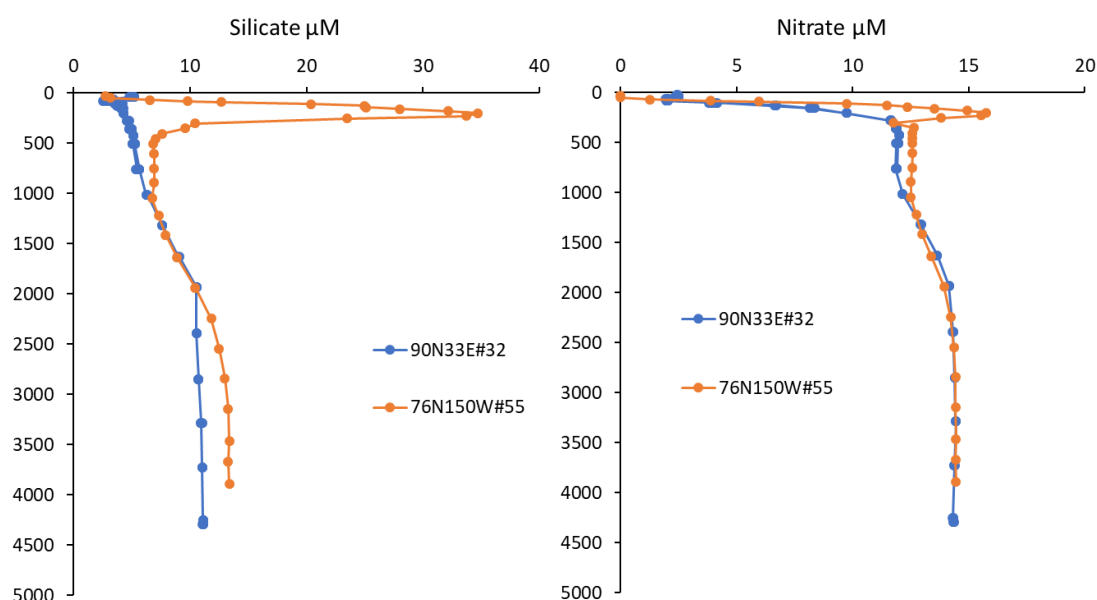
Close to the North Pole in Amundsen Basin ( $88\text{--}89^\circ\text{N}$ ), Olli *et al.* (2007) found a relatively shallow euphotic zone with light attenuation coefficients of  $0.1\text{--}0.4 \text{ m}^{-1}$  in the upper 15-m water layer. These values are relatively high and can be compared to a value of  $0.07 \text{ m}^{-1}$  for attenuation coefficient for PAR ( $K_{\text{PAR}}$ ) in clear water in the Barents Sea (and  $0.02\text{--}0.025 \text{ m}^{-1}$  for the clearest ocean water, close to distilled water; Sakshaug *et al.*, 2009). The light level at 15 m was about  $5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and the depth of the euphotic zone (1% light) was not much more than 20 m (Olli *et al.*, 2007). The relatively low transparency may reflect that the station was located in the Transpolar Drift, with a large proportion of river water containing light-absorbing colored dissolved organic matter (DOM).



### 4.3.2 Nutrients

Nitrate and inorganic phosphate are main nutrients for phytoplankton growth, with silicate additionally required for the growth of diatoms with siliceous tests. Ammonium and urea are two forms of reduced nitrogen (N) compounds that are also used as nutrients for growth by algae. Nitrate accumulates in the upper water layer during winter, and growth based on nitrate is denoted as new production (see [Section 4.5.1](#)). Ammonium and urea are released by grazing zooplankton and microbial degradation of organic material, and algae growth based on this recycled N is denoted as regenerated production (RP; Dugdale and Goering, 1967; Sakshaug, 2004).

Nutrient concentrations in the upper polar mixed layer are relatively low due to the strong salinity stratification, which limits vertical mixing and upward transport of nutrients from deeper layers with higher nutrient concentrations. In general, nutrient concentrations in the upper layer are higher in Eurasian Basin than in Amerasian Basin (Codispoti *et al.*, 2013; Bluhm *et al.*, 2015) and generally higher on the shelves than in the CAO ([Figure 4.11](#); Randelhoff *et al.*, 2020).



**Figure 4.11.** Vertical profiles of silicate (left panel) and nitrate (right panel) in the Canada Basin (station #55 at 76°N, 150°W) and at the North Pole in the Amundsen Basin (station #32). Data from U.S. Arctic GEOTRACES cruise in 2015 (<https://www.ncei.noaa.gov/data/oceans/ncei/ocads/data/0156924/>).

Atlantic water from the WSC that flows into Nansen Basin has winter nutrient concentrations of about 11–12  $\mu\text{mol l}^{-1}$  nitrate, 0.7–0.8  $\mu\text{mol l}^{-1}$  phosphate, and 5–6  $\mu\text{mol l}^{-1}$  silicate (Rey, 2004, 2012). The winter convection is relatively deep in the western Nansen Basin, down to 100 m or deeper, which contributes to the relatively high winter nutrient concentrations in the upper layer (Rudels *et al.*, 2004; Packard and Codispoti, 2007; Codispoti *et al.*, 2013; Ulfsbo *et al.*, 2014). Nutrient concentration values are lacking for the eastern Nansen Basin, but they are presumably lower than in the western part. Relatively high summer nutrient concentrations (5–8  $\mu\text{mol l}^{-1}$  nitrate) have been found in the slope waters in southern Nansen Basin, from north of Svalbard to Severnaya Zemlya (Gilg *et al.*, 2010, citing Colony and Timokhov, 2001; Codispoti *et al.*, 2013). Nutrient concentrations in Amundsen Basin are lower than in Nansen Basin, with winter concentrations of about 5  $\mu\text{mol l}^{-1}$  nitrate in the North Pole region (Codispoti *et al.*, 2013).

Concentrations of nutrients are very low in the Beaufort Gyre in Canada Basin, even in winter, with nitrate concentrations typically  $< 1 \mu\text{mol l}^{-1}$  in the upper mixed layer (McLaughlin and Carmack, 2010; Codispoti *et al.*, 2013; Varela *et al.*, 2013). This is related to the clockwise (anticyclonic) circulation, with doming and downwelling in the centre of the gyre. However, below the upper mixed layer in Canada Basin lies nutrient-rich Pacific water in the upper halocline. Pacific water has a much higher nutrient content than Atlantic water, by a factor of about 3 for nitrate and phosphate and up to about 10 for silicate (Sakshaug, 2004; Carmack and McLaughlin, 2011; Codispoti *et al.*, 2013). Bering slope water has a nitrate concentration of about  $30 \mu\text{mol l}^{-1}$  when it flows onto the northern Bering shelf, and the average nitrate concentration of the water that flows through Bering Strait in late winter (pre-bloom) is about  $20 \mu\text{mol l}^{-1}$  (Codispoti *et al.*, 2009, 2013).

Pacific water in Amerasian Basin can be separated into winter water and summer water. These two types are layered above each other in the upper and middle halocline. Pacific summer water is lighter (less saline) and warmer, and sits on top of the colder winter water. In vertical profiles, they can be distinguished by the local temperature maxima and minima between the cold upper mixed layer and the warmer Atlantic layer, with core depths of around 50 m and 150 m, respectively. Off Mackenzie Delta, in the southeastern Beaufort Sea, the nitrate concentration is about  $17 \mu\text{mol l}^{-1}$  (with corresponding concentrations of  $2.3 \mu\text{mol l}^{-1}$  phosphate and  $33 \mu\text{mol l}^{-1}$  silicate; Macdonald *et al.*, 1987; Carmack *et al.*, 2004). Winter profiles from northern Beaufort Sea have shown nitrate concentrations of  $15\text{--}17 \mu\text{mol l}^{-1}$  at  $150\text{--}200$  m depth (Codispoti *et al.*, 2013). While these concentrations are higher than those in the Atlantic layer below ( $11\text{--}12 \mu\text{mol l}^{-1}$ ), inorganic phosphate and silicate are present in relatively higher concentrations and are better indicators of Pacific water. This is believed to be caused by the loss of nitrate through denitrification due to the degradation of organic matter, which stems from the high production in the Bering Strait and Chukchi Sea region, and is associated with low N/P and N/Si nutrient ratios (Codispoti *et al.*, 1991, 2013). Phosphate concentrations can be up to  $1.7 \mu\text{mol l}^{-1}$  in Pacific water as it leaves the Arctic Ocean through Lancaster Sound or Fram Strait, while silicate may be up to  $25 \mu\text{mol l}^{-1}$  (which is four- to fivefold higher than in Atlantic winter water in the Nordic Seas; Jones and Coote, 1980; Codispoti *et al.*, 1991). Nutrient characteristics can be used to trace the distribution and circulation of Pacific halocline water in Amerasian Basin and into adjacent parts of Eurasian Basin (Codispoti *et al.*, 2013).

Nutrient-rich Pacific water, particularly summer water that lies directly below the polar upper mixed layer, has the potential to enrich the upper layer through convective mixing in winter and by upwelling in canyons along adjacent slopes (Carmack and Kulikov, 1998; Pickart *et al.*, 2009, 2011, 2013a, 2013b). Much of the Pacific summer water flows north in the western Amerasian Basin (west of the Beaufort Gyre) from the Chukchi Borderland towards the North Pole region (Steele *et al.*, 2004). This is a zone of potentially higher algal production if convection or uplift of density gradients, related to shifts in circulation, brings nutrients up into the euphotic zone.

Nutrients in the western Canada and Makarov basins are not depleted from the surface layer in summer, but occur with concentrations of  $1\text{--}4 \mu\text{mol l}^{-1}$  nitrate (Gosselin *et al.*, 1997). In Amundsen Basin, close to the North Pole, Olli *et al.* (2007) recorded  $3 \mu\text{mol l}^{-1}$  nitrate in the upper layer in late summer (mid-August 2001). Data compiled by Codispoti *et al.* (2013) and Bluhm *et al.* (2015) show that nitrate is generally present in the surface layer in summer, with higher values in the Eurasian than in the Amerasian Basin. This suggests that nutrients do not become limiting for phytoplankton growth in much of the CAO, and that, therefore, light is the main limiting factor.

In broad terms, PP in Amerasian Basin appears to be nutrient-limited, while PP in Eurasian Basin is potentially more light-limited. This is reflected by the very low nutrient concentrations

in Canada Basin, e.g. nitrate  $< 1 \mu\text{mol l}^{-1}$  even in winter in the Beaufort Gyre, whereas nutrients are somewhat higher ( $2\text{--}4 \mu\text{mol l}^{-1}$  nitrate) and may not be seasonally depleted in Eurasian Basin.

## 4.4 Biomass

### 4.4.1 Phytoplankton

Algae biomass is generally recorded as Chl *a*, which is a relative index of biomass. The Chl *a* content of algal cells varies among species and with physiological conditions. Thus, the ratio of Chl *a* to C (the main constituent of biomass) may vary by an order of magnitude (Sakshaug, 2004). Chl *a* content is generally higher in cells adapted to low light relative to high-light conditions. A deep Chl maximum towards the bottom of the euphotic zone is a common feature in the CAO, notably in the Beaufort Gyre (Ardyna *et al.*, 2013). Higher Chl content of cells as a response to low light may contribute to these deep maxima, making them appear more prominent than if they were expressed in other units of biomass such as C. It might be desirable to express phytoplankton biomass in units of C, but this is difficult to achieve in practice. Cell counts can be converted to C (based on C content per cell), but it is very time consuming and associated with uncertainty due to variable cell size and the presence of heterotrophs (e.g. Booth and Horner, 1997). The determination of particulate organic C (POC) includes phytoplankton biomass, but also heterotrophic microplankton and dead organic material (detritus).

Chl *a* levels in the water column are generally low in the CAO, typically  $< 0.1\text{--}0.3 \text{ mg m}^{-3}$ . Particularly low values ( $0.01\text{--}0.1 \text{ mg Chl } a \text{ m}^{-3}$ ) have been recorded in the upper layer in Canada Basin (Lee and Whitledge, 2005; Lee *et al.*, 2010; Yun *et al.*, 2012). In this oligotrophic area, there is a pronounced deep Chl maximum layer (located at  $40\text{--}60 \text{ m}$  depth), with much higher Chl *a* concentrations, generally  $0.2\text{--}1.0 \text{ mg m}^{-3}$  (Lee and Whitledge, 2005; Lee *et al.*, 2010; McLaughlin and Carmack, 2010; Yun *et al.*, 2012; Ardyna *et al.*, 2013; Varela *et al.*, 2013). In the Amundsen and Makarov basins in the North Pole region, Chl *a* concentrations were  $0.03\text{--}0.3 \text{ mg m}^{-3}$  in the surface layer (upper  $20 \text{ m}$ ), while being generally low at greater depths ( $< 0.02 \text{ mg m}^{-3}$ ; Olli *et al.*, 2007). However, a deep Chl maximum ( $0.2\text{--}0.3 \text{ mg m}^{-3}$ ) was also found there at some stations. In the Nansen and Amundsen basins, Metfies *et al.* (2016) recorded Chl *a* concentrations of  $< 0.3 \text{ mg m}^{-3}$  at most stations, with 60–90% made up of small picoplankton cells.

Vertically integrated Chl *a* is commonly around  $5\text{--}10 \text{ mg m}^{-2}$  in the CAO. Values of  $1\text{--}25 \text{ mg Chl } a \text{ m}^{-2}$  were recorded on the Arctic Ocean Section cruise in 1994, between the Chukchi Borderland region, across the North Pole, and into the Amundsen Basin ( $74\text{--}90\text{--}86^\circ\text{N}$ ), with mean values of 12 and  $7 \text{ mg Chl } a \text{ m}^{-2}$  in the western Canada Basin and Makarov Basin, respectively (Gosselin *et al.*, 1997). Olli *et al.* (2007) recorded  $0.5\text{--}6 \text{ mg Chl } a \text{ m}^{-2}$  along a section from Nansen Basin ( $82^\circ\text{N}$ ), via the North Pole, and into Makarov Basin. Values of  $2\text{--}4 \text{ mg Chl } a \text{ m}^{-2}$  were reported from Eurasian Basin in summer (Fernández-Méndez *et al.*, 2014). Mean values of 7.3 (s. d. 5.0) and 10.8 (s. d. 5.7)  $\text{mg Chl } a \text{ m}^{-2}$  were recorded in Canada Basin in summer 2002 and 2005 (Lee and Whitledge, 2005; Lee *et al.*, 2010), while Yun *et al.* (2012) reported a mean of 6.0 (s. d. 1.9)  $\text{mg Chl } a \text{ m}^{-2}$  in late summer 2009.

Nöthig *et al.* (2020) summarized a large dataset on vertically integrated Chl *a* from cruises in the CAO between 1993 and 2015. They reported median values of 12.6, 7.0, and  $8.0 \text{ mg Chl } a \text{ m}^{-2}$  in the Nansen, Amundsen, and Amerasian (mostly Makarov) basins, with most values (95% of 43–57 stations)  $< 35 \text{ mg Chl } a \text{ m}^{-2}$  in Nansen Basin and  $< 20 \text{ mg Chl } a \text{ m}^{-2}$  in the Amundsen and Makarov basins. The integrated Chl *a* values were associated with median POC values of  $2.3\text{--}4.4 \text{ g C m}^{-2}$ , giving C: Chl *a* ratios of about 300–500 for the median values from the three basins (Nöthig *et al.*, 2020). The C: Chl *a* ratio of Arctic phytoplankton has, in most cases, been

found to be in the range 25–100 (Sakshaug, 2004), with a value of about 30 reported by Booth and Horner (1997) for the Arctic Ocean Section cruise in 1994. The range of 25–100 corresponds to biomass values of 0.2–0.7 g C m<sup>-2</sup> for the median Chl *a* value of 7 mg m<sup>-2</sup> in Amundsen Basin, and to 0.3–1.3 g C m<sup>-2</sup> for the median value of 12.6 mg Chl *a* m<sup>-2</sup> in Nansen Basin. These indicated phytoplankton C values, based on Chl *a*, suggest that most of the C recorded as POC is not phytoplankton, but includes considerable fractions of dead organic matter (detritus) and heterotrophic organisms like microzooplankton.

English (1961) described the seasonal development of phytoplankton recorded as integrated Chl *a* biomass m<sup>-2</sup> in the upper 20 m based on detailed sampling from early June through October at Drift Station Alpha in 1957 and 1958. The results showed a consistent seasonal pattern, with build-up of Chl *a* from low values in June to high values in July and August (10–25 mg Chl *a* m<sup>-2</sup> in 1957 and 3–60 mg Chl *a* m<sup>-2</sup> in 1958; see Figures 4 and 5 in English, 1961). These values are high compared to the more recent values summarized above. Station Alpha drifted in the northern Canada Basin and the Makarov Basin between 80 and 86°N and 100–180°W. It is not known whether the high values obtained by English were due to methodological differences. Samples (4 l filtered onto a 47-mm HA Millipore filter) were analysed spectrophotometrically on acetone extract, based on the method of Richards and Thompson (1952) and Creitz and Richards (1955). Apollonio (1959) reported values up to over 20 mg m<sup>-2</sup> at Drift Station Bravo (on Fletcher's Ice Island - T-3) in summer 1957 (July–August) using a similar method (the analyses were done at Woods Hole Oceanographic Institution). Pautzke (1979) described the seasonal development of Chl *a* at T-3 for six years (1968–1973), when the station drifted at about 85°N between 160 and 80°W over Alpha Ridge. The results showed large interannual variability. High values of 30–50 mg Chl *a* m<sup>-2</sup> were recorded in 1968 when the station drifted in the northwestern Canada Basin at 83–84°N. In three of the subsequent years (1969, 1970, and 1972), the Chl *a* concentration was 10–25 mg m<sup>-2</sup>, while it was lower, at 5–15 mg m<sup>-2</sup>, in the two remaining years (1971, 1973). Pautzke (1979) reported even lower values (around 5–7 mg Chl *a* m<sup>-2</sup>) at Drift Station AIDJEX in the Canada Basin (74–77°N, 135–150°W).

Newer data for the seasonal pattern of Chl have been obtained using ice-tethered profiling instruments (ITP; Laney *et al.*, 2014). Deployments in Canada Basin (73–81°N 130–160°W) showed a deep Chl maximum (< 0.2 mg Chl *a* m<sup>-3</sup>) and very low concentrations in the upper layer. A year-long deployment showed that elevated Chl occurred from June to October. Deployments further north at about 85°N (in Makarov Basin and over Alpha Ridge) showed a different pattern, with high Chl in the upper layer (30 m) and concentrations up to 0.4 mg Chl *a* m<sup>-3</sup> (Laney *et al.*, 2014). The seasonal Chl build-up started in late June and the bloom lasted until September.

#### 4.4.2 Ice algae

Determining the biomass of ice algae is challenging for at least two reasons. The first reason is the difficulty of sampling them adequately and representatively. Algae that are loosely attached to the underside of the ice may be swept away during the sampling process, and algae that reside in the interior matrix of the ice may not be included if only the bottom few cm are sampled (Gradinger, 1999). The second reason is that the high spatial variability at fine scales makes representative sampling difficult from a statistical perspective. Nevertheless, there are many studies that have reported the biomass of ice algae, recorded as Chl *a*. Leu *et al.* (2015) presented a detailed review and summary of studies, most of which were outside the CAO and in land-fast ice, including the coastal Beaufort Sea, Franklin Bay in Amundsen Gulf, Resolute in the Canadian Arctic Archipelago, North Water Polynya, Greenland, Svalbard, and the White Sea. A few studies were included on drifting pack ice, including from the Chukchi Sea (Ambrose *et al.*, 2005; Gradinger, 2009), North Water Polynya (Tremblay *et al.*, 2006), Greenland Sea



(Gradinger, 1999; Gradinger *et al.*, 1999), and Barents Sea (Gradinger and Zhang, 1997; Tamelander *et al.*, 2009). Studies from pack ice in the CAO are summarized later in this section.

The Chl *a* biomass in land-fast sea ice often reaches values up to 10–50 mg Chl *a* m<sup>-2</sup> (Leu *et al.*, 2015, their Table 3). The most extensive studies of ice algae have been done in the Resolute area (north of Barrow Strait) in the Canadian Arctic Archipelago, and address many aspects of ice-algae biology, ecophysiology, and ecology (e.g. Smith *et al.*, 1988; Welch and Bergman, 1989; Cota *et al.*, 1991; Cota and Smith, 1991; Bergman *et al.*, 1991; Michel *et al.*, 1996; Mundy *et al.*, 2005). The seasonal development of ice algae at Resolute was found to be strongly dependent on snow and ice conditions (Welch and Bergman, 1989; Mundy *et al.*, 2005). The maximum biomass of ice algae reflects the balance between increased light, which allows growth, and increased melting, which causes a loss of ice algae through sloughing. Self-shading, through absorption of light by algal Chl, reduces the rates of growth and biomass build-up to the seasonal maximum (Welch and Bergman, 1989; Bergman *et al.*, 1991), which was theoretically calculated to be 100–200 mg Chl *a* m<sup>-2</sup> under the snow and ice conditions at Resolute (Smith *et al.*, 1988). The extensive dataset from Resolute is in agreement with this prediction, with just a few values up in this high range. Leu *et al.* (2015) showed that high values were associated with low snow cover (< 10 cm), while the seasonal growth of ice algae was delayed and slower with a thicker snow cover, and reached values up to a maximum of 50 mg Chl *a* m<sup>-2</sup>.

The biomass of ice algae in the pack ice of the CAO is generally much lower (by an order of magnitude) than values reported from fast-ice and drift ice farther south in the Arctic sea ice domain (Leu *et al.*, 2015). Gradinger (1999) found values from < 0.01 to 7 mg Chl *a* m<sup>-2</sup> (median value of 1.6 mg Chl *a* m<sup>-2</sup>) for stations in the Nansen, Amundsen, and Makarov basins, most of them located north of 85°N. The median biomass as C (determined from cell counts) was 112 mg C m<sup>-2</sup> (range 13–457 mg C m<sup>-2</sup>), which gives a C: Chl *a* ratio of 70. Ice algae had a wide vertical distribution, often with maxima in the interior of the ice and not in the bottom layer (Gradinger, 1999). Fernández-Méndez *et al.* (2014) reported biomass values of 1.2–1.7 and 0.1–3.7 mg Chl *a* m<sup>-2</sup> for ice algae communities dominated by pennate diatoms and aggregates of such diatoms, respectively, in the Nansen and Amundsen basins (82–88°N, 32–132°E) in 2011 and 2012. Higher values of 8 and 14–44 mg Chl *a* m<sup>-2</sup> were found where *Melosira arctica* occurred as filaments and aggregates, respectively. Fernández-Méndez *et al.* (2015) reported values of 0.3–1.7 mg Chl *a* m<sup>-2</sup> for six stations, and a higher value (8 mg Chl *a* m<sup>-2</sup>) for two more stations in the same area (for the same cruise in 2012, PS80). However, Lange *et al.* (2017a) demonstrated that mean Chl *a* content in sea ice based on ice-core measurements was underestimated considerably (by up to a factor of two) when compared to larger-scale measurements derived from under-ice profiling platforms at eight of nine sites sampled on the PS80 cruise. They concluded that ice-core-based estimates of ice algal Chl *a* biomass often do not representatively capture spatial variability, implying considerable uncertainties for pan-Arctic estimates based on traditional ice core observations. All these studies (RV Polarstern cruises) were in late summer, mostly August–September.

During the Arctic Ocean Section in 1994 (transpolar Canada–USA cruise), the biomass of ice algae was found to be in a similar low range of 0.1–4 mg Chl *a* m<sup>-2</sup> for stations in the Canada, Makarov, and Amundsen basins, with one higher value of 14 mg Chl *a* m<sup>-2</sup> at a station in Makarov Basin (Wheeler *et al.*, 1996; Gosselin *et al.*, 1997). Melnikov *et al.* (2002) reported ice algae biomass as concentrations of Chl *a* (µg l<sup>-1</sup>) in ice profiles collected during the SHEBA drift station in Canada Basin (75–80°N, 144–166°W). The maximum average concentration in MYI was 1 µg Chl *a* l<sup>-1</sup> in July, which corresponds to 2–3 mg Chl *a* m<sup>-2</sup> for ice 2–3 m thick. The maximum concentration in first-year ice was 0.3 µg Chl *a* l<sup>-1</sup>. The vertical distribution of Chl *a* in the ice was wide, with a maximum in the ice interior in several cases, although the highest concentration overall (about 10 µg Chl *a* l<sup>-1</sup>) was recorded in the bottom layer of ice (MYI in July; Melnikov *et al.*, 2002). The method used at SHEBA to sample Chl *a* in ice algae was the same as

that used previously at Russian ice-drift stations (Melnikov, 1979, 1997). Results from the Russian NP-22 station in 1976, as seasonal averages, were somewhat higher for MYI ( $0.35 \mu\text{g Chl } a \text{ l}^{-1}$ ) and lower for FYI ( $0.07 \mu\text{g Chl } a \text{ l}^{-1}$ ), when compared to the SHEBA results (Melnikov *et al.*, 2002). The seasonal data for NP-23 showed concentrations of  $0.2\text{--}1.4 \mu\text{g Chl } a \text{ l}^{-1}$  for summer (June–October), with higher values (by a factor of about 2) for the lower layer of the ice relative to the middle and upper portions (Melnikov, 1997, his Figure 28).

Lange *et al.* (2017b) reported comparable low values from the Lincoln Sea, with mean bottom-ice Chl for multiyear hummock ice of  $1.5 \text{ mg Chl } a \text{ m}^{-2}$  (range  $0.6\text{--}3.6 \text{ mg Chl } a \text{ m}^{-2}$ ). Lower values were found in young first-year ice, with an average of  $0.7 \text{ mg Chl } a \text{ m}^{-2}$ . The higher values under hummocks (elevated ice surfaces) were explained as a result of lower snow cover compared to surrounding ice (Lange *et al.*, 2017b).

Chl biomass in drifting ice in Fram Strait ( $81^\circ\text{N}$ ) was low,  $0.1\text{--}0.9 \text{ mg Chl } a \text{ m}^{-2}$ , with a mean of  $0.46$  (Glud *et al.*, 2014). This was for a melting ice floe about  $1 \text{ m}$  thick in late June 2010. Chl *a* here was also distributed broadly inside the ice, but with generally higher concentrations (up to a maximum of  $3 \mu\text{g Chl } a \text{ l}^{-1}$ ) in the lower half portion of the ice. South of Fram Strait, in Greenland Sea, low biomass values of  $0.1\text{--}3 \text{ mg Chl } a \text{ m}^{-2}$  were recorded in drifting pack ice by Gradinger (1999) and Gradinger *et al.* (1999).

Results from the CAO, including the older Russian ice-drift stations, SHEBA, and RV Polarstern cruises, are consistent in showing low biomass of ice algae in the range  $0.1\text{--}10 \text{ mg Chl } a \text{ m}^{-2}$  and commonly  $1\text{--}2 \text{ mg Chl } a \text{ m}^{-2}$ . Comparable low values have also been recorded in the outflow region in Fram Strait and Greenland Sea. In contrast, higher values have been recorded in drift ice in the Chukchi Sea. Gradinger (2009) reported values of  $10\text{--}100 \text{ mg Chl } a \text{ m}^{-2}$  for stations on the Chukchi shelf in spring 2002, while much lower values of about  $0.2\text{--}6 \text{ mg Chl } a \text{ m}^{-2}$  were recorded in slope waters in the adjacent Beaufort Sea. Ambrose *et al.* (2005) reported values of  $0.3\text{--}123 \mu\text{g Chl } a \text{ l}^{-1}$  in the bottom  $10 \text{ cm}$  of sea ice in the northeastern Chukchi Sea in summer (June 1998). Most values were  $< 10 \text{ mg Chl } a \text{ m}^{-2}$ , with two high values of  $51$  and  $123 \text{ mg Chl } a \text{ m}^{-2}$ . Relatively high values were also reported for the North Water Polynya in northern Baffin Bay, with mean values of  $21$  and  $63 \text{ mg Chl } a \text{ m}^{-2}$  for the bottom layer of ice in May and June, respectively (Tremblay *et al.*, 2006).

The reason for the low ice-algae biomass in the CAO, measured both previously and more recently, is probably the low light levels under ice. With snow cover, there is very little light in and under the ice. Light conditions improve as melting progresses, but this is also associated with loss of ice algae from the ice due to sloughing. Light enters the water through leads and openings, which allows growth of phytoplankton as well as ice algae, such as filaments of *Melosira arctica* hanging from the underside of ice near the edges of floes. MYI hummocks may support a higher biomass of ice algae due to reduced snow coverage. Accounting for the effect of hummocks has been demonstrated to increase the area of MYI estimated to be suitable for ice algal growth (Lange *et al.*, 2017b).

## 4.5 Primary production

### 4.5.1 Concepts and terminology

Primary production (PP) is the production and growth of plants at the base of the trophic ladder, and is the basis for energy flow and material cycling in an ecosystem. While this is clear in principle, PP is defined, expressed, and measured in different ways, making it a complex issue. The following list gives some of the types of PP recognized:

1. Gross primary production (GPP) is the total amount of organic material produced by algae through photosynthetic C fixation.
2. Net primary production (NPP) is the GPP minus algal respiration.
3. Net community production (NCP) is the NPP minus heterotrophic respiration by microorganisms and zooplankton.
4. Export production (EP) is the part of the PP that leaves the euphotic zone through sinking and sedimentation.
5. New production (NP) is PP based on new input of nutrients to the euphotic zone, technically defined as growth of algae based on nitrate.
6. Regenerated production (RP) is PP based on recycled nutrients in the euphotic zone, technically defined as growth of algae based on ammonium and, in some cases, urea.
7. Harvestable production is usually equated with NP, and is the production that can be removed by harvest without impoverishing the system.

The basic equation for photosynthetic C fixation is:



The basic equation for respiration is the same in reversed form. The primary organic material formed by photosynthesis, and used as the basic substrate in respiration, is carbohydrate glucose. Biochemistry in organisms is more complex, and inorganic nutrients (N and P) are used to form amino acids, proteins, and other biochemical constituents, such as nucleotides and nucleic acids. In stoichiometric versions, the equations for photosynthesis and respiration form the basis for the Redfield ratios (Redfield, 1934; Redfield *et al.*, 1963):



These ratios are relatively robust, and can be used to convert the results obtained with different methods, such as C fixation, uptake of N (nitrate, ammonium), and evolution of O<sub>2</sub>.

In a steady state and non-advective regime (basically an isolated and vertically connected water column), EP is equal to NP (i.e. over the annual cycle, the input of nutrients by mixing from below into the upper euphotic layer equals the loss from this layer by sedimentation). NPP in the euphotic layer, in the forms of C fixation, O<sub>2</sub> evolution, and N uptake by algae, balances the respiratory remineralization of the produced organic material taking place both in the euphotic zone and in the deeper part of the water column below. The seasonal draw-down of nitrate in the euphotic zone, from maximum values in winter to minimum values in summer, is an expression of NP, where any input of nitrate into the euphotic zone by mixing across the deeper boundary during the vegetative period also needs to be counted. Through EP, a similar amount of nitrate is produced by remineralization of sedimenting material in the water column below the euphotic zone. For C (CO<sub>2</sub>) and O<sub>2</sub>, the gaseous exchange with the atmosphere needs to be taken into account when considering equilibrium budgets over the water column.

The concept of NCP is much used in the literature, although it is not easily defined in practice. It represents the difference between algae GPP and respiration by all organisms including algae, heterotrophic microorganisms, and zooplankton. Averaged over the water column and an annual cycle, NCP is zero in a steady-state system. That is, all material produced by algae is recycled and remineralized. If NCP is calculated for the euphotic zone, it may be taken to represent NP, since RP is based on respiratory remineralization and recycling of nutrients. From a practical perspective, NCP is frequently estimated using incubation methods (see

[Section 4.5.2](#)). This may exclude larger organisms, e.g. zooplankton, to an unknown extent from the measurement. A question is if, and to what extent, incubations lead to underestimation of the real NCP in the euphotic zone.

Williams (1993) reviewed the concepts and definitions of the various types of PP, and Codispoti *et al.* (2013) provided a recent summary of the topic. They concluded that despite the complexities, there is a broad consensus that total production estimated from  $^{15}\text{N}$  incubations roughly equals PP estimated from  $^{14}\text{C}$  incubations, and that NP roughly equals NCP.

Photosynthesis is a complex of biochemical reactions, which starts with harvesting the energy in light (photons) through Chl *a* and other accessory pigments, and then uses the chemically bound energy, in the form of ATP, to synthesize glucose, and, subsequently, proteins and other biochemical constituents. In eukaryotic cells, Chl and other parts of the light-harvesting apparatus sit in chloroplasts inside the cell, and the apparatus consists of two parts, photosystems I and II (PSI and PSII). In addition to energy, reducing power (in the form of the reductant NADPH) is generated in the light-dependent processes, as part of the electron transfer involved in photosynthesis. Turnover of ATP and reductant is rapid (seconds or ms), which means that the harvesting of light and synthesis of glucose from  $\text{CO}_2$  (or bicarbonate  $\text{HCO}_3^-$ ) are coupled in real time. However, subsequent steps, where photosynthetically produced glucose is used as a basis to synthesize proteins, nucleic acids, and other biochemical substances, may take place with a time-delay related to the day–night cycle and the cycle of division and self-replication of cells. A part of the energy for these dark processes "downstream" from the light-dependent processes may, therefore, stem from respiratory ATP generation. Thus, the relationship between photosynthesis and  $\text{O}_2$  can be complex.  $\text{O}_2$  is generated from C fixation and the reduction of  $\text{CO}_2$  (and  $\text{H}_2\text{O}$ ), but  $\text{O}_2$  can also be utilized in biosynthesis, which is a part of PP.

The complexity of photosynthesis is not only of academic interest to plant physiologists, but has a practical bearing on how we regard PP in a marine ecosystem. This is primarily because respiration comes into play for how we define and interpret the different types of PP, e.g. distinguishing between GPP and NPP, and interpreting NCP. It also has a practical implication for how we measure rates of photosynthesis, e.g. using dark bottles for incubations measuring  $^{14}\text{C}$  uptake or  $\text{O}_2$  evolution. It is a paradox that this most fundamental of all processes for the functioning of marine ecosystems is still not so well understood. This has particularly large implications for an oligotrophic system like the CAO, where rates of PP are low (as we will detail in the following sections) and the relative role of respiration is large over the annual cycle.

#### 4.5.2 Methods for determining primary production

There is a wide range of methods in use for determining or estimating PP rates. They can be broadly grouped in five categories:

- incubations [ $^{14}\text{C}$ ,  $^{13}\text{C}$ ,  $^{15}\text{N}$  (nitrate, ammonium, urea), oxygen];
- chemical properties in the water column (carbonate system, oxygen, inorganic nutrients,  $^{234}\text{Th}$ );
- sediment traps;
- remote sensing; and
- mathematical modelling.

The  $^{14}\text{C}$  method has been the classical method for measuring PP since it was introduced by Steemann Nielsen (1952; see [Section 4.5.5](#)). It is perhaps surprising that it is still not clear what the  $^{14}\text{C}$  method is measuring, although there is consensus that it lies somewhere between GPP and NPP (Sakshaug *et al.*, 1997). The  $^{14}\text{C}$  method has more recently been supplemented by using



the stable isotope  $^{13}\text{C}$ , often in combination with measurements of uptake of  $^{15}\text{N}$ -labelled nitrate and ammonium (and occasionally urea). In short, isotope-labelled substrates (e.g.  $^{14}\text{C}$ - or  $^{13}\text{C}$ -labelled bicarbonate) are added to small-volume water samples (typically 100–250 ml) which are incubated for a period from a few to 24 hours. At the end of incubation, the water samples are filtered, and the amounts of isotopes taken up by the algae (usually retained on a filter) are measured and expressed as rates of PP.

Incubations for C uptake are done in basically three different ways:

1. *In situ* incubations where bottles are incubated suspended at their respective light depths across the euphotic zone (commonly down to 1% light).
2. Simulated *in situ* incubations, where bottles are incubated in an incubator and screens are used to simulate light levels corresponding to different light depths.
3. P vs. E incubations where bottles from selected depths are incubated at different light levels to determine the relationship between rate of C fixation and light level (irradiance, E), in the so-called P-E curve. The PP rates are then calculated or modelled from light, biomass (Chl *a*), and photosynthetic parameters from the P-E curve (where P is normalized per unit of Chl *a*).

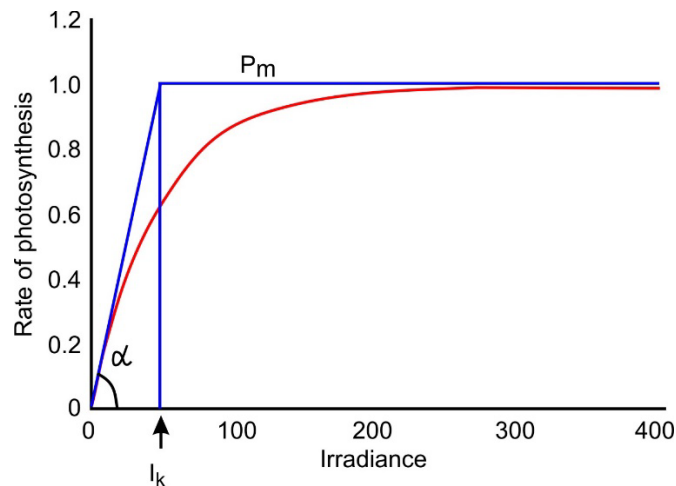
The primary unit for expressing PP rates based on uptake of  $^{14}\text{C}$  or  $^{13}\text{C}$  is the amount of C taken up (incorporated as new biomass) per unit time and unit volume of water, e.g.  $\text{mg C m}^{-3} \text{ h}^{-1}$ . Depending on the length of incubation, hourly rates are used to estimate daily rates by integrating over the 24-hour cycle ( $\text{mg C m}^{-3} \text{ d}^{-1}$ ). Daily rates from specific sampling depths are used to estimate the daily PP rates by phytoplankton per unit of sea surface area, e.g.  $\text{mg C m}^{-2} \text{ d}^{-1}$ , by integration over the water column. When sampling at different times during the productive season, daily rates can be used to estimate annual rates of PP, typically expressed as  $\text{g C m}^{-2}$ . Extrapolation from rates determined in small-volume samples, to daily rates over the water column, and to annual rates over the seasons, is a difficult issue and is associated with assumptions and uncertainties. In principle, it can be done in three different ways: (i) strict mathematical interpolation between samples in depth and time; (ii) modelling, where shifting light conditions and biomass of algae are taken into account; or (iii) a combination of the two.

Rates of PP are often normalized relative to the biomass of algae (typically Chl *a*), e.g.  $\text{mg C mg Chl}^{-1} \text{ h}^{-1}$ . This is commonly done when expressing the so-called P-E curve (Figure 4.12; see Section 4.5.6), which describes the relationship between PP and light intensity (E, typically PAR expressed in units of  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ). The P-E curve is asymptotic and is described by two parameters: initial slope and asymptote. These are the two basic photosynthetic parameters, denoted  $\alpha$  and  $P_m$ . When expressed per unit Chl *a*, they are denoted as  $\alpha^B$  and  $P_m^B$ , or  $\alpha^*$  and  $P_m^*$  (Sakshaug *et al.*, 1997), where the superscript B or \* stands for biomass (biomass-normalized).

NP is often estimated using the f-ratio, which is the ratio of uptake of nitrate to uptake of the sum of N nutrients (nitrate plus ammonium, and sometimes also urea) determined from uptake of  $^{15}\text{N}$ -labelled nutrients. The f-ratio can be used, along with measurements of PP from uptake of  $^{14}\text{C}$  or  $^{13}\text{C}$ , to estimate NP. Uptake of N from  $^{15}\text{N}$ -labelled substrates can be converted to units of C using Redfield ratio or study-specific empirical ratios.

Incubations measuring oxygen evolution from photosynthetic C fixation were more commonly used earlier. In principle, rates of C uptake and fixation and  $\text{O}_2$  evolution should correspond, since they are stoichiometrically related in the basic equation for photosynthesis. The ratio of  $\text{O}_2$  produced per  $\text{CO}_2$  fixed is called the photosynthetic quotient (PQ), and should ideally be 1 (on a molar basis) from the stoichiometric equation. However, the PQ is larger than unity, since a part of the harvested energy is used to reduce nitrate in addition to C fixation (Sakshaug *et al.*,

1997). With mixed populations in natural water samples that include heterotrophic microorganisms, the processes involving oxygen can be more complex. A technical issue is the use of dark bottles that are incubated to correct the measurements in light bottles. There is a dark uptake of  $^{14}\text{C}$ , which is not well understood, but is subtracted from the light value, while the dark respiration is subtracted to obtain the net production, as the difference between incubation in light and dark.



**Figure 4.12. P vs. E curve.** Relationship between rate of primary production (P) vs. irradiance (E) for phytoplankton samples incubated at different light intensities. The relation is an asymptotic curve described by two parameters: initial slope ( $\alpha$ ) and maximum rate of production ( $P_m$ ). In the example given, the unit of P is the hourly rate of C fixed normalized per unit Chl *a* ( $\text{mg C (mg Chl } a)^{-1} \text{ h}^{-1}$ ), and the unit of E is the amount of photons per surface area and time ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ). Typical values of  $0.02 \text{ mg C (mg Chl } a)^{-1} \text{ h}^{-1}$  ( $\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$  for  $\alpha^*$ , and  $1.0 \text{ mg C (mg Chl } a)^{-1} \text{ h}^{-1}$  for  $P_m^*$  have been used (the \* denotes biomass-normalized values of  $\alpha$  and  $P_m$ ). The parameter  $E_k$  (which is the ratio of  $P_m$  to  $\alpha$ ; shown as  $I_k$  in the figure) is 50.

Methods based on changes in chemical properties in the water column include measurements of concentration of  $\text{O}_2$ ,  $\text{CO}_2$ , and dissolved inorganic C (DIC, including bicarbonate and carbonate ions; see [Section 4.5.7](#)). Increases in  $\text{O}_2$  concentration and decreases in DIC in the euphotic zone can be used to estimate NCP, using appropriate corrections for gaseous exchange with the atmosphere across the sea surface. The opposite trend, with decreases in  $\text{O}_2$  and increases in DIC in the water column below the euphotic layer, can be used to estimate respiratory remineralization of organic material, reflecting EP.

The seasonal drawdown of DIC in the euphotic zone, between the winter maximum and the summer minimum, is used as a measure of annual (or seasonal) NP. The same is the case for integrated contents of inorganic nutrients, notably nitrate and phosphate.

Sediment traps deployed below the euphotic zone are used to measure the vertical flux of POC and other variables, such as particulate organic N (PON), Chl *a*, and phaeopigments. This can provide a direct measurement of EP (see [Section 4.5.8](#)).

Satellite remote sensing of ocean color is used to estimate PP (see [Section 4.5.9](#)). This is done with algorithms that convert the ocean colour recorded by sensors into estimates of Chl *a* and NPP based on empirical relationships. This method has limitation in the CAO, since satellites can only “see” Chl in nearly ice-free waters (up to about 10% ice cover), which excludes most of the area.

Coupled physical–biological models (see [Section 4.5.10](#)), including nutrients and biochemistry, are used to estimate PP. With 3D physics included, the models take horizontal advection into

account, but a challenge is how well the vertical mixing processes are represented for the strongly stratified and seasonably variable Arctic Ocean.

### 4.5.3 Role of advection

The steady-state situation, with a vertically connected water column, does not apply to the strongly stratified CAO. There are basically four main water layers: 1) polar upper mixed layer (ca. 0–50 m), 2) halocline gradient layer (ca. 50–200 m), 3) Atlantic layer (ca. 200–1000 m), and 4) deep water (ca. 1000–4000 m). The top layer moves more or less independently from the Atlantic layer deeper down. For example, the Transpolar Drift traverses over the circulating branches of Atlantic water steered by the deep ridges and basin slopes.

The halocline layer receives the sedimenting material falling out of the euphotic zone as EP. This layer is then moved around in the CAO with pathways at least partly different from those of the top layer. The halocline layer carries productivity signals from upstream source regions on the Atlantic and Pacific sides. The signal may be in the form of organic material (both particulate and dissolved), which represents a biological oxygen demand (BOD), leading, in turn, to a decrease in  $O_2$  concentrations and an increase in concentrations of nitrate and DIC. The signal may also be in the form of a nitrate deficit (relative to the preformed winter concentrations), as demonstrated by the study of Olsson *et al.* (1999). They showed a fairly high nitrate deficit in the Atlantic halocline layer stemming from production in upstream areas in the Barents and Norwegian seas. This is an example of an advective signal that, if it were taken to represent processes in a vertically connected water column, would lead to a strong overestimation of production in the upper layer of the water column above.

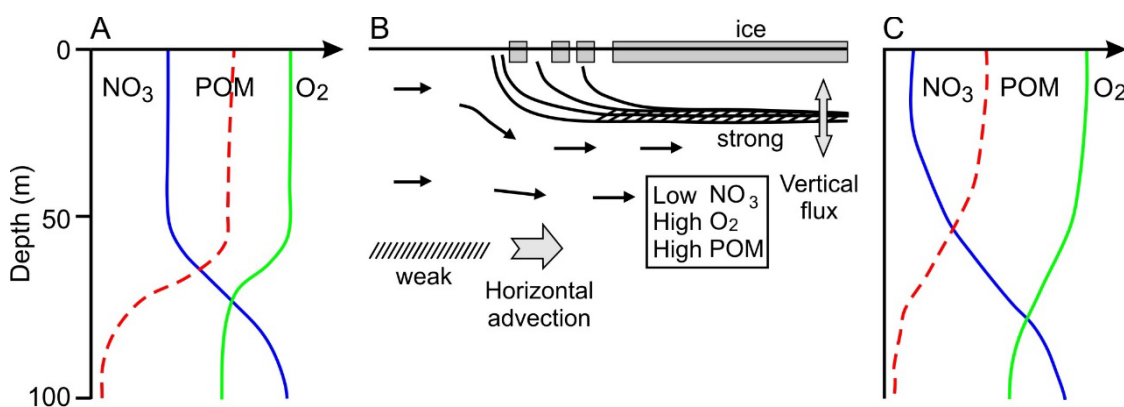


Figure 4.13. Schematic illustration of potential effects of algal production in upstream Atlantic and Pacific waters becoming submerged as part of the halocline, under the upper polar mixed layer which contains the euphotic zone in the CAO. (A) Idealized vertical profiles in upstream waters of nitrate,  $O_2$ , and particulate organic matter (POM), with decreased nitrate and increased POM (mainly as algal biomass and detritus) and  $O_2$  above the relatively weak seasonal pycnocline (thermocline), reflecting the spring growth of phytoplankton. (B) Transect where Atlantic (or Pacific) water flows submerged under (or has flowing over it) lighter water of the upper polar mixed layer with ice cover, located above a strong pycnocline that results from ice-melt and salinity stratification. The submerged water brings with it signatures of surface production in the form of reduced nitrate and elevated  $O_2$  and POM below the strong pycnocline. (C) Vertical profiles of nitrate, POM, and  $O_2$  resulting from the combined effect of local production in the upper polar mixed layer, advection from upstream production in the layer below, and vertical flux exchanges between the upper polar mixed layer and the underlying water.

The example above demonstrates the complexity in interpreting measurements through the water column in the CAO. There may be signals from at least three different processes embedded into the observed concentrations in the halocline layer (Figure 4.13): 1) a productivity signal from upstream regions, with reduced nitrate and increased  $O_2$  and DIC; 2) a different

productivity signal from upstream regions in the form of BOD, leading to reduced O<sub>2</sub> and increased nitrate and DIC; and 3) a similar signal resulting from EP in the water column above. These three and opposing processes may be difficult to disentangle, and the first two (advected signals with opposing signs) may lead to overestimates of *in situ* production if they are not carefully corrected for.

#### 4.5.4 Level of primary production in the CAO

Rates of PP are often given as daily rates per unit surface area (integrated over the water column as mg C m<sup>-2</sup> d<sup>-1</sup>) or integrated as annual rates (g C m<sup>-2</sup> year<sup>-1</sup>). There is general consensus that the rates and level of PP in the CAO are low, and that the CAO is an oligotrophic sea (Sakshaug, 2004; Codispoti *et al.*, 2013; Bluhm *et al.*, 2015). Just how low PP is, is an issue addressed in subsequent parts of this Section 4. Apollonio (1959) and English (1961) obtained very low estimates for annual PP of about 1 g C m<sup>-2</sup> based on their pioneering work from ice-drift stations. This was two orders of magnitude lower than annual rates in other sea areas, and categorized the CAO as a virtual desert and an ultraoligotrophic sea. Later studies (e.g. the joint Canada-US Arctic Ocean Section in 1994; Gosselin *et al.*, 1997) obtained higher rates, which suggested that the annual PP could be an order of magnitude higher than suggested by the studies of Apollonio (1959) and English (1961). These rates are still an order of magnitude lower than typical levels of PP in temperate and boreal seas. For reference, the global average annual PP has been estimated to be about 150 g C m<sup>-2</sup> year<sup>-1</sup> for the world's oceans (Field *et al.*, 1998; Falkowski *et al.*, 1998; Carr *et al.*, 2006). The annual PP for the Barents Sea is about 100 g C m<sup>-2</sup> year<sup>-1</sup> on average, with somewhat higher values of 100–150 g C m<sup>-2</sup> year<sup>-1</sup> for the open-water southern part (Wassmann *et al.*, 2006a, 2006b; Hunt *et al.*, 2013). Higher values of 150–300 g C m<sup>-2</sup> year<sup>-1</sup> were reported for the slope region of the Bering Sea (Springer *et al.*, 1996), and even higher values, of up to 500 g C m<sup>-2</sup> year<sup>-1</sup> or more, have been reported for the wider Bering Strait region (McRoy *et al.*, 1987; Hansell *et al.*, 1993; Springer and McRoy, 1993).

PP of the CAO is ultimately driven by the input of nutrients from the Atlantic inflow with the Barents Sea and Fram Strait branches, and from the Pacific inflow through Bering Strait and Chukchi Sea. Most of the nutrients in the Atlantic water do not become available for production since they are in the bulk Atlantic layer between about 200 and 1000 m depth. Nutrients from the Atlantic water are provided to the top layer in the western Nansen Basin, where the heat of the inflowing water melts sea ice and creates a two-layered system (Rudels *et al.*, 2004; Rudels, 2012, 2015). Nutrients are also provided by Atlantic water that forms the cold halocline in the eastern Nansen Basin, some of which may be mixed into the upper layer by winter convection and processes such as upwelling along shelf edges. Nutrient-rich Pacific water is separated into summer and winter waters, which form layers at about 50–70 and 100–150 m depth in the halocline, respectively. Some nutrients, particularly from the Pacific summer water, are mixed up into the top layer by winter convection and other processes.

Annual inputs and reservoirs of nutrients supplied by Atlantic and Pacific waters set the upper limit of the total annual NP in the CAO. Anderson *et al.* (1998) calculated that the total annual input of nitrate by Atlantic and Pacific waters in the upper ca. 200 m corresponded to an annual NP of 12 g C m<sup>-2</sup> when converted to units of C. This assumes that all the nitrate is utilized, which is likely not the case. However, the calculation illustrates an upper maximum for overall production in the CAO.

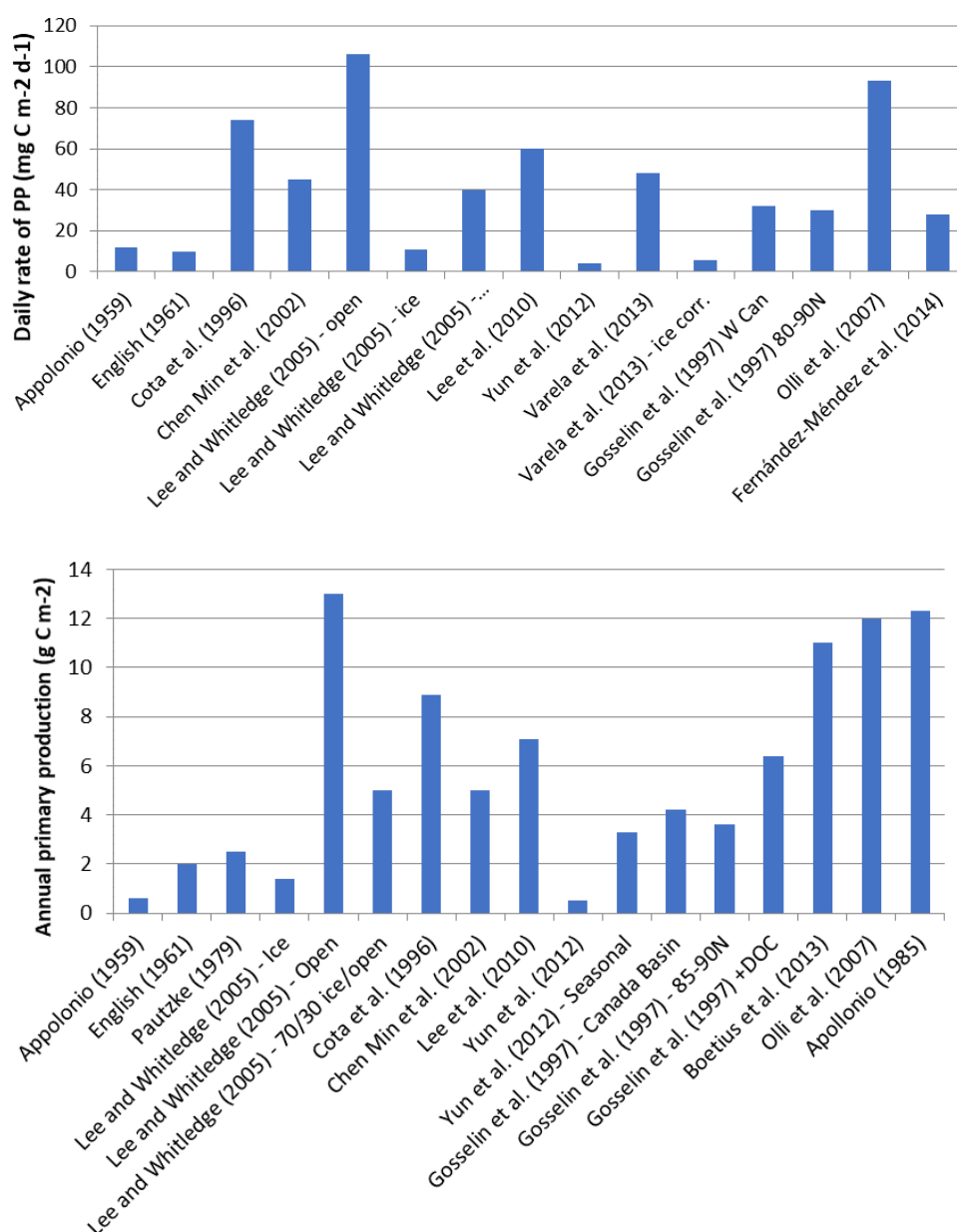
The following sections (sections 4.5.5–4.5.11) review the many studies of PP in the CAO. This includes several previous reviews on PP in Arctic marine waters, e.g. Subba Rao and Platt (1984), Sakshaug (2004), and Codispoti *et al.* (2013), that have included information on the CAO. Many different methods have been used to determine or estimate PP in the CAO, falling under the five groups of methods listed in Section 4.5.2. Sections 4.5.5–4.5.10 summarize the results



obtained by the various methods, starting with the classical  $^{14}\text{C}$  method, which is often used for "ground-truthing" other methods. Section 4.5.11 concludes with an overall evaluation of the likely level of PP for the CAO.

#### 4.5.5 Results from $^{14}\text{C}$ and $^{13}\text{C}$ incubations

The rates of daily and annual phytoplankton PP in the CAO obtained in studies using incubation with  $^{14}\text{C}$  or  $^{13}\text{C}$  are shown in [Figure 4.14](#). Daily rates are commonly 10–100  $\text{mg C m}^{-2} \text{d}^{-1}$ . In most studies they are extrapolated to annual rates by multiplying daily rates by the length of the vegetative season, set as 120 days. This conversion produces annual PP estimates of roughly 1–10  $\text{g C m}^{-2} \text{year}^{-1}$ . There are two factors that have clear effects on the results: sea ice conditions, and time (date) within the vegetative season.



**Figure 4.14.** Daily (upper panel) and annual (lower panel) estimates of PP from C fixation determined with  $^{14}\text{C}$  or  $^{13}\text{C}$  incubations. The studies are identified by literature reference. I/O is a weighted average for ice covered and open waters in Lee and Whitledge (2005). CB – Canada Basin; 85–90 – the North Pole region between 85 and 90°N. See text for more information on the various studies.

Lee and Whitley (2005), working in Canada Basin, found mean rates of about  $100 \text{ mg C m}^{-2} \text{ d}^{-1}$  in open waters, with lower rates by a factor of 10 (about  $10 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) in ice-covered waters. Translated to annual rates (120 days) this gave values of 13 and  $1.4 \text{ g C m}^{-2} \text{ year}^{-1}$  for open and ice-covered waters, respectively. An estimated  $5 \text{ g C m}^{-2} \text{ year}^{-1}$  was obtained for a comparable situation with 30% open and 70% ice-covered waters. Other estimates for Canada Basin, mostly in open waters, are in the range of  $5\text{--}9 \text{ g C m}^{-2} \text{ year}^{-1}$  (Cota *et al.*, 1996; Chen *et al.*, 2002; Lee *et al.*, 2010). Varela *et al.* (2013) obtained a daily rate of  $48 \text{ mg C m}^{-2} \text{ d}^{-1}$  on average for stations in Canada Basin and Beaufort Sea. When corrected for ice cover, the value was reduced to  $15 \text{ mg C m}^{-2} \text{ d}^{-1}$ . NP (based on uptake of  $^{15}\text{N}$ ) was estimated to be about  $5 \text{ mg C m}^{-2} \text{ d}^{-1}$  when corrected for ice cover.

Yun *et al.* (2012), working late in the season (September–October) in Canada Basin, obtained low rates, with a mean of  $4 \text{ mg C m}^{-2} \text{ d}^{-1}$ , corresponding to  $0.5 \text{ g C m}^{-2} \text{ year}^{-1}$  if extrapolated to 120 days. The authors noted the pronounced seasonal pattern, with lower rates late in the vegetative season. By combining data that spanned the productive season, they obtained an annual estimate of  $3.3 \text{ g C m}^{-2} \text{ year}^{-1}$  (based on the studies of Gosselin *et al.*, 1997; Lee and Whitley, 2005; Lee *et al.*, 2010; Yun *et al.*, 2012).

The early studies from ice-drift stations by Apollonio (1959) and English (1961) obtained low rates, around  $10 \text{ mg C m}^{-2} \text{ d}^{-1}$  corresponding to about  $1 \text{ g C m}^{-2} \text{ year}^{-1}$ . These low rates have been questioned, due to a lack of awareness of the importance of clean methodology at the time (e.g. Pomeroy, 1997), but the results are in broad agreement with later results. Pautzke (1979) did a comprehensive study over four seasons (1971–1975), from late winter to autumn, at ice-drift stations in Amerasian Basin (Station T-3 in the northern part over the Alpha Ridge 1971–1973, and AIDJEX in Canada Basin in 1975). Pautzke did frequent P-E experiments to determine photosynthetic parameters (initial slope and maximum rate), and used these to calculate (model) annual PP using light and Chl *a* as input parameters. He obtained a mean annual production over the four years of  $3.2 \text{ g C m}^{-2} \text{ year}^{-1}$  (values for single years were  $5.8$  (1971),  $2.2$  (1972),  $2.5$  (1973), and  $2.1 \text{ g C m}^{-2} \text{ year}^{-1}$  (1975).

During the Arctic Ocean Section cruise in 1994, from the Chukchi Sea to Fram Strait via the North Pole, Gosselin *et al.* (1997) obtained mean daily rates of about  $30 \text{ mg C m}^{-2} \text{ d}^{-1}$  for stations in the Canada, Makarov, and Amundsen basins. This translates into annual PP of about  $4 \text{ g C m}^{-2} \text{ year}^{-1}$ , assuming a 120-day growth period. Gosselin *et al.* (1997) also measured the DOC fraction of  $^{14}\text{C}$  uptake, which gave a total annual production (POC + DOC) of about  $6.5 \text{ g C m}^{-2} \text{ year}^{-1}$  for phytoplankton. They also measured rates of PP by ice algae of a similar magnitude to those of phytoplankton, giving a total annual PP of  $15 \text{ g C m}^{-2} \text{ year}^{-1}$  for the ice-covered part of the CAO. This included release of DOC, which constituted about a third of the total PP (Gosselin *et al.*, 1997). Gosselin *et al.* (1997) obtained a much higher rate (about  $500 \text{ mg C m}^{-2} \text{ d}^{-1}$  at one station in the northern Nansen Basin (not included in [Figure 4.14](#)).

Fernández-Méndez *et al.* (2014) recorded similar rates ( $25\text{--}30 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) in the Nansen and Amundsen basins as those obtained by Gosselin *et al.* (1997) for phytoplankton (particulate), while Olli *et al.* (2007) found somewhat higher rates of particulate production ( $50\text{--}140 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) in the North Pole region in Amundsen and Makarov basins. The mean daily rate in the study of Olli *et al.* (2007) gave an annual rate of about  $11 \text{ g C m}^{-2} \text{ year}^{-1}$  for a productive period of 120 days. This could possibly be an overestimate by a factor of 2 or more, since the effective vegetative season is shorter than 120 days (60–90 days; see English, 1961, and Pautzke, 1979), and the high rates measured are probably not representative for the whole season (see Yun *et al.*, 2012). Fernández-Méndez *et al.* (2015) reported rates of  $18\text{--}308$  (mean 95)  $\text{mg C m}^{-2} \text{ d}^{-1}$  for open water and  $0.1\text{--}232$  (mean 33)  $\text{mg C m}^{-2} \text{ d}^{-1}$  for ice-covered waters in Eurasian Basin. Mean total rates (including ice algae) declined from 54 to  $34 \text{ mg C m}^{-2} \text{ d}^{-1}$  from

August to September due to decreasing light conditions. Total annual production in the Eurasian Basin in 2012 was estimated to be  $9 \text{ g C m}^{-2} \text{ year}^{-1}$  (Fernández-Méndez *et al.*, 2015).

The annual rate of about  $12 \text{ g C m}^{-2} \text{ year}^{-1}$  reported by Apollonio (1985) was for a coastal bay (Dumbell Bay) at the north coast of Ellesmere Island, where most of the production took place in a short ice-free period in late summer.

Rates of PP by ice algae were reviewed by Leu *et al.* (2015). Most values from drifting pack ice were in the range  $1\text{--}50 \text{ mg C m}^{-2} \text{ d}^{-1}$ , e.g.  $4\text{--}30 \text{ mg C m}^{-2} \text{ d}^{-1}$  in the Chukchi and Beaufort Sea (Gradinger, 2009),  $< 1\text{--}55 \text{ mg C m}^{-2} \text{ d}^{-1}$  in the northern Barents Sea (Hegseth, 1998; McMinn and Hegseth, 2007), and  $1\text{--}10 \text{ mg C m}^{-2} \text{ d}^{-1}$  in the Fram Strait region and Greenland Sea (Mock and Gradinger, 1999; Assmy *et al.*, 2013). Values in the high end of this range ( $50 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) would give an annual production of  $3 \text{ g C m}^{-2}$ , if maintained over a growth period of two months. Higher daily values, of up to nearly  $500 \text{ mg C m}^{-2} \text{ d}^{-1}$ , have been recorded for ice algae in fast ice in the Resolute area in the Canadian Arctic Archipelago ( $21\text{--}463 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Smith *et al.*, 1988;  $< 1\text{--}280 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Bergmann *et al.*, 1991). These two studies gave estimates of annual production of  $1\text{--}23 \text{ g C m}^{-2}$  and  $1\text{--}11 \text{ g C m}^{-2}$ , respectively. The ranges represent different snow and ice conditions. A value of  $5 \text{ g C m}^{-2}$  was given as a representative mean value for fast ice in the Barrow Strait–Lancaster Sound region (Bergmann *et al.*, 1991; Welch *et al.*, 1992).

During the Arctic Ocean Section cruise in 1994, ice algae PP was found to be  $1\text{--}50 \text{ mg C m}^{-2} \text{ d}^{-1}$ , except for one higher value ( $310 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) for a station in Makarov Basin (Gosselin *et al.*, 1997). Mean values were low for stations in the northern Canada Basin ( $76\text{--}80^\circ\text{N}$ ) and Amundsen Basin ( $2\text{--}3 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Wheeler *et al.*, 1996). Driven by the one high value, the mean daily PP was  $57 \text{ mg C m}^{-2} \text{ d}^{-1}$  for the central part of the CAO ( $81\text{--}90^\circ\text{N}$ ), which gives an annual production of  $3.4 \text{ g C m}^{-2}$  for a growth period of 60 days. Including released DOC ( $12 \text{ mg C m}^{-2} \text{ d}^{-1}$ ), the total production by ice algae would be about  $4 \text{ g C m}^{-2}$ . The much lower values recorded for the Canada and Amundsen basins would lower this estimate to about half for the entire CAO.

Production by ice algae in the Eurasian Basin was found to be  $< 1\text{--}13 \text{ mg C m}^{-2} \text{ d}^{-1}$  for situations where pennate diatoms dominated, and  $13\text{--}40 \text{ mg C m}^{-2} \text{ d}^{-1}$  for aggregates of *Melosira arctica* (Fernández-Méndez *et al.*, 2014). The high end of these daily rates corresponds to values of 0.8 and  $2.4 \text{ g C m}^{-2}$  for a growth period of 60 days ( $1.2$  and  $3.6 \text{ g C m}^{-2}$  for 90 days). In a subsequent study, Fernández-Méndez *et al.* (2015) found that ice algae contributed 6% to the total PP in Eurasian Basin. Their contribution was up to  $> 50\%$  at several stations where the production of phytoplankton (and total production) was very low.

#### 4.5.6 Estimates based on photosynthetic parameters

The two parameters of the P-E curve (photosynthesis vs. light; [Figure 4.12](#)), the initial slope  $\alpha^*$  and the maximum photosynthetic rate  $P_m^*$  (normalized per unit of Chl *a*), are informative for the production potential of algae. The rate of photosynthesis (or PP) is expressed as amount of C fixed per unit of Chl *a* and unit of time ( $\text{mg C (mg Chl } a)^{-1} \text{ d}^{-1}$ ).  $\alpha^*$  gives the increase in PP per increase in unit of light at a low light level (starting from zero).  $P_m^*$  is the asymptotic value, and indicates the maximum PP at light saturation. Photoinhibition is a negative effect on the rate of PP. It occurs at high light levels and can be represented as a negative photoinhibition parameter  $\beta^*$  (with the same unit as  $\alpha^*$ ) in mathematical versions of the P-E curve (Platt *et al.*, 1980; Sakshaug *et al.*, 1997).  $\alpha^*$  is called the maximum light utilization coefficient and gives the production potential under low light (light-limitation). It is related to the maximum quantum yield  $\phi_m$ , which is PP relative to the absorbed PAR (while  $\alpha^*$  is PP relative to ambient or received PAR).  $P_m^*$  is the maximum rate of PP under light saturation.

The ratio between  $P_m^*$  and  $\alpha^*$  is called the light saturation index ( $E_k$ ) and has units of light. It is the amount of PAR at the intersection between the initial slope ( $\alpha^*$ ) and the asymptote ( $P_m^*$ ), and it indicates how many units of light it takes, with the rate at  $\alpha^*$ , to reach the maximum  $P_m^*$ .  $E_k$  is used as an index of the photoacclimation state of algae, with lower values for cells adapted to low light than for cells adapted to high light (Sakshaug *et al.*, 1997). It could be expected that the two parameters  $\alpha^*$  and  $P_m^*$  are independent, since  $\alpha^*$  reflects the maximum of the light-harvesting part of the photosystems, while  $P_m^*$  reflects the capacity of the "dark" metabolic processes downstream from them. Nevertheless, they are often found to co-vary and to be correlated in datasets from the Arctic (Harrison and Platt, 1986; Behrenfeld *et al.*, 2004). This feature makes  $E_k$  stable and insensitive to changes in the two main photosynthetic parameters. The covariation of  $P_m^*$  and  $\alpha^*$  is considered a mystery that is not yet resolved. Behrenfeld *et al.* (2004) suggested that it could reflect respiratory energy generation (ATP) driven by a variable fraction of the reductant formed through photochemistry in the cells.

The photosynthetic parameters are adaptive and change with physiological state and environmental conditions, as well as varying among species. Consequently, there is a wide range of reported values for  $\alpha^*$  and  $P_m^*$ . Part of this variability can also be methodological, especially for  $\alpha^*$ , since there are measurement uncertainties at low rates of PP as well as influences from curve-fitting methods (Sakshaug *et al.*, 1997). Extensive sets of P-E measurements from Arctic waters were reported by Harrison and Platt (1986) for the eastern Canadian Arctic, and by Rey (1991) for Barents Sea. Sakshaug and Slagstad (1991) found that most reported values were in the range 0.01–0.03 mg C (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup> (μmol m<sup>-2</sup> s<sup>-1</sup>)<sup>-1</sup> for  $\alpha^*$  and 0.3–2.0 mg C (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup> for  $P_m^*$ . A more recent dataset from the Beaufort Sea gave median values of 0.017 for  $\alpha^*$  (most values were < 0.04) and 0.5 for  $P_m^*$  (with most values < 2; Huot *et al.*, 2013). Fernández-Mendéz *et al.* (2015) found values of 0.002–0.05 for  $\alpha^*$  and 0.1–3.5 for  $P_m^*$  for melt ponds, sea ice, and water in Eurasian Basin, with average values of 0.025 ( $\alpha^*$ ) and 1.2 ( $P_m^*$ ) across eight datasets from August and September (2012).

Newer data from the CAO are in general agreement with previous data from the Arctic, as summarized by Sakshaug and Slagstad (1991). The early and extensive study by Pautzke (1979), from ice-drift stations T-3 and AIDJEX in Amerasian Basin, gave mean annual values of 0.02–0.13 [mg C (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup> (μmol m<sup>-2</sup> s<sup>-1</sup>)<sup>-1</sup>] for  $\alpha^*$  and 1.0–3.3 [mg C (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup>] for  $P_m^*$ . The somewhat higher values for  $\alpha^*$  found by Pautzke (1979) could reflect that they are mean values from a highly skewed distribution (see e.g. Harrison and Platt, 1986; Huot *et al.*, 2013) where a few high values may strongly influence (increase) the mean values.

The light saturation index  $E_k$  ( $P_m^*/\alpha^*$ ) is used to indicate physiological adaptation to light, with low values indicating an adaptation to low light. Huot *et al.* (2013) found a clear pattern in the Beaufort Sea, with decreasing values of  $E_k$  from about 60 μmol m<sup>-2</sup> s<sup>-1</sup> in the surface layer to about 10 μmol m<sup>-2</sup> s<sup>-1</sup> at the bottom of the euphotic zone. This change mainly reflected a decrease in  $P_m^*$  from values around 1 to about 0.2 mg C (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup> over the depth range. While this indicates a decrease in photosynthetic capacity with increasing depth and lower light, a corresponding increase in the Chl *a*: C ratio (more Chl *a* at low light levels) may counter this effect, if rates of PP are expressed per unit C instead of Chl *a* (Sakshaug and Slagstad, 1991).  $P_m^*$  is related to the maximum growth rate of algae, which is temperature-dependent (Smith and Sakshaug, 1990; Sakshaug and Slagstad, 1991). Eppley (1972) found a relationship between maximum growth rate (as doubling per day) and temperature, which predicts a maximum of 0.85 d<sup>-1</sup> at 0 °C. A  $P_m^*$  value of 1–2 mg C (mg Chl *a*)<sup>-1</sup> h<sup>-1</sup> corresponds to a growth rate, in units of C, of 0.25–0.5 d<sup>-1</sup> if we assume a daylength of 12 h and a C: Chl *a* ratio of 50.

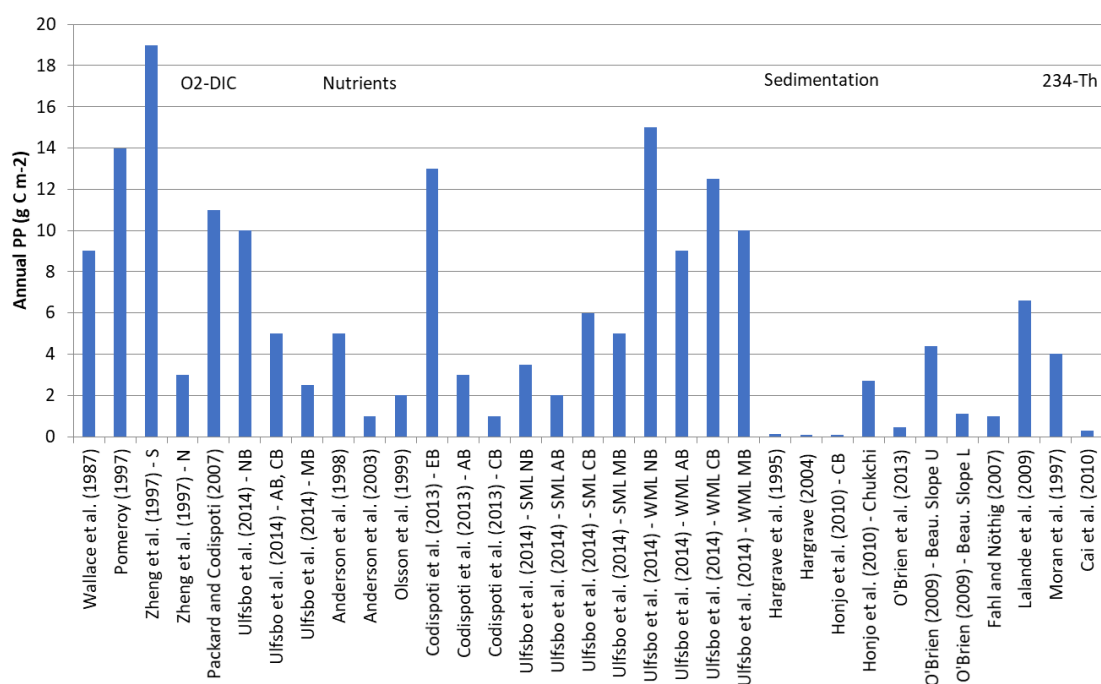
Values of  $\alpha^*$  and  $P_m^*$  can be used in combination with data on light and Chl *a* to calculate rates of PP (e.g. Pautzke, 1979; Fernández-Mendéz *et al.*, 2015). We have previously seen that typical light levels may be 10–60 μmol m<sup>-2</sup> s<sup>-1</sup> under sea ice and 100–300 μmol m<sup>-2</sup> s<sup>-1</sup> for open water in



the CAO. Typical Chl *a* biomass values are 5–10 mg m<sup>-2</sup> for phytoplankton and 1–5 mg m<sup>-2</sup> for ice algae. Using values of 0.02 for  $\alpha^*$  and 1.0 for  $P_m^*$  and assuming 12-h daylength (as an average for the productive period), light-limited production with 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$  irradiance (PAR) gives daily production rates of 2.4–24 mg C m<sup>-2</sup> d<sup>-1</sup> for 1–10 mg Chl *a* m<sup>-2</sup>. The chosen values of  $\alpha^*$  and  $P_m^*$  correspond to an  $E_k$  of 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , which marks the transition to light-saturated conditions for production. The light-saturated PP for irradiances > 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$  is 12–120 mg C m<sup>-2</sup> d<sup>-1</sup> for 1–10 mg Chl *a* m<sup>-2</sup>. These theoretical considerations, based on the photosynthetic parameters, give a range of production that agrees well with the measurements shown in [Figure 4.14](#). Since the photosynthetic parameters are normalized to Chl *a*, PP scales proportionally with the Chl *a* concentration when using this method of estimation. The light-saturated PP would be 300–600 mg C m<sup>-2</sup> d<sup>-1</sup> for 25–50 mg Chl *a* m<sup>-2</sup>.

#### 4.5.7 Estimates based on chemical properties in the water column

Estimates of annual PP based on seasonal changes of chemical properties in the water column are shown in [Figure 4.15](#). Estimates are based on changes, caused by the growth of algae during the growing season from winter to summer, in concentrations or inventories of 1) O<sub>2</sub>, 2) DIC/CO<sub>2</sub>, and 3) nutrients. Estimates based on the increase in O<sub>2</sub> or the decrease in DIC are related to NCP, while estimates based on seasonal drawdown of inorganic nutrients generally reflect NP. NCP and NP production are assumed to be roughly equivalent (Codispoti *et al.*, 2013).



**Figure 4.15.** Estimated annual PP (g C m<sup>-2</sup> year<sup>-1</sup>) in the CAO based on seasonal changes in chemical properties of the water column. The first set of studies (from Wallace *et al.*, 1987 to Ulfssbo *et al.*, 2014 MB) are based on changes in O<sub>2</sub> or DIC/CO<sub>2</sub>; the next set (from Anderson *et al.*, 1998 to Ulfssbo *et al.*, 2014 WML MB) are based on changes in concentrations and inventories of inorganic nutrients. Abbreviations: AB – Amundsen Basin, CB – Canada Basin, MB – Makarov Basin, NB – Nansen Basin, EB – Eurasian Basin; SML – summer mixed layer, WML – winter mixed layer; N and S – North and South; U and L – upper and lower.

The estimates summarized in [Figure 4.15](#) range from 1 to 19 g C m<sup>-2</sup> year<sup>-1</sup>, with most of them lying in the range 1–15 g C m<sup>-2</sup> year<sup>-1</sup>. Many of the estimates based on nutrient inventories are

low ( $1\text{--}6 \text{ g C m}^{-2} \text{ year}^{-1}$ ), while some of the estimates based on  $\text{O}_2$  or DIC are relatively high ( $9\text{--}19 \text{ g C m}^{-2} \text{ year}^{-1}$ ).

#### 4.5.7.1 $\text{O}_2$ and $\text{CO}_2/\text{DIC}$

Ulfssbo *et al.* (2014) reported results from a cruise with RV Polarstern, which crossed the Nansen, Amundsen, Canada, and Makarov basins in late summer (mid-August–September 2011), and used four different approaches to estimate NCP. Estimates based on  $\text{O}_2$  (supersaturation in the upper mixed layer) and DIC (underway  $\text{pCO}_2$  and DIC profiles) were given as ranges:  $0\text{--}10 \text{ g C m}^{-2} \text{ year}^{-1}$  for Amundsen Basin, Canada Basin, and Mendeleev Ridge,  $0\text{--}5 \text{ g C m}^{-2} \text{ year}^{-1}$  for Makarov Basin, and  $5\text{--}15 \text{ g C m}^{-2} \text{ year}^{-1}$  for Nansen Basin (these are shown as midpoint values for the ranges in [Figure 4.15](#)).

Pomeroy (1997) used the seasonal increase in  $\text{O}_2$  concentration under the ice, as recorded from ice-drift stations (Station Alpha; English, 1961; and Station NP-22; Melnikov and Pavlov, 1978), to estimate an annual production of  $13$  and  $15 \text{ g C m}^{-2} \text{ year}^{-1}$  for the two sites, respectively. Adding a correction for loss of  $\text{O}_2$  to the atmosphere (equivalent to  $6 \text{ g C m}^{-2} \text{ year}^{-1}$ ) gave an estimated annual NCP of about  $20 \text{ g C m}^{-2} \text{ year}^{-1}$  for Station Alpha, where English (1961) did his early  $^{14}\text{C}$  work.

Zheng *et al.* (1997) applied a method based on tritium/ $^3\text{He}$  aging and  $\text{O}_2$  concentrations to estimate  $\text{O}_2$  utilization rates and PP in the western Nansen Basin. Rates of apparent  $\text{O}_2$  utilization below the euphotic zone, when vertically integrated and converted to units of C, gave estimates of EP of  $19 \text{ g C m}^{-2} \text{ year}^{-1}$  for the southern part (south of  $83^\circ\text{N}$ ) and  $3 \text{ g C m}^{-2} \text{ year}^{-1}$  for the northern part of a section across Nansen Basin. These values were considered to represent estimates of local NP. However, it is likely that the  $\text{O}_2$  consumption reflected advection from upstream production, particularly for the stations in the southwestern Nansen Basin.

Wallace *et al.* (1987) used a similar method [using chlorofluorocarbon (CFC) compounds for age determination] to estimate apparent  $\text{O}_2$  utilization rate at the CESAR ice-drift station over Alpha Ridge in Amerasian Basin. They derived EP estimates of about  $5\text{--}13 \text{ g C m}^{-2} \text{ year}^{-1}$  based on depth-integrated  $\text{O}_2$  utilization down to  $155 \text{ m}$  in the halocline layer.

Packard and Codispoti (2007) used an enzymatic assay method [respiratory electron transport system (ETS)] to determine  $\text{O}_2$  utilization rates in the water column below an ice-drift station in northern Fram Strait at  $83^\circ\text{N}$  in April 1981. Integrating respiration from  $50 \text{ m}$  to about  $500 \text{ m}$  depth and converting to C using Redfield ratio gave an EP estimate of about  $11 \text{ g C m}^{-2} \text{ year}^{-1}$ .

An important issue with EP estimates based on  $\text{O}_2$  consumption in the CAO is the extent to which they reflect advective transport of production (organic matter and associated BOD) from upstream highly productive areas. This could be particularly the case near the inflow region of Atlantic water in the southwestern Nansen Basin, and could have contributed to the high rates recorded by Zheng *et al.* (1997) and Packard and Codispoti (2007). It could also have affected the estimate of Ulfssbo *et al.* (2014) for Nansen Basin, where there was a discrepancy between estimates based on  $\text{pCO}_2/\text{DIC}$  ( $10\text{--}15 \text{ g C m}^{-2} \text{ year}^{-1}$ ) and estimates based on  $\text{O}_2$  ( $0\text{--}5 \text{ g C m}^{-2} \text{ year}^{-1}$ , from their Figure 5, panel c).

#### 4.5.7.2 Nutrients

The role of advection on productivity signals was clearly demonstrated by Olsson *et al.* (1999) who estimated nitrate deficits (apparent nitrate utilization, as the difference between observed and preformed source water nitrate concentrations) converted into units of C using the C/N Redfield ratio. There was a positive nitrate deficit (reflecting use of nitrate in production) through the entire halocline layer, shifting to a negative deficit (more nitrate) reflecting

remineralization below 300–400 m depth in Eurasian Basin. Olsson *et al.* (1999) interpreted the positive nitrate deficit in the halocline layer as an advective signal stemming from EP on the shelves rather than local production. They estimated a mean shelf EP of  $15 \text{ g C m}^{-2} \text{ year}^{-1}$  into the basins of the CAO. The nitrate deficit was weakened by remineralization as it was transported around in Eurasian Basin. Olsson *et al.* (1999) used this deficit to estimate an EP of  $2 \text{ g C m}^{-2} \text{ year}^{-1}$  for Amundsen Basin.

Anderson *et al.* (2003) used a similar approach based on phosphate deficit to estimate EP and NP. The vertically integrated phosphate deficit in the upper 50 m, converted to units of C, represented from 2.9 to  $8.4 \text{ g C m}^{-2}$  for the Eurasian, Makarov, and Canada basins. These deficits were accumulated over several years. When taking estimates of the age of surface water (5–15 years) into account, the phosphate deficit suggested an annual EP of about  $0.5 \text{ g C m}^{-2} \text{ year}^{-1}$ . Adding a term for vertical mixing of phosphate into the upper 50 m layer, Anderson *et al.* (2003) suggested a total EP or NP of about  $1 \text{ g C m}^{-2} \text{ year}^{-1}$  for the CAO.

Anderson *et al.* (1998) estimated the total annual input of nitrate to the upper mixed and halocline layers from inflowing Atlantic water, Pacific water, and river run-off (a total of  $0.7 \times 10^{12} \text{ mol year}^{-1}$ ). About 70 and 30% of this came from Pacific and Atlantic waters, respectively, with only about 1% from rivers. Converted to units of C and normalized to a total area of about 5 million  $\text{km}^2$  for the CAO basins and slopes, this is equivalent to a mean production of  $12 \text{ g C m}^{-2} \text{ year}^{-1}$ . This is interesting as a theoretical maximum production, assuming all nutrients in the upper layers (down to about 200 m) are used. In reality, much of the nitrate is not used, perhaps only in the order of one-third to one-half (Anderson *et al.*, 1998). This would give an NP estimate of about  $5 \text{ g C m}^{-2} \text{ year}^{-1}$  based on annual nitrate input to the CAO.

Another approach to using nutrient data is to estimate the seasonal drawdown of inorganic nutrients (nitrate and phosphate) relative to the observed or calculated winter concentrations. There are some practical difficulties with this for the CAO because winter data are scarce and the difference between winter and summer concentrations is relatively small. This leads to considerable uncertainties in such estimates.

Codispoti *et al.* (2013) used nutrient data to estimate NCP, assumed to be equivalent to NP for a wider Arctic area. Their estimate for the Eurasian Basin was  $10 \text{ g C m}^{-2} \text{ year}^{-1}$  based on a qualitative analysis, and  $13 \text{ g C m}^{-2} \text{ year}^{-1}$  based on the average for a limited number of grid cells. They obtained an estimate of  $3 \text{ g C m}^{-2} \text{ year}^{-1}$  for the Amerasian Basin (north of about  $75^\circ\text{N}$ ) and a low value of about  $1 \text{ g C m}^{-2} \text{ year}^{-1}$  for the Beaufort Gyre region in Canada Basin (their Beaufort Northern subregion). For the western part of Amerasian Basin, they gave a value of around  $10 \text{ g C m}^{-2} \text{ year}^{-1}$  (their Northern Chukchi and Northern East Siberian Sea subregions). Codispoti *et al.* (2013) suggested a mean value of  $8 \text{ g C m}^{-2} \text{ year}^{-1}$  for the entire CAO (Amerasian and Eurasian basins combined).

Ulfso *et al.* (2014) produced estimates of NCP based on seasonal drawdown of inorganic nutrients from the upper summer mixed and winter mixed layers, respectively. The summer mixed layer is formed by the melting of sea ice and is separated from the lower part of the winter mixed layer by a seasonal halocline. Ulfso *et al.* (2014) used nutrient concentrations at the temperature minimum, below the seasonal halocline, to represent winter concentrations, from which observed concentrations during the cruise in late summer were subtracted. The seasonal drawdown of nutrients represented annual NP of  $2\text{--}6 \text{ g C m}^{-2} \text{ year}^{-1}$  (values were given as ranges:  $2\text{--}5 \text{ g C m}^{-2} \text{ year}^{-1}$  for Nansen Basin,  $5\text{--}8$  for Amundsen Basin,  $2\text{--}10$  for Canada Basin,  $5\text{--}10$  for the Mendeleev Ridge area, and  $0\text{--}10$  for Makarov Basin; shown as midpoint values in [Figure 4.15](#)).

The nutrient drawdown was much higher for the winter mixed layer, with values up to 5–25 g C m<sup>-2</sup> year<sup>-1</sup> for Nansen Basin and 10–30 g C m<sup>-2</sup> year<sup>-1</sup> for the Mendeleev Ridge region (Ulfsbo *et al.*, 2014). The mean (midpoint) values for the winter mixed layer is two- to fourfold higher than those for the summer mixed layer. The average mixed layer depth in summer was 21.5 m, while the winter mixed layer varied from a mean of 40 m for the northwestern Canada Basin to a mean of 63 m for Nansen Basin. Nutrient profiles (nitrate) presented by Codispoti *et al.* (2013) for the late summer period (20 August–29 September) in Eurasian Basin (their Figure S2 in Supplementary material) show two things: 1) nitrate in the upper summer mixed layer is not depleted, but occurs with concentrations of 2–6 µmol l<sup>-1</sup>, and 2) nitrate concentrations increase more or less gradually below 20 m, through the cold halocline layer and down to about 200 m for the ensemble of profiles. This suggests that it may be difficult to estimate the correct winter concentration for the upper layer from concentrations in a gradient below. If the value is taken too deep and, therefore, is too high, this will lead to an overestimation of the seasonal nutrient (nitrate) drawdown between winter and late summer. It is an open question whether such large amounts of nutrients are being vertically mixed into the upper summer mixed layer from the layer below, as the difference between the NP calculated for the summer and winter mixed layers by Ulfsbo *et al.* (2014) would suggest. This could be examined by considering the effect of ice melt on salinity, which would also be affected by the vertical mixing across the seasonal halocline.

#### 4.5.8 Estimates based on rates of sedimentation

The vertical C flux in the layer below the euphotic zone can be used as an estimate of EP. Annual rates from studies with long-term deployment of sediment traps (commonly about one year) are summarized in [Figure 4.15](#).

Very low rates of 0.1–0.5 g C m<sup>-2</sup> year<sup>-1</sup> have been recorded in Canada Basin. Honjo *et al.* (2010), in a comprehensive study with drifting (ice-tethered) sediment traps at 150–200 m depth in two long-term deployments, obtained rates of about 0.1 g C m<sup>-2</sup> year<sup>-1</sup> (0.08 and 0.12 g C m<sup>-2</sup> year<sup>-1</sup> for the two deployments). A higher rate of 2.7 g C m<sup>-2</sup> year<sup>-1</sup> was recorded when one of the traps drifted across the Chukchi Rise area. Similar low rates of about 0.1 g C m<sup>-2</sup> year<sup>-1</sup> were recorded with drifting sediment traps over Alpha Ridge (0.07 g C m<sup>-2</sup> year<sup>-1</sup>; Hargrave, 2004) and on the shelf north of Ellesmere Island (0.13 g C m<sup>-2</sup> year<sup>-1</sup>; Hargrave *et al.*, 1994). Hwang *et al.* (2015) recorded low values (0.07–0.27 g C m<sup>-2</sup> year<sup>-1</sup>) with traps at about 3000 m depth at four stations in Canada Basin.

O'Brien *et al.* (2013) recorded slightly higher values of 0.2–0.7 g C m<sup>-2</sup> year<sup>-1</sup> for three annual cycles using moored sediment traps in the southern Canada Basin. Higher values of 1.1 and 3.8–4.9 g C m<sup>-2</sup> year<sup>-1</sup> were recorded over the lower and upper slopes, respectively, off the Mackenzie shelf (recorded with a trap at 400 m over a water depth of 2700 m, and traps at 300–500 m over water depth of 700 m). The POC content of the sedimenting material was low (3–6%), and most of the sedimenting material (75–85%) was considered of terrigenous origin (O'Brien, 2009).

Fahl and Nöthig (2007) recorded a vertical C flux of 1.0 g C m<sup>-2</sup> year<sup>-1</sup> with a mooring over the eastern (Siberian) end of Lomonosov Ridge. This represented C from marine production. The total C flux was 1.5 g C m<sup>-2</sup> year<sup>-1</sup>, of which about a third was estimated to be of terrigenous origin. At a nearby location on the Laptev slope (1350 m water depth), Lalande *et al.* (2009) measured annual rates of 4.1 and 9 g C m<sup>-2</sup> year<sup>-1</sup> for two consecutive annual periods. The fraction of terrigenous material was not quantified, but terrigenous POC from the Lena River and resuspended sediments from the Laptev shelf probably contributed to the relatively high vertical fluxes on the Laptev slope (Lalande *et al.*, 2009). Lalande *et al.* (2019) presented additional results from moorings at the East Siberian Sea slope and in the eastern Amundsen

and Nansen basins, with low annual rates of  $0.4\text{--}0.6\text{ g C m}^{-2}\text{ year}^{-1}$  (measured as POC flux in sediment traps at about 250 m depth). The contribution of phytoplankton C at these three sites, and two additional stations at the base of Lomonosov Ridge and the Laptev slope, was  $0.01\text{--}0.1\text{ g C m}^{-2}\text{ year}^{-1}$ , or 1–14% when compared to the POC flux (Lalande *et al.*, 2019).

Two studies have used the  $^{234}\text{Th}$  (thorium) /  $^{238}\text{U}$  (uranium) method to estimate vertical C flux.  $^{234}\text{Th}$  is a particle-reactive and short-lived radionuclide (half-life of 24 days) produced *in situ* from  $^{238}\text{U}$ , which has a very long half-life (4.5 billion years) and is found dissolved as a conservative salt in seawater (Coale and Bruland, 1985). The basis for the method is that  $^{234}\text{Th}$  is scavenged by sedimenting particles that leave the euphotic zone. Moran *et al.* (1997) obtained a relatively high estimate of  $4\text{ g C m}^{-2}\text{ year}^{-1}$  based on mean daily values of  $36\text{ mg C m}^{-2}\text{ d}^{-1}$  for stations across the CAO (Arctic Ocean Section 1994) extrapolated to 120 days. Moran *et al.* (1997) considered their results an upper estimate of POC flux for several reasons (e.g. small vs. large particles, recycling of POC).

A much lower estimate of about  $0.3\text{ g C m}^{-2}\text{ year}^{-1}$  was obtained in a comprehensive study with improved methodology by Cai *et al.* (2010) during a RV Polarstern cruise to the CAO in 2007. The mean daily rate was more than an order of magnitude lower than that obtained by Moran *et al.* (1997; 2.5 vs.  $36\text{ mg C m}^{-2}\text{ d}^{-1}$ ). Methodological improvements may have contributed to the difference. According to Cai *et al.* (2010), they conducted a high-resolution study which they considered resulted in one of the most complete and theoretically accurate  $^{234}\text{Th}$  datasets ever collected.

#### 4.5.9 Satellite remote sensing

Satellite remote sensing has been used to quantify PP in the Arctic Ocean. The method is based on algorithms that convert the recorded ocean colour to units of Chl *a* and estimated rates of PP using input data for temperature and light (Arrigo *et al.*, 2008; Pabi *et al.*, 2008; Renaut *et al.*, 2018). There are two main limitations for using the remote sensing method in the Arctic: (i) even low amounts of sea ice (down to 10% areal cover) mask the ocean colour signal seen by the satellite, which basically limits the method to open water (< 10% ice cover), and leaves most of the CAO blank (no records); and (ii) the influence of coloured DOM (CDOM) and suspended solids from the many large rivers that discharge into the Arctic Ocean. While this latter issue can be dealt with by removing pixels with obvious influence by rivers, the resulting maps still show quite high values in the major river plumes, which are possibly mainly artifacts (Arrigo *et al.*, 2008; Pabi *et al.*, 2008; Matrai *et al.*, 2013).

Arrigo and colleagues have provided PP estimates for longitudinal sectors of the Arctic Ocean (Arrigo *et al.*, 2008; Pabi *et al.*, 2008; Arrigo and van Dijken, 2011). The obtained data are mainly from the surrounding shelves and the peripheral part of the CAO with seasonally open water. They observed increasing production trends over the last two decades, which reflect the increase in open water due to both the decrease in sea ice cover in winter and the longer open-water season in areas where there was winter ice (Arrigo *et al.*, 2008; Arrigo and van Dijken, 2011; Renaut *et al.*, 2018).

Detailed examinations of satellite-based estimates of Chl *a* and PP, along with *in situ* data for the wider Arctic Ocean (south to  $60\text{--}65^\circ\text{N}$ ), were carried out for the surface layer by Matrai *et al.* (2013) and for the integrated water column by Hill *et al.* (2013). Satellite-based and observed ( $^{14}\text{C}$ ) PP for the surface layer were only weakly and not significantly correlated ( $r^2 = 0.11$ ; Matrai *et al.*, 2013). The estimated integrated production based on satellite data were low for the CAO basin, with a value of  $1.4\text{ Tg C year}^{-1}$  given by Hill *et al.* (2013). This is two orders of magnitude lower than the net (new) PP determined based on seasonal nutrient draw-down ( $119\text{ Tg C year}^{-1}$ ; Codispoti *et al.*, 2013). This discrepancy both reflects the fact that satellites lack



information from much of the CAO due to the presence of sea ice, and that the estimate based on seasonal drawdown of nitrate is uncertain and possibly an overestimate.

#### 4.5.10 Modelling

Arctic Ocean PP rates (daily to annual) have been estimated using mathematically coupled physical–biological models. Using a nested coupled model (SINMOD; Slagstad and McClimans, 2005; Wassmann *et al.*, 2006a), Slagstad *et al.* (2011) simulated mean annual rates for the Arctic basins of 10 and 3 g C m<sup>-2</sup> year<sup>-1</sup> for GPP and NPP, respectively. In Eurasian Basin, modelled annual GPP was 17 and 7 g C m<sup>-2</sup> year<sup>-1</sup> at 86 and 90°N, respectively (Slagstad *et al.*, 2011). Simulating a future summer ice-free Arctic Ocean gave a total GPP of about 35 g C m<sup>-2</sup> year<sup>-1</sup> for the CAO (Slagstad *et al.*, 2011).

Popova and colleagues simulated PP in the Arctic Ocean using physical and ecological models (NEMO and MEDUSA). Popova *et al.* (2010, 2012, 2013) obtained annual PP values of < 10 g C m<sup>-2</sup> year<sup>-1</sup> for the central ice-covered part and 10–20 g C m<sup>-2</sup> year<sup>-1</sup> for the peripheral areas with more open-ice conditions in summer. Popova *et al.* (2012) compared modelled PP using five coupled physical and biological ocean models. The models differed in many respects (numerical representation, parameterization, grid resolution, initial and boundary conditions, and complexity), but, despite this, they gave broadly the same results for the CAO, with indicated production values of < 10 and 10–20 g C m<sup>-2</sup> year<sup>-1</sup> in broad areas, although with some differences in the proportion of these categories among the models. Popova *et al.* (2013) used the NEMO–MEDUSA model to examine the role of the advection of nutrients in sustaining PP in the CAO. The time-scale for supplying nutrients from Atlantic- and Pacific-source waters into the subsurface layer of CAO was about 5–15 years, while nutrient supply from the surrounding shelves occurred on a time-scale of about five years.

Castellani *et al.* (2017) used a new sea ice model for bottom algae (SIMBA) coupled with a three-dimensional sea ice–ocean model to simulate the growth and production by ice algae in the CAO. The model was run with input data for 2012 and was compared to observations from a cruise that year. There was fair agreement between the observed and modelled biomass of ice algae in September, with the highest simulated biomass in the heaviest sea ice in the Lincoln Sea area north of Greenland (up to 10 µg Chl *a* l<sup>-1</sup>). The simulated monthly mean PP rates by ice algae were up to 15 mg C m<sup>-2</sup> d<sup>-1</sup>, being highest in May for the southern region of the CAO (70–80°N) and in June for the central region (80–90°N). The simulated daily rates are equivalent to an annual rate in the order of 0.5 g C m<sup>-2</sup>. Tedesco *et al.* (2019) used a sea-ice biogeochemical model to simulate production by ice algae under historical and future climate conditions (RCP 8.5 scenario). The model predicted that in the future scenario, linked to a change to annual ice, there would be an increase in production by a factor of about 2 at 83°N in the CAO. However, this simulated increase was from a very low to a still very low level of annual production (from 0.1 to 0.2 g C m<sup>-2</sup>).

#### 4.5.11 Summary and evaluation of level of primary production

There is a span of two orders of magnitude in the annual production values summarized in [figures 4.14](#) and [4.15](#) from EP of around 0.1 g C m<sup>-2</sup> year<sup>-1</sup> to NP or NCP of about 20 g C m<sup>-2</sup> year<sup>-1</sup> based on O<sub>2</sub> and nutrient data. Nevertheless, they all agree in showing that annual PP is relatively low.

The <sup>14</sup>C and <sup>13</sup>C data converge to give a fairly consistent picture of phytoplankton annual PP (not including ice algae) of about 1–4 g C m<sup>-2</sup> year<sup>-1</sup> in ice-covered waters and around 10 g C m<sup>-2</sup> year<sup>-1</sup> in seasonally open waters. As an average over the still largely ice-covered CAO, a value of 5 g C m<sup>-2</sup> year<sup>-1</sup> seems appropriate as a first approximation for the phytoplankton component of the annual PP.

The other methods shown in [Figure 4.15](#) reflect PP of ice algae in addition to phytoplankton, with both components affecting  $O_2$ ,  $CO_2/DIC$ , nutrients, and vertical C flux. EP, as recorded by sediment traps and the  $^{234}Th$  method, is generally low. Very low rates were recorded in the Canada, Amundsen, and Nansen basins ( $0.1\text{--}0.6\text{ g C m}^{-2}\text{ year}^{-1}$ ), with some higher values found over the surrounding slopes in the Beaufort and Laptev seas ( $1\text{--}5\text{ g C m}^{-2}\text{ year}^{-1}$ ). This is in agreement with higher production over the shelves being exported out into the basins and contributing to an increased vertical C flux along the slopes. However, a considerable fraction of the C flux here is of terrestrial origin. The generally low vertical C flux and EP is apparently not sufficient to cover the C demand of the benthos in the CAO (Wiedmann *et al.*, 2020). The authors suggested that the discrepancy may be due to episodic flux events (not recorded in sediment traps), such as rapidly sinking aggregates of ice algae (e.g. Boetius *et al.*, 2013) and dead zooplankton.

Most of the estimates based on  $O_2$ ,  $CO_2/DIC$ , and inorganic nutrients are in the range  $1\text{--}10\text{ g C m}^{-2}\text{ year}^{-1}$ . Some of the higher values ( $> 10\text{ g C m}^{-2}\text{ year}^{-1}$ ) based on  $O_2$  were estimated for the southern Nansen Basin, and may be due to advected signals from upstream production in the Barents and Norwegian seas. Some of the estimates based on seasonal drawdown of inorganic nutrients (primarily nitrate) are also high, e.g. the value of Codispoti *et al.* (2013) for the Eurasian Basin and the values of Ulfsbo *et al.* (2014) for the winter mixed layer.

There is an apparent discrepancy between the relatively high values obtained from seasonal drawdown of nutrients, which represent NP, and the  $^{14}C\text{--}^{13}C$  results and estimates of EP measured with sediment traps and the  $^{234}Th$  method. This is possibly due to uncertainty in the winter nitrate concentration in the upper mixed layer, leading to an overestimate of production based on the seasonal drawdown. Model results (Popova *et al.*, 2013, see their Figure 3c) indicate that the vertical winter mixing is limited, resulting in low maximum nitrate concentration in the surface layer. The uncertainty associated with the seasonal drawdown of nutrients should be addressed with a more careful analysis of the seasonal vertical physics, rates of algae production, and available nutrient data.

Besides the seasonal and regional variability of PP values from the Arctic Ocean, the method used and the spatial representativeness of sampling constitute significant sources of variability, particularly in ice-covered waters. In the past, most PP estimates were based on single-point measurements from water or ice core samples, which are associated with large statistical uncertainty. In recent years, under-ice profiling platforms have been successfully used to overcome the spatial bias of single-point measurements, both for under-ice phytoplankton (Massicotte *et al.*, 2019) and ice algae (Lange *et al.*, 2017a, 2017b).

Taken together, the data reviewed here suggest a NPP level of about  $10\text{ g C m}^{-2}\text{ year}^{-1}$  in the CAO. Production is probably lower in the central area, with heavier ice cover (even when ice algae are included), and higher ( $10\text{--}20\text{ g C m}^{-2}\text{ year}^{-1}$ ) in the peripheral parts, with seasonal ice cover and slope regions. Spatially, there is also a pattern of higher production in Nansen Basin, associated with the inflowing Atlantic water, and lower production in Canada Basin, associated with the anticyclonic Beaufort Gyre. In a recent review, Wiedmann *et al.* (2020) used a value of  $13\text{ g C m}^{-2}\text{ year}^{-1}$  in a proposed C budget for the CAO.

Overall, the CAO is an extremely oligotrophic system, implying low ecological transfer potential to higher trophic levels. The significant fraction of production released as DOC (about a third) is mostly processed in the microbial loop, with little left for use by higher trophic consumers due to the large number of trophic steps involved (e.g. bacteria–protozoans–crustaceans–fish or seal). Phytoplankton are mostly small, with a substantial fraction of picoplankton ( $< 2\text{ }\mu\text{m}$ ). These small algae are themselves part of the microbial loop and need to pass through an extra step in the foodweb leading up to higher trophic consumers (compared to diatoms which can be grazed by large calanoid copepods directly).

## 5 Zooplankton and invertebrate ice fauna

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### 5.1 Introduction

The beginning of zooplankton investigations in the CAO was marked by the Fram expedition in 1893–1896. The samples collected were analysed by the zoologist G. O. Sars, who described 15 new species of copepods (out of a total of 28 species recognized; Sars, 1900). From the 1930s, during the period of Soviet and US ice-drift stations, comprehensive investigations of zooplankton were carried out, including seasonal studies with sampling throughout the year (e.g. Virketis, 1957; Minoda, 1967; Kosobokova, 1978, 1980, 1983; Vinogradov and Melnikov, 1980). From the 1980s, in the era of expeditions with ice-breaker research vessels, more extensive sampling and studies of zooplankton have been carried out with the most modern equipment available (e.g. Hirche and Mumm, 1992; Mumm *et al.*, 1998; Kosobokova and Hirche, 2000, 2009; Kosobokova *et al.*, 1998, 2011; Kosobokova and Hopcroft, 2010; Matsuno *et al.*, 2012).

These studies have provided a rather good overview and understanding of the zooplankton component of the CAO ecosystem. The Census of Marine Life programme provided an incentive and focus for some of the more recent studies and synthesis work (e.g. Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). This section of the report builds on these syntheses.

During the Fram expedition, Nansen (1906) noted the fauna of unicellular organisms and invertebrates that lived inside and on the underside of sea ice. With a similar sequence over time as for zooplankton, sea-ice biota has been investigated first from ice-drift stations and subsequently from research vessels. Igor Melnikov has had a central role in this research since his first participation in the Soviet North Pole 22 ice-drift station in 1975. He has frequently been to the CAO, in the most recent years sampling from the Russian Barneo station established near the North Pole in spring. Melnikov has synthesized information on sea-ice biota and the cryopelagic or sympagic ecosystem (Melnikov, 1997, 2009). Bluhm *et al.* (2017a, 2017b) provided more recent syntheses.

Sea-ice fauna has two main components: (i) meiofauna that lives in brine channels inside the matrix of the ice (Bluhm *et al.*, 2017a, 2017b, 2018; Kiko *et al.*, 2017), and (ii) macrofauna that lives associated to the underside of the ice (Gulliksen and Lønne, 1991; Melnikov, 1997; Hop *et al.*, 2000; David *et al.*, 2015; Bluhm *et al.*, 2017a; Ehrlich *et al.*, 2020). Amphipods are the most important group among the latter. There is a close connection between ice fauna and zooplankton, and some species of zooplankton may be found under the ice as part of the under-ice fauna ([Figure 5.1](#)). Sea-ice amphipods have generally been observed to live associated with sea ice. However, it is currently unclear if they are obligate ice fauna, or if they can also live in the pelagic as zooplankton when there is no ice (Werner *et al.*, 1999, Berge *et al.*, 2012, Kunisch *et al.*, 2020).

This section provides faunistic overviews and describes the main species patterns, life histories, and distributions (vertical and horizontal) of zooplankton ([Section 5.2](#)) and sea ice invertebrate fauna ([Section 5.3](#)). [Section 5.4](#) summarizes information on abundance and biomass of zooplankton and sea ice fauna, and [Section 5.5](#) provides information on trophic links of these groups in the CAO foodwebs.

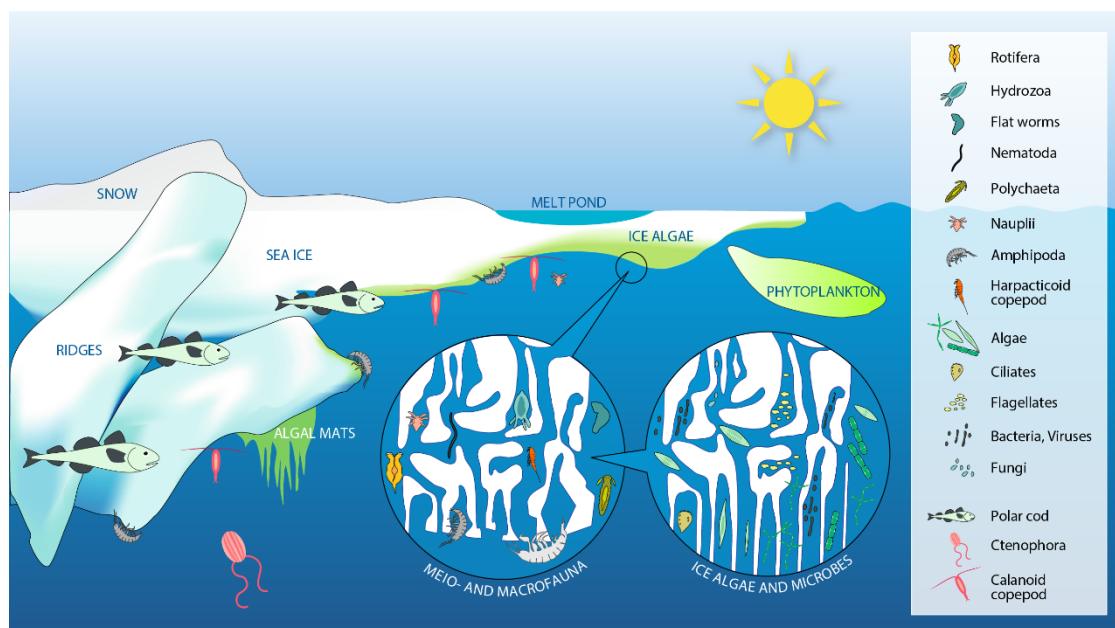


Figure 5.1. Schematic illustration of floating sea ice with associated sea ice biota of ice algae, microbes, meiofauna, and macrofauna (e.g., amphipods) living inside or on the underside of the ice. Planktonic forms including calanoid copepods and ctenophores may come up into the sub-ice zone underneath the ice. Reproduced with permission from Bluhm *et al.* (2017b).

## 5.2 Zooplankton

### 5.2.1 Number of species

The zooplankton community of the Arctic Ocean is dominated by copepods in terms of number of species, abundance, and biomass. Species inventories for the Arctic Ocean have been prepared by Sirenko (2001) for invertebrates in general, and by Kosobokova and Hirche (2000), Kosobokova and Hopcroft (2010), and Kosobokova *et al.* (2011) for zooplankton in the Eurasian and Amerasian basins. Kosobokova and Hirche (2000) listed 106 species, of which 76 were copepods (63 calanoids, nine cyclopoids, four harpacticoids), 6 amphipods, and 20 non-crustacean species (including 11 hydromedusae, 3 chaetognaths, 2 pteropods, and 2 appendicularian species). Kosobokova and Hopcroft (2010) listed 111 species recorded in Canada Basin in 2005: 55 species of copepods, 11 amphipods, 5 ostracods, 2 euphausiids, one decapod, 12 hydromedusae, one scyphomedusae, 4 siphonophores, 4 ctenophores, 2 pteropods, 4 larvaceans, 4 chaetognaths, 5 polychaetes, and 1 foraminiferan (74 crustacean and 37 other species). The total number included three new species that were recognized and under description. In addition, there were several small deep-water calanoids (about 12 species, predominantly belonging to the family Discoidae) and oncaeids (ca. 6 species) that could not be identified to the species level and included in the species number (some of these were also considered to be new undescribed species; Kosobokova and Hopcroft, 2010).

Kosobokova *et al.* (2011; their Table 1) provided an overview of previous inventories of zooplankton in the Arctic Ocean going back to Shirshov (1938). Their most recent inventory included a total of 174 species, with crustaceans (121 species) and gelatinous forms [28 species of cnidarians (17 hydromedusae, 4 scyphomedusae, 7 siphonophores), and 9 species of ctenophores] making up 70 and 21% of the total species number, respectively. Copepods were the dominant group with 91 species (52% of the total number of species). Other crustaceans listed were 16 amphipods, 5 ostracods, 4 euphausiids, 4 mysids, and 1 decapod. Other groups included 4 chaetognaths, 4 larvaceans, 2 pteropods, 5 polychaetes, and 1 nemertin worm.

Kosobokova *et al.* (2011) provided information on the recorded occurrence of the 174 species in each of the four main basins (Nansen: 136 species, Amundsen: 134 species, Makarov: 124 species, and Canada: 141 species), as well as information on their preferred depth range (epi-, meso-, and bathypelagic; their Table 2). Twenty-six of the 174 species were considered expatriates, recorded only as late developmental stages and non-reproducing adults (Table 3 in Kosobokova *et al.*, 2011). The list of 174 species represented an increase of 40 species from a previous compilation, with 21 species not recorded before in the CAO and 19 species recently described as new species to science, including 11 copepods and 4 ctenophores (Kosobokova *et al.*, 2011).

The first investigation of zooplankton in the Arctic Ocean was made during Nansen's Fram expedition in 1893–1896. G. O. Sars analysed the samples and reported 28 species of copepods, 15 of which he described as new species (Sars, 1900; *Augaptilus glacialis*, *Chiridius obtusifrons* (Sars, 1903), *Drepanopus bungei* (Sars, 1898), *Gaetanus brevispinus*, *G. tenuispinus*, *Heterorhabdus compactus*, *Microcalanus pygmeus*, *Pseudocalanus major*, *Pseudochirella spectabilis*, *Scaphocalanus brevicornis*, *Spinocalanus longicornis*, *Temorites brevis*, *Undinella oblonga*, *Xanthocalanus borealis*, and *Lubbockia glacialis*). Brodsky (1950) described 14 new species of copepods from the Arctic Ocean (Brodsky, 1956, 1957, 1967; *Chiridella abyssalis*, *Euaugaptilus hyperboreus*, *Haloptilus pseudooxycephalus*, *Lucicutia anomala*, *L. polaris*, *Metridia pacifica*, *Pareuchaeta polaris*, *Pseudaugaptilus polaris*, *Scaphocalanus polaris*, *Scolecitricella minor* var. *occidentalis*, *Spinocalanus elongatus*, *S. longispinus*, *S. polaris*, and *Xanthocalanus polaris*). Several new species of copepods were described more recently by Markhaseva (1984, 1998, 2002), Markhaseva and Kosobokova (1998), Markhaseva *et al.* (2001), and Andronov and Kosobokova (2011), including *Chiridella reductella*, *C. sarsi*, *Disco triangularis*, *Onchocalanus cristogerens*).

Most copepods (as well as species of other groups) have broad vertical ranges, although various species tend to be found either epipelagically in the upper water layer, or deeper in the water column in the mesopelagic or bathypelagic zones (Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). The upper polar mixed layer is where most, if not all, primary production (PP) takes place during summer, and it constitutes an important part of the epipelagic zone, which extends down to include the halocline layer. The mesopelagic zone corresponds principally to the Atlantic layer at 200–1000 m depth, while the bathypelagic zone consists of the deep and bottom waters of the basins. The greatest number of species are found in the mesopelagic and bathypelagic zones, with 40–45 species of copepods recorded between 300 and 2000 m in the Canada and Eurasian basins, compared to 20–25 species in the upper 100 m (Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). Multivariate community analyses have shown a strong vertical organization of the zooplankton species patterns, with clustering and ordination by depth strata (Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011).

### 5.2.2 Overview of dominant or important species or groups

Copepods (Figure 5.2) generally make up more than 90% of the abundance (in number of individuals) and 70% or more of the biomass of mesozooplankton sampled with common zooplankton nets. Four species of relatively large calanoid copepods make up the bulk of the zooplankton biomass in the upper 25–50 m in summer: *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, and *Metridia longa* (Figure 5.3). *Calanus hyperboreus* is found throughout the Arctic Ocean and is overall the most important species in terms of biomass, making up about 30% of the biomass in Canada Basin (Kosobokova and Hopcroft, 2010), about 70–90% in Canada Basin and over the Northwind Ridge and Chukchi Cap (Ashjian *et al.*, 2003), about 60% in the central parts of the Amundsen and Makarov basins (Auel and Hagen, 2002), and 15–45% in the easternmost parts of the Amundsen and Makarov basins across Lomonosov Ridge near the Laptev Sea (Kosobokova and Hirche, 2000). *Metridia longa* also has a wide distribution in the



basins, while *Calanus glacialis* seems to be distributed in high abundance in the peripheral parts, closer to the surrounding shelves. *Calanus finmarchicus* is found mainly in Nansen Basin, where it is transported with inflowing Atlantic water, and is not found in Canada Basin (Jaschnov, 1966; Hirche and Mumm, 1992; Mumm, 1993; Kosobokova and Hirche, 2000, 2009; Hirche and Kosobokova, 2007; Kosobokova *et al.*, 2011). Other large calanoid copepods which contribute somewhat to biomass are the carnivorous *Paraeuchaeta glacialis* (1–8%) and *Scaphocalanus magnus* (1.1–3.5 %). Both of these species are typically found in the upper mesopelagic layer (50–300 m; Mumm, 1993; Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010).

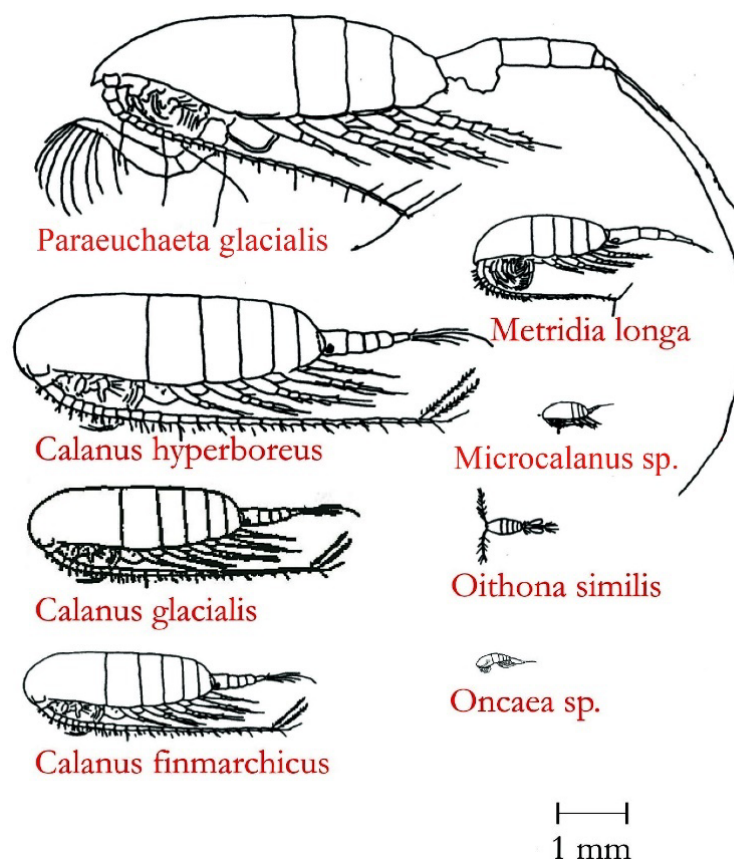


Figure 5.2. Drawings (to same relative scale) of small and large copepods that are common and important species in the CAO. Redrawn from G. O. Sars – "An account of the Crustacea of Norway", 1901–1921 (Sars, 1903).

Small copepods (Figure 5.2) are the dominant component in terms of numbers of mesozooplankton individuals. The quantitatively most important species are *Microcalanus pygmaeus* (a small calanoid) and the cyclopoid species *Oithona similis* and *Oncaea borealis* (Auel and Hagen, 2002; Hopcroft *et al.*, 2005; Kosobokova and Hopcroft, 2010). In the central parts of the Arctic Ocean (Amundsen and Makarov basins), *Oithona similis* dominates strongly (by numbers) in the upper 50 m, whereas *Oncaea borealis* tends to be more important in the subsurface layer below 50 m (Kosobokova, 1983; Auel and Hagen, 2002). *Oithona similis*, and *Oncaea* and *Microcalanus* species each make up about 20% of the numerical abundance (sampled with 150- $\mu$ m mesh net) in Canada Basin. Due to their small size, *Oithona* and *Oncaea* constitute only a few percent of the biomass, whereas the somewhat larger *Microcalanus* makes up 6% of the total mesozooplankton biomass (Kosobokova and Hopcroft, 2010).

There are several more species of copepods that live in the meso- and bathypelagic zones (mostly small but also some larger ones). The small cyclopoid *Neomormonilla minor* (or

*Mormonilla minor*) is found in relatively high abundance in the mesopelagic layer (200–1000 m; 1–3% of the total numerical abundance; Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010). The calanoid *Spinocalanus longicornis* is another mesopelagic species, and is most abundant at 100–500 m depth in the Atlantic layer. Along with other *Spinocalanus* species (including *S. antarcticus*), it was found to make up 6–8% of the total mesozooplankton abundance and about 4% of the total biomass (Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010). *Gaetanus tenuispinus* is found in fair numbers in the upper mesopelagic (100–500 m) in the Atlantic water in Nansen Basin and across the base of Lomonosov Ridge, but it is scarce in the central parts of the Arctic Ocean and in Canada Basin (Mumm *et al.*, 1998; Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010). *Scaphocalanus brevicornis* is also found in the Atlantic layer, with the largest numbers at 200–1000 m depth (0.6–1% of total biomass; Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010).



Figure 5.3. Two dominant *Calanus* species in the CAO: *Calanus hyperboreus* (upper panel) and *C. glacialis* (lower panel). Photos: Maria Włodarska-Kowalczyk and Russ Hopcroft.

Among bathypelagic species, the most abundant copepods are *Aetidiopsis rostrata*, *Spinocalanus polaris*, *S. longispinus*, and *S. elongatus*. They occur with largest numbers at 750–1500 m depth or deeper (Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010). Nine species of copepods are found only in the deep water below 1000 m in the Arctic Ocean: *Lucicutia anomala*,

*L. polaris*, *L. pseudopolaris*, *Mimocalanus damkaeri*, *Scaphocalanus polaris*, *Pseudaugaptilus polaris*, *Disco triangularis*, *Onchocalanus cristogerens*, and *Hyalopontius typicus*. With the exception of the last one (described by G. O. Sars in 1909), these species are described from, and known only as endemic species of, the Arctic Ocean (Sars, 1900; Brodsky, 1950, 1967; Heptner, 1969; Damkaer, 1975; Markhaseva and Kosobokova, 1998; Kosobokova and Hirche, 2000; Kosobokova *et al.*, 2011). While it was previously suggested that the Canada Basin hosted a unique deep-water endemic fauna (Brodsky and Pavshits, 1976), newer studies have shown that the species composition in the Canada and Eurasian basins is the same, and that Lomonsov Ridge does not serve as an effective zoogeographic barrier (Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011).

Besides copepods, two other groups of crustaceans that contribute to the abundance and biomass of zooplankton in the Arctic Ocean are amphipods and ostracods. Amphipods are typically larger forms, and some of them are considered macro- rather than mesozooplankton. The large Arctic species *Themisto libellula* (Figure 5.4) and the somewhat smaller boreo-arctic *Themisto abyssorum* are both common in the Arctic Ocean, and they were each found to constitute nearly 1% of the zooplankton biomass in Canada Basin (Kosobokova and Hopcroft, 2010). However, the biomass of amphipods and other macrozooplankton may be considerably underestimated by studies using mesozooplankton nets due to their ability to avoid the nets (Sameoto *et al.*, 2000; Skjoldal *et al.*, 2013). Several amphipods are dominant components of the ice biota, including *Gammarus wilkitzkii*, *Apherusa glacialis*, *Onisimus glacialis*, and *O. nansenii* (see Section 5.3.2), and they can also be found occasionally in the water column (Kosobokova *et al.*, 2011). These amphipods are characteristically endemic fauna elements of the Arctic, and their occurrence in the pelagic may be part of the mechanisms whereby they survive and recolonize sea ice as it melts and reforms in the Arctic Ocean (Berge *et al.*, 2012).



**Figure 5.4.** The hyperiid amphipod *Themisto libellula* grows to a maximum length of 5–6 cm and is a very important species in the CAO ecosystem. Photo: Maria Włodarska-Kowalczyk.

Ostracods have been found to make up around 3–4 % of the total mesozooplankton biomass in the Arctic Ocean (Mumm, 1993; Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010). *Boroecia maxima* (called *Conchoecia* in some literature) is the most common species in the Arctic Ocean, where it is found predominantly in cold waters in the upper layers (0–200 m) and in lower densities in deeper waters (Chavtur and Bashmanov, 2007; Bashmanov and Chavtur, 2009). *Boroecia borealis* is another common species found mainly in the mesopelagic Atlantic layer (Bashmanov and Chavtur, 2008).

The CAO is not part of the habitat of krill, but four species have been recorded there, brought in by currents (Kosobokova *et al.*, 2011). The most common is *Thysanoessa longicaudata*, which is a basin species transported with Atlantic water in Nansen Basin east to the Laptev Sea (Mumm, 1993; Kosobokova *et al.*, 1998). *Thysanoessa inermis* and *T. raschii* are also found in the slope waters of the Laptev Sea, as well as farther east in the Makarov and Canada basins (Kosobokova *et al.*, 1998, 2011). The larger Atlantic species *Meganctiphanes norvegica* has also been recorded from Nansen Basin, with one specimen collected by the Fram expedition (Sars, 1900). Among other crustaceans, the decapod *Hymenodora glacialis* is found as a wide-spread deep-water species in the Arctic Ocean (Kosobokova *et al.*, 2011).

Chaetognaths and larvaceans (appendicularians) are two common groups among the non-crustacean forms of zooplankton in the Arctic Ocean. Chaetognaths are relatively large forms, and contribute more to biomass than to abundance in terms of numbers of individuals. They are important carnivores, with *Eukrohnia hamata* as the predominant form in the CAO, and they make up 12–18% of the total zooplankton biomass in both the Eurasian and Canadian basins (Kosobokova and Hirche, 2000, 2009; Kosobokova and Hopcroft, 2010). *Parasagitta* (or *Sagitta*) *elegans* is a common species in the Atlantic water inflow region in Nansen Basin (Mumm, 1993; Kosobokova and Hirche, 2000, 2009; David *et al.*, 2015; Ehrlich *et al.*, 2020). Two species of larvaceans are common, the Arctic *Oikopleura vanhoeffeni* and the more boreal *Fritillaria borealis*. *O. vanhoeffeni* is found mainly in the upper 50 m, whereas *F. borealis* tends to occur somewhat deeper in the Atlantic layer (Kosobokova and Hirche, 2000). Larvaceans (mainly *Oikopleura*) have been found to make up about 1–4% of the zooplankton biomass in the Arctic Ocean (Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010), but they can be highly variable and dominate the zooplankton biomass locally (David *et al.*, 2015; Ehrlich *et al.*, 2020).

Several species of gelatinous zooplankton (hydromedusae, scyphomedusae, siphonophores, and ctenophores) are found in the Arctic Ocean, both epipelagically and deeper in the water column (Kosobokova *et al.*, 2011, listed 17 hydrozoan, 4 scyphozoan, 7 siphonophore and 9 ctenophore species, including 3 new species of ctenophores). Gelatinous zooplankton are difficult to sample and preserve due to their often extreme fragility. In addition, larger forms are dispersed or patchily distributed, and are not collected representatively with small nets (Raskoff *et al.*, 2005). Therefore, information about gelatinous forms in the Arctic Ocean is more limited than for the crustacean component of zooplankton. Observations with ROVs under the ice and in deep water in Canada Basin revealed more than 50 gelatinous taxa (including larvaceans and pteropods), with ctenophores and siphonophores dominating over slope and ridge areas (in the Chukchi borderlands), while medusae dominated at the deep stations in the basin (Raskoff *et al.*, 2005, 2010; [Figure 5.5](#)). The trachy-medusae *Sminthea arctica* and a new species of narcomedusae were the two most common species, accounting for more than half (54%) of all observed specimens (Raskoff *et al.*, 2010). These are meso- and bathypelagic species, found at depths of 200–2000 m and 1000–2500 m, respectively. Two other common meso- and bathypelagic species were *Botrynema ellinorae* and *B. brucei* (Raskoff *et al.*, 2010). The large medusae *Chrysaora melanaster* and *Cyanea capillata* were found to be widely distributed in surface waters of Canada Basin (Purcell *et al.*, 2010; Raskoff *et al.*, 2010).

Epipelagic ctenophores include *Mertensia ovum* and *Bolinopsis infundibulum*, which have been found as common species in the upper layer of Canada Basin during summer (Raskoff *et al.*, 2005, 2010; Purcell *et al.*, 2010). These two species are also found in Eurasian Basin and the adjacent Barents Sea, and are important predators of copepods and other zooplankton (Swanberg and Båmstedt, 1991a, 1991b; Purcell *et al.*, 2010; Kosobokova *et al.*, 2011). *Beroe cucumis* and *Dryodora glandiformis*, which are specialist predators of other ctenophores and larvaceans, respectively, were found to be common species in surface waters of the Canada and Eurasian basins (Purcell *et al.*, 2010; David *et al.*, 2015). Ctenophores (including undescribed



species) were also observed by ROV in the meso- and bathypelagic zones of Canada Basin (Rascoff *et al.*, 2010).

A final group of plankton that should be mentioned is the pteropod molluscs, which occur with two species, *Limacina helicina*, a filter-feeder, and *Clione limacina*, assumed to be a specialist predator on *Limacina*. *Limacina helicina* has been found to be common in the upper 50–100 m in the Arctic Ocean, where it can comprise a few % of the total number of mesozooplankton (Kobayashi, 1974; Mumm, 1993; Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010). *Clione limacina* can be locally abundant in the ice–water interface layer (David *et al.*, 2015; Ehrlich *et al.*, 2020).

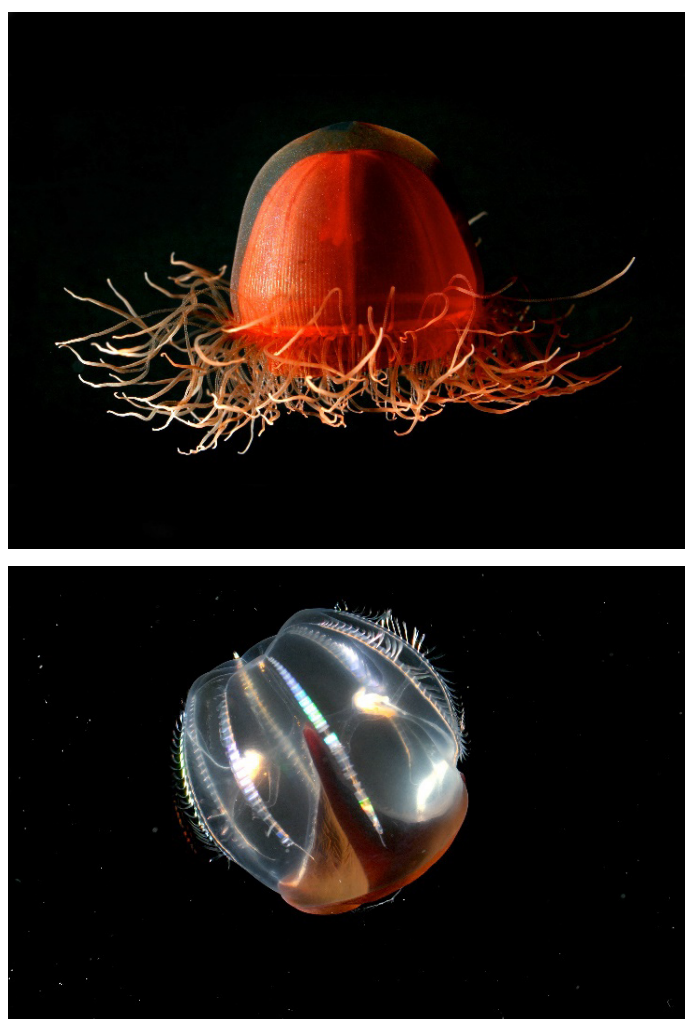


Figure 5.5. Two gelatinous zooplankton species from deep water in the CAO: the small bathypelagic hydrozoan *Crossota norvegica* (upper panel), and an undescribed species of ctenophore (lower panel). Photos by Kevin Raskoff, Monterey Peninsula College.

### 5.2.3 Biogeography

Zooplankton in the Arctic Ocean are largely of Atlantic origin, reflecting the open connection to the northern North Atlantic through deep Fram Strait. The majority of the species in the Arctic Ocean are also found in adjacent parts of the North Atlantic, and many also have a wider distribution (including cosmopolitan and bipolar species). In their compilation of information on zooplankton species in the Arctic Ocean, Kosobokova *et al.* (2011) noted that 25% of the species (19% of copepods) were found in the North Atlantic, 10% (10% of copepods) were also found in the North Pacific, 25% (28% copepods) had a wide distribution, and 9% (10%



copepods) had a bipolar distribution. They listed only 7% of the species (10% of copepods) as Arctic endemics, 6% (4% of copepods) as Arctic cryopelagic, and 13% (17% of copepods) as new Arctic species (newly described or undescribed). The relatively high percentage of new species reflects the large emphasis on basic faunistic investigations in the Arctic Ocean in recent decades, not least through the Census of Marine Life programme (e.g. Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). In contrast to the large number of Atlantic species, the Arctic Ocean harbours few species that elsewhere can only be found in the North Pacific and not in the North Atlantic (1–2%; Kosobokova *et al.*, 2011).

For the majority of zooplankton species, the CAO is part of their habitat and distribution area, and they can be considered residents (148 species out of a total of 174, or 85%; Kosobokova *et al.*, 2011). These species are actively reproducing in the Arctic Ocean, as corroborated by the presence of younger life stages (Kosobokova *et al.*, 2011). For the Arctic endemic species (including newly described species), it is an open question whether the species are endemic to the Arctic Ocean *per se* or are also found in the Nordic seas portion of the Arctic Mediterranean Sea (the area north of the ridge system between Scotland and Greenland). Apart from the cryopelagic (ice-associated) species, most of the endemic species are deep-water forms, such as the eight copepod species mentioned previously. Since the meso- and bathypelagic realms are openly connected with the circulation of Atlantic layer and deep waters through Fram Strait, it would be somehow surprising if the species found in the Eurasian Basin were not also found in the basins of the Nordic seas, which have similar physical oceanographic conditions.

In addition to the residents, there is a faunal element of expatriates. These are species that have been advected with currents into the Arctic Ocean, but are unable to reproduce or only able to reproduce poorly, and thus are not able to maintain populations. Expatriates can be grouped in three categories: Atlantic, Pacific, and neritic (shelf) expatriates (Figure 5.6; Kosobokova and Hirche, 2000; Kosobokova *et al.*, 2011). *Calanus finmarchicus* is the most important of the Atlantic expatriates, being transported with Atlantic water east in Nansen Basin to the Laptev Sea region (Jaschnov, 1966, 1970; Hirche and Mumm, 1992; Kosobokova *et al.*, 1998, 2011; Mumm *et al.*, 1998; Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Hirche and Kosobokova, 2007). *C. finmarchicus* is abundant, it contributes to the high zooplankton biomass in the southern Nansen Basin, and it can also be found in the recirculating current branches of Atlantic water in Amundsen Basin and in the area of Lomonosov Ridge (Mumm *et al.*, 1998; Thibault *et al.*, 1999; Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Hirche and Kosobokova, 2007). *C. finmarchicus* has been recorded in Makarov Basin, but not in Canada Basin (Kosobokova and Hirche, 2000, 2009; Kosobokova *et al.*, 2011). Other Atlantic expatriates include the krill *Thysanoessa longicaudata*, the copepods *Oithona atlantica*, *Metridia lucens*, and *Paraeuchaeta norvegica*, and the siphonophore *Dimophyes arctica* (Jaschnov, 1966; Kosobokova *et al.*, 2011).

Pacific expatriates include the five common oceanic copepods in the Bering Sea: *Eucalanus bungii*, *Metridia pacifica*, *Neocalanus cristatus*, *N. flemingeri*, and *N. plumchrus* (Kosobokova *et al.*, 2011). These copepods are advected northward through the Bering Strait region in large amounts (Springer *et al.*, 1989) and with Pacific water (presumably mainly summer water) into the western Canada Basin adjacent to the northern Chukchi shelf (Matsuno *et al.*, 2011). Pacific copepod species have been recorded from ice-drift stations in the Canada and Makarov basins, but not in Eurasian Basin (Brodsky and Nikitin, 1955; Pavshits, 1971; Brodsky and Pavshits, 1977; Kosobokova and Hirche, 2000; Nelson *et al.*, 2014). They were recorded in low abundance (around 0.5 individuals m<sup>-2</sup>) during a cruise in the western Canada Basin in July 2005 (Kosobokova and Hopcroft, 2010). A few individuals were also collected from Canada Basin in 2008 (Matsuno *et al.*, 2012). In contrast, *Neocalanus cristatus* was not recorded during a cruise to the slope region in the same area in July–August 2002 (Lane *et al.*, 2008). However, *Neocalanus cristatus* was collected (0–0.92 individuals m<sup>-2</sup> d<sup>-1</sup>) throughout the year from a sediment trap

moored at Northwind Abyssal Plain (Matsuno *et al.*, 2014). Out of the two other *Neocalanus* species, which are advected north through the Bering Strait, *Neocalanus plumchrus* has (perhaps surprisingly) not been recorded in Canada Basin, while *N. flemingeri* has been observed at low abundance (Matsuno *et al.*, 2012). Successful reproduction for *N. flemingeri* was reported in the Chukchi Sea (Matsuno *et al.*, 2015). *Metridia pacifica* was found to be fairly abundant (although an order of magnitude less so than *Metridia longa*) in a region over Northwind Ridge and Chukchi Plateau during the SHEBA ice-drift station (Ashjian *et al.*, 2003).

The third group of expatriates comprises neritic species advected from adjacent shelves into the CAO. They include brackish or euryhaline coastal-water species such as the copepods *Drepanopus bungei*, *Acartia longiremis*, and *Pseudocalanus major*, which are transported from the Siberian shelf seas and found in the eastern Nansen and Amundsen basins (Kosobokova *et al.*, 1998; Kosobokova and Hirche, 2000). Other brackish or neritic species include the copepods *Jaschnovia tolli*, *Pseudocalanus acuspes*, and *P. minutus*, and the medusa *Cyanea capillata* (Kosobokova *et al.*, 1998, 2011).

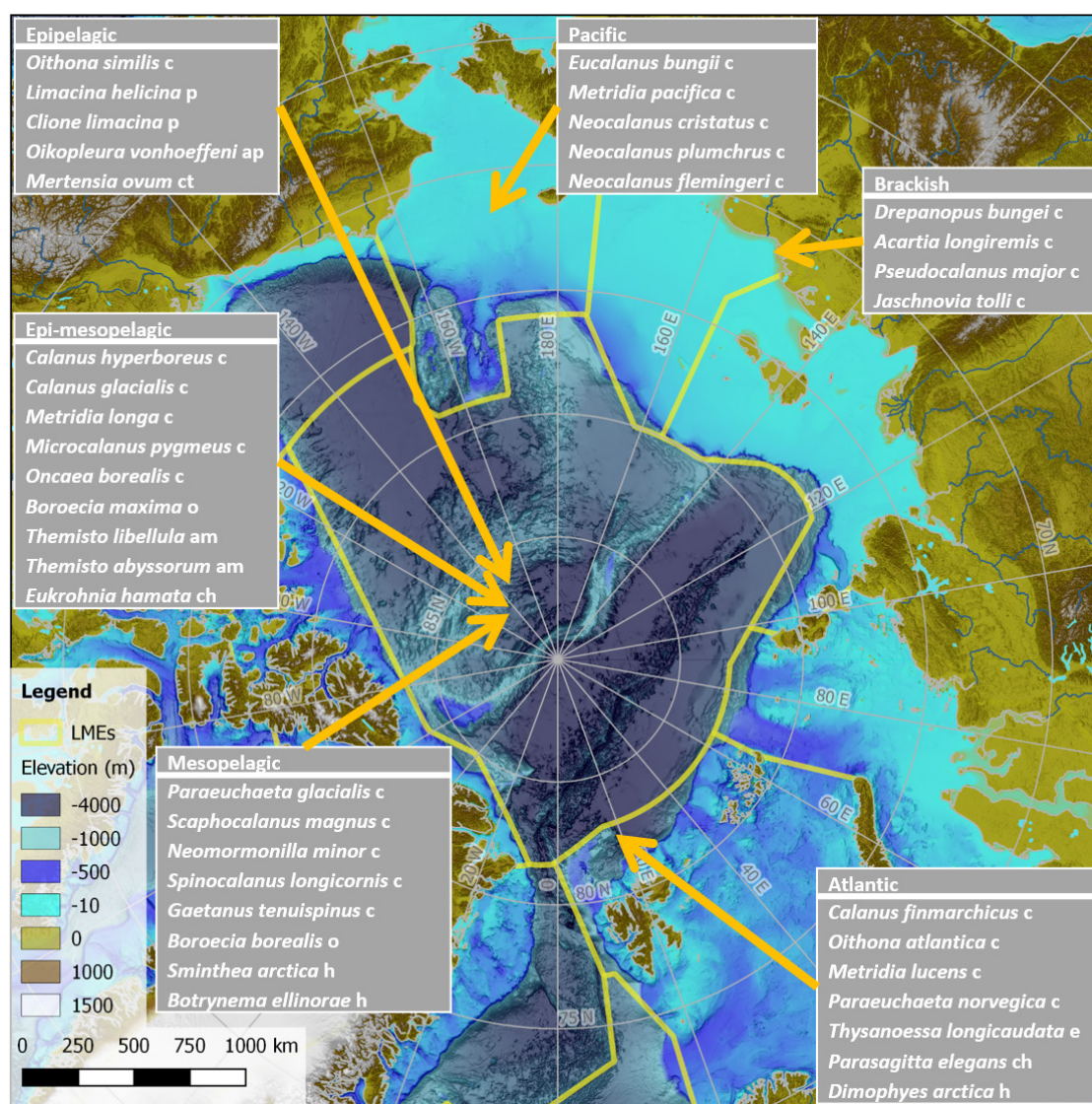


Figure 5.6. Common resident species of zooplankton in the epipelagic and mesopelagic layers of the CAO and expatriated species transported into the CAO through the Atlantic and Pacific gateways and from estuarine and neritic habitats on the adjacent Arctic shelves. Abbreviations: am – amphipod, ap – appendicularian, c – copepod, ct – ctenophore, ch – chaetognath, e – euphausiid, h – hydromedusae, o – ostracod, p – pteropod.

### 5.2.4 Life history and vertical and seasonal distribution

Two main life-history strategies have been recognized for Arctic copepods, the dominant group of zooplankton: (i) pulsed reproduction timed to the short productive period in summer; and (ii) sustained reproduction over a large part of the year (Ashjian *et al.*, 2003). The first strategy is used by the large calanoid copepods, notably the *Calanus* species, which can have a multiyear life cycle in the Arctic Ocean to complete their generational development. These large copepods are predominantly herbivores or omnivores and can survive long periods without feeding during winter, which they spend at depth as part of an ontogenetic migration (Conover, 1988; Conover and Huntley, 1991). Smaller species and some other (e.g. deeper-living) copepods are, to a larger extent, omnivores, detritivores, and carnivores and are not so directly dependent on algae production during summer. They utilize the second life-history strategy, with reproduction taking place over a longer period, and conduct little to no ontogenetic vertical migration (Kosobokova, 1983; Ashjian *et al.*, 2003).

Most recent studies conducted from icebreakers have been in summer and lack seasonal resolution. However, they have provided data with high vertical resolution in the upper 500 m (Mumm, 1993; Mumm *et al.*, 1998; Thibault *et al.*, 1999) or throughout the water column (e.g. Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010). In contrast, studies using ice-drift stations have sampled over extended periods, including winter, and have provided data on seasonal or annual cycles (e.g. Brodsky and Pavshits, 1977; Dawson, 1978; Kosobokova, 1983; Geynrikh *et al.*, 1983; Rudyakov, 1983; Grainger, 1989; Ashjian *et al.*, 2003). Combined, both types of studies provide a fairly clear and detailed picture of the main features of the vertical organization and seasonal changes in zooplankton in the Arctic Ocean basins.

In Arctic summer, most zooplankton (in terms of abundance and biomass) are found in the surface layer corresponding to the upper polar mixed layer (upper 25–50 m; Brodsky and Pavshits, 1977; Kosobokova, 1982, 1989; Grainger, 1989; Mumm *et al.*, 1998; Kosobokova *et al.*, 1998, 2011; Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010). There is a more or less exponential decrease in abundance and biomass with depth, reaching an order of magnitude lower values than at the upper polar mixed layer by a depth of about 200 m (transition between the halocline and the Atlantic layer), and a further order of magnitude lower values by a depth of about 1500 m (upper part of the deep water below the Atlantic layer; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). Depth is the main factor structuring the species assemblages or communities, with broadly similar patterns observed in the Eurasian and Amerasian basins (Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). Species sort themselves into primarily epipelagic, mesopelagic, or bathypelagic groups, although most species occur with wide vertical ranges and are commonly found in two or more of the vertical water layers (polar mixed, halocline, Atlantic, deep water; Grainger, 1989; Kosobokova *et al.*, 2011). Therefore, the very clear pattern of separation by depth layers based on species composition data reflects, to a large extent, changes in relative species abundance rather than differences in species composition. However, differences in species composition do play a role for the more widely separated depth layers, e.g. surface layer vs. bottom-water layers; Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011).

There is seasonal and ontogenetic vertical migration for some species, but there appears to be limited or no diurnal vertical migration in the upper layer during summer (Bogorov, 1946; Grainger, 1989). Kosobokova (1978) reported results from four 24-h stations and one 48-h station taken from the North Pole 22 drift station in the CAO (83–84°N, 140–170°W) from April to September in 1975 and 1976 (Melnikov, 1976a, 1976b). The results suggested no diurnal vertical migration for adult female *Calanus hyperboreus* or copepodite stage CV of *Calanus glacialis*, but indicated a weak migration tendency of female *C. glacialis* in summer. Groendahl and Hernroth

(1986) interpreted data obtained during day and night (not at the same stations) north of Svalbard by the Ymer 1980 expedition to suggest that some species (*Oncaea borealis* and *Metridia longa*) did perform diurnal vertical migration. However, a recent and more extensive study at Svalbard suggested that zooplankton did not perform diurnal vertical migration at these high latitudes with continuous light during summer (Blachowiak-Samolyk *et al.*, 2006).

## 5.2.5 Life cycles of dominant species

### 5.2.5.1 *Calanus hyperboreus*

*Calanus hyperboreus* is an abundant species in the Greenland Sea basins south of Fram Strait, where it reproduces successfully, but apparently requires 3–4 years to complete its life cycle (Hirche, 1997). In this area, a high abundance of young copepodite stages CI–II occurs in early summer (May–June), resulting from spawning the previous winter. They develop further to CIII until August, when they descend to a depth of 1000 m or more to overwinter (Hirche and Niehoff, 1996; Hirche, 1997). The population of *C. hyperboreus* in the Greenland Sea in 1988–1995 was around 5000–15 000 individuals  $\text{m}^{-2}$ , with adult females making up about 10–20%, or around 1000–1500 individuals  $\text{m}^{-2}$  (Hirche, 1997). The biomass of *C. hyperboreus* in the Greenland Sea Gyre area was estimated to be between 5 and 16 g dry weight (dw)  $\text{m}^{-2}$  (mean 9 g  $\text{m}^{-2}$ ) in 1988/1989 and 3–6 (mean 4) g dw  $\text{m}^{-2}$  in 1993 (Hirche, 1997). These values of abundance and biomass of *C. hyperboreus* in the Greenland Sea can serve as a reference when evaluating the status of this dominant species in the Arctic Ocean.

Vertical and seasonal patterns in biomass distribution in the CAO reflect the patterns of the main zooplankton species, notably the large calanoid copepods which make up most of the biomass. The seasonal cycle of the dominant *C. hyperboreus* has been described from samples obtained from ice-drift stations. Dawson (1978) reported results from nearly two years of sampling from the T-3 Ice Island in the northern part of Canada Basin (over the Alpha Ridge area north of Ellesmere Island at 84–85°N and 86–112°W; February 1970–January 1972). Young copepodite stages (CII and particularly CIII; roughly 4000 individuals  $\text{m}^{-2}$ ) were found distributed in the Atlantic layer at about 200–600 m during the first winter (March–April 1970), but not in the second. CIIIs moved up into the surface layer (upper 50 or 100 m) during summer, where they apparently developed into CIVs and some also into CVs, which were found in relatively small numbers in the upper 50 m during July–August (roughly 1–2 individuals  $\text{m}^{-3}$ ). CIVs and CVs descended into the Atlantic layer (200–600 m) during winter and appeared to ascend to the surface layer the next summer. Adult females showed a complex pattern, with many found in the upper layer (0–100 m) during mid-winter (December–February), and descending to depths of 200–300 m during spring. Some females were present in the surface layer (0–50 m) in summer (July), and 20–30% of the female population was found to be mature (gravid) in late winter (March–April). The winter population of female *C. hyperboreus* had an abundance around 500–1000 individuals  $\text{m}^{-2}$  (read from Figure 3 in Dawson, 1978).

Dawson (1978) interpreted his observations to show that the population underwent development, but that the rate was low, requiring at least three years to complete the life cycle. The relatively large numbers of CII and CIII in the first winter (but not the second) showed that recruitment was taking place at least in some years. However, the lack of recorded offspring from the gravid females that were found in spring of both years indicated that successful reproduction in the high-latitude part of the CAO takes place only occasionally or perhaps generally not. Thus, the population would be dependent on advective transport of copepodites from more productive peripheral regions closer to the surrounding shelves (Dawson, 1978). Dawson (1978) cited Harding (1966), who found large numbers of CII in September that remained as CII and CIII through winter in the Arctic Ocean (sampling from ice drift station T-3 in Canada Basin at 81°N, 137°W).



Rudiyakov (1983) reported results on *C. hyperboreus* from the Russian North Pole ice-drift stations (SP-2–5, 1950–1956; original data published by Brodsky and Nikitin, 1955; Virketis, 1957, 1959; mesh No. 23/3 and 15/0). The geographical area covered by the ice-drift stations was in the Canada and Makarov basins. The mean density of the population was roughly 500–1000 individuals  $\text{m}^{-2}$ , formed predominantly by older copepodite stages (CIII–CVI) with around 200 females  $\text{m}^{-2}$ . Copepodite stage CIII showed a pronounced seasonal variation, with the highest values in winter (November–January) and values declining to a minimum in August (Figure 1 in Rudiyakov, 1983). All copepodite stages, including adult females, were concentrated in the surface layer (upper 50 or 100 m) in summer, from May to September, while they were found deeper, mainly in the Atlantic layer, during winter. There are both similarities and differences between the results of Rudiyakov and those reported by Dawson (1978). One difference is the complexity of the seasonal vertical distribution by adult females, which were found in the upper layer in winter and descending in spring in the results of Dawson (1978). It is possible that the averaging of the datasets reported by Rudiyakov may have contributed to masking a feature like this, or it could be that the difference is real and reflects the diversity and flexibility in life history of this large calanoid copepod.

Copepodite stages CII and, particularly, CI were found in small numbers, and Rudiyakov (1983) noted that this was perplexing. It indicated that the population of *C. hyperboreus* in the CAO was dependent on advective transport of young stages from areas with more active reproduction. This is perhaps illustrated by the results reported by Ashjian *et al.* (2003) from the SHEBA Ice Station in the western Canadian Basin. Copepodite stages CI and CII of *C. hyperboreus* were observed in some abundance only in summer (July–August) when the station drifted over Chukchi Plateau. These young stages resulted from spawning in spring and were found concentrated in the upper 25 m in summer (Ashjian *et al.*, 2003). The CIs developed into stage CII which descended below the halocline into the Atlantic layer during autumn (September). CII copepodites were not observed the previous autumn and winter (October–March) when the station drifted over the deep Canada Basin, suggesting that these waters had not received an input of new recruits stemming from spawning during the preceding spring. Johnson (1963) reported results from Station Alpha drifting in the northern Canada Basin (81–85°N, 155–170°W; north of Northwind Ridge and Chukchi Plateau) from June 1957 to February 1958. He observed few CI–II, but large proportions of CIII copepodites (23–48%) of the *C. hyperboreus* population in winter, at the end of the study period (December–February). While the results were obtained with a coarse-mesh net (about 0.6 mm) that is likely to have undersampled the youngest stages (see Skjoldal *et al.*, 2013), the large proportion of CIII demonstrates recruitment of young stages, which could have been transported in the Beaufort Gyre from the Chukchi Borderland region in the western Canada Basin.

Relatively large numbers of young copepodite stages of *C. hyperboreus* (CI–CIII, about 1000–2000  $\text{m}^{-2}$ ) have been found in the slope waters of the southwestern Nansen Basin north of Svalbard (at around 81.5°N) in summer (July–August), demonstrating recruitment in this area with the core Atlantic inflow from Fram Strait (Hirche and Mumm, 1992). Active recruitment was also corroborated by another study that found large proportions of young stages (CI–II, 30–80%) in waters around northwestern Svalbard in spring (May; Søreide *et al.*, 2008). *C. hyperboreus* also spawns and recruits in the central Barents Sea, with nauplii (up to 15 000  $\text{m}^{-2}$ ) and young copepodites (CI–II, 500–1000  $\text{m}^{-2}$ ) found there in spring and early summer (May–June; Melle and Skjoldal, 1998). Hirche and Mumm (1992) detected a change in the population of *C. hyperboreus* in the western Nansen Basin in deep water beyond the slope (north of 82°N). Here, the population was dominated by adult females (about 100–300  $\text{m}^{-2}$ ) and CVs, with very few young copepodites (CI–CIII). All stages were found at their highest densities in the upper 25 m, with almost the entire population (>90%) found in the upper 50 m, which suggests active feeding on phytoplankton in the upper layer. All females had immature gonads, indicating that



they were not ready to spawn, but they were, presumably, preparing for overwintering (Hirche and Mumm, 1992).

Compiling data from several cruises, Kosobokova and Hirche (2009) found that the biomass of *C. hyperboreus* was highest in a band along the southern margins of the deep basins on the Eurasian side, with typical values of 2–3 g dw m<sup>-2</sup> extending from the western Nansen Basin to the eastern Amundsen Basin. The maximum biomass value (4 g dw m<sup>-2</sup>) was observed over the eastern base of Lomonosov Ridge (Kosobokova and Hirche, 2000, 2009). Similar high values of 2–4 g dw m<sup>-2</sup> (1–2 g C m<sup>-2</sup>) were recorded by Ashjian *et al.* (2003) from the SHEBA drift station in the western margin of Canada Basin, with the highest values over Northwind Ridge and Chukchi Plateau. The mesozooplankton biomass here was dominated (70–90%) by older copepodite stages (CIV–VI) of *C. hyperboreus*, with typical abundances of 2000–6000 (maximum 14 000) individuals m<sup>-2</sup>. Over the deeper Canada Basin, biomass and abundance were found to be generally lower (around 2 g dw m<sup>-2</sup> and 1000–2000 individuals m<sup>-2</sup>; Ashjian *et al.*, 2003). Kosobokova and Hopcroft (2010) found a mean biomass of *C. hyperboreus* of 1.0 g dw m<sup>-2</sup> and a mean abundance of 1080 individuals m<sup>-2</sup> in the same general area of the western Canada Basin during the Hidden Ocean cruise in 2005.

In the northern part of the Nansen, Amundsen, and Makarov basins (> 85°N), Auel and Hagen (2002) recorded biomass values of about 1–1.5 g dw m<sup>-2</sup> for *C. hyperboreus* (out of a total mesozooplankton biomass of about 2 g dw m<sup>-2</sup>) and abundances of 1000–1500 individuals m<sup>-2</sup>. Mumm *et al.* (1998) reported abundances of about 100–1300 individuals m<sup>-2</sup> in the upper 500 m on a transect from north of Svalbard to the North Pole region, with biomass values of 0.5–0.8 g dw m<sup>-2</sup> of *C. hyperboreus* in the Nansen, Amundsen, and Makarov basins. Olli *et al.* (2007) recorded biomass values of 0.6–1.1 g dw m<sup>-2</sup> (0–200 m) for *C. hyperboreus* in Amundsen Basin close to the North Pole (88–89°N). *C. hyperboreus* made up about 40–50% of the total mesozooplankton biomass (1.6–2.0 g dw m<sup>-2</sup>) with about 500–1000 individuals m<sup>-2</sup>. Adult females were the most dominant stage, at about 250 individuals m<sup>-2</sup>, followed by copepodite stage CI at about 200 m<sup>-2</sup> (Olli *et al.*, 2007). These observations are in line with the general pattern reported by Kosobokova and Hirche (2009) of lower biomass of *C. hyperboreus* in the northern parts of the basins beyond the maximum zone along the southern slopes. Kosobokova (1982) reported a biomass of *C. hyperboreus* of about 1 g dw m<sup>-2</sup> in the northern Canada Basin (60% of a total mesozooplankton biomass of about 1.5 g dw m<sup>-2</sup>; from NP-22 drift station, at 83–85°N).

In summary, the biomass and abundance of *C. hyperboreus* in the Arctic Ocean are lower than in the Greenland Sea Gyre by a factor of up to 10 (Figure 5.7, panel A). The maximum biomass recorded in the Arctic Ocean (about 4 g dw m<sup>-2</sup> in the Lomonosov Ridge region in the eastern Arctic; Kosobokova and Hirche, 2000, 2009) is in the lower end of the values for the Greenland Sea reported by Hirche (1997; 3–16 g dw m<sup>-2</sup>). The reported biomass values for *C. hyperboreus* in the Arctic Ocean can be grouped broadly into zones of high biomass around the southern rim of the basins on the Eurasian side (2–4 g dw m<sup>-2</sup>) and zones of lower biomass (0.5–1.5 g dw m<sup>-2</sup>) in the northern and central part of the basins (Kosobokova, 1982; Mumm *et al.*, 1998; Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Ashjian *et al.*, 2003; Kosobokova and Hopcroft, 2010).

The biomass and stage composition data suggest that active recruitment takes place primarily in the peripheral parts of the CAO on the Eurasian side. From here, young copepodite stages are transported with the currents into the central parts of the CAO, where they continue to develop over several years, but may not be able to reproduce regularly and successfully. This is in agreement with the results of a modelling study that suggested that *C. hyperboreus* was not able to develop from egg to the first wintering diapause stage (CIII) in the central parts of the Arctic Ocean (Ji *et al.*, 2012). The critical development time to reach CIII was estimated to be about 70 days at 0°C (or about 100 days at –1.6°C), and these conditions were modelled to occur

only in the peripheral parts south of 80–83°N on the Eurasian side and in the Beaufort Sea (Ji *et al.*, 2012). Lack of successful reproduction in the central part of the Arctic Ocean was also suggested by Olli *et al.* (2007), who considered *C. hyperboreus* (and also *C. glacialis*) to be expatriates in the central region, dependent on advective transport from the peripheral and more productive regions.

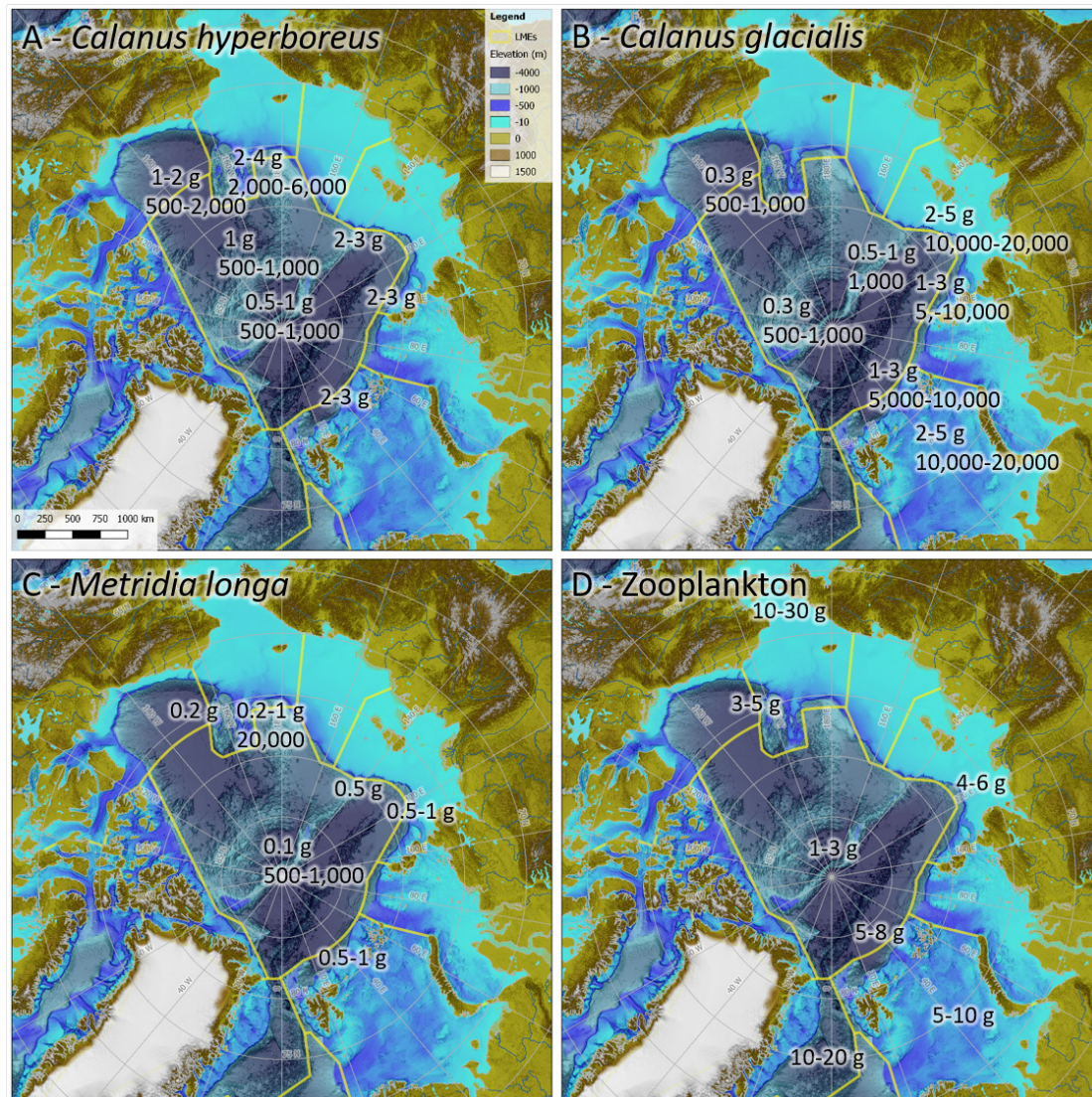


Figure 5.7. Integrated biomass (g dry weight m<sup>-2</sup>) and numerical abundance (number of copepodites m<sup>-2</sup>) of (A) *Calanus hyperboreus*, (B) *C. glacialis*, (C) *Metridia longa*, and (D) total zooplankton biomass (g dry weight m<sup>-2</sup>) in the CAO. See the text for more details and sources of information

The general lack of successful reproduction does not preclude that some reproduction by *C. hyperboreus* can take place under favourable conditions, e.g. under conditions with low ice coverage and stimulated growth of the algae that provide food for the copepods. Indeed, some young copepodite stages have been found in the high-latitude part of the CAO, although infrequently and in small numbers and proportions (Dawson, 1978; Rudyakov, 1983; Olli *et al.*, 2007). In a recent paper, Ershova and Kosobokova (2021) compiled data on *C. hyperboreus* and *C. glacialis* from cruises between 1993 and 2015. Young stages of *C. hyperboreus* were occasionally found in the central part of the CAO, but generally in small numbers, with the population dominated by the older copepodite stages CIV–VI, which typically made up > 90% of the total abundance.



#### 5.2.5.2 *Calanus glacialis*

*Calanus glacialis* is generally considered a shelf species, and its occurrence in the Arctic Ocean presumably depends, to a large extent, on production and development in the surrounding shelf areas with seasonal ice cover. However, the species is found throughout the CAO, suggesting a continuous distribution range in the high Arctic (Kosobokova *et al.*, 2011; David *et al.*, 2015). It reproduces successfully in the Arctic water mass of the northern Barents Sea, where egg production occurs at the onset of the spring phytoplankton bloom when Chl *a* concentration increases (Melle and Skjoldal, 1998; Hirche and Kosobokova, 2003). Abundances of young copepodite stages (CI–III) were found to be 20 000–40 000 individuals  $\text{m}^{-2}$  in summer in the central Barents Sea (Melle and Skjoldal, 1998) and even higher (around 150 000 individuals  $\text{m}^{-2}$ ) on the northern Barents shelf at 79–81°N (Slagstad and Tande, 1990). *C. glacialis* has been suggested to have a predominantly 2-year life cycle in the Barents Sea (Tande *et al.*, 1985, Slagstad and Tande, 1990). The abundance of adult females in summer (after presumably two years of development) is around 500–1000 individuals  $\text{m}^{-2}$  (Slagstad and Tande, 1990; Melle and Skjoldal, 1998; Hirche and Kosobokova, 2003). These abundance values for the northern Barents Sea can serve as a reference when we consider abundances in the CAO (Figure 5.7, panel B).

*C. glacialis* is found as an epipelagic species in the Arctic Ocean in summer, with the highest abundance commonly in the upper water layer (0–50 m) and even at the surface (0–25 m; Grainger, 1965, 1989; Brodsky and Pavshchikov, 1977; Hirche and Mumm, 1992; Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Olli *et al.*, 2007; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). *C. glacialis* has been reported from the ice–water interface layer under sea ice in the CAO, where it feeds on ice algae (Melnikov, 1997; David *et al.*, 2015; Kohlbach *et al.*, 2016). In Canada Basin (at 72–76°N) in summer (July 2005), the large majority of the population was found in the upper 50 m, with highest mean abundance (about 25 individuals  $\text{m}^{-3}$ ) in the top 25 m (Kosobokova and Hopcroft, 2010). During the SHEBA ice drift in the southwestern Canada Basin (at about 75–80°N), *C. glacialis* was found mainly in the Atlantic layer below the halocline (at about 200–500 m depth) in winter, in the upper 100 m (with highest concentration in the upper 50 m) during summer, and in the halocline layer around 150 m during autumn (Ashjian *et al.*, 2003).

Kosobokova and Hirche (2009) described a horizontal distribution pattern for *C. glacialis*, with a band of high biomass values, typically up to 1.5–2 g dry weight  $\text{m}^{-2}$ , along the outer shelf margin and the continental slope on the Eurasian side of the basins. Very high values of 2–8 and up to 9 g dw  $\text{m}^{-2}$  were recorded in the northern Kara Sea northwest of Severnaya Zemlya, and in the Laptev Sea off the New Siberian Islands, respectively (Kosobokova and Hirche, 2009). On transects from the shelves into the basins, there was a clear shift in dominance from *C. glacialis* over the outer shelf to *C. hyperboreus* over the basin (Kosobokova and Hirche, 2009). The relative importance of *C. glacialis* was high in the Laptev Sea region, where it made up 50–90% of the mesozooplankton biomass (Kosobokova and Hirche, 2009). The high biomass in the Laptev Sea and the northeastern Kara Sea reflects favorable conditions for reproduction in these regions and possibly also advection from the nearby northern Barents Sea (Kosobokova and Hirche, 2001, 2009; Hirche and Kosobokova, 2003, 2007).

Lower biomass values have typically been recorded in Canada Basin. Kosobokova and Hopcroft (2010) recorded a mean biomass of 0.33 g dw  $\text{m}^{-2}$  (9% of total mesozooplankton biomass) in the southwestern Canada Basin and a mean abundance of about 1000 individuals  $\text{m}^{-2}$ . Similar values were recorded by Ashjian *et al.* (2003) for the SHEBA ice-drift station, with a biomass of typically 0.2–0.4 g dw  $\text{m}^{-2}$  (0.1–0.2 g C  $\text{m}^{-2}$ ; 5–10% of total mesozooplankton), and an abundance of typically 250–500 individuals  $\text{m}^{-2}$  in autumn and winter and 500–1000 individuals  $\text{m}^{-2}$  in summer. Kosobokova (1982) reported a similar value of about 0.3 g dw  $\text{m}^{-2}$  for drift station

NP-22 in the northern Canada Basin, and a somewhat higher value of about 0.9 g dw m<sup>-2</sup> for NP-23.

Similar biomass values of around 0.3–0.4 g dw m<sup>-2</sup> have been recorded in the northern Nansen, Amundsen, and Makarov basins (Hirche and Mumm, 1992; Mumm, 1993; Mumm *et al.*, 1998; Auel and Hagen, 2002). On a transect across the western Nansen Basin, Hirche and Mumm (1992) recorded a biomass of *C. glacialis* of about 0.2–1 g dw m<sup>-2</sup> (0.2–0.8 g ash-free dw m<sup>-2</sup>), with abundances of copepodite stage CV and adult females of 100–500 individuals m<sup>-2</sup>. *C. glacialis* made up about 10% of the mesozooplankton biomass on average in Canada Basin, with a mean biomass of about 0.35 g dw m<sup>-2</sup> (Mumm, 1993). Mumm *et al.* (1998) recorded mean biomass values of 0.24–0.37 g dw m<sup>-2</sup> for *C. glacialis* in the Nansen, Amundsen, and Makarov basins, making up 15–22% of the total mesozooplankton biomass in the upper 500 m. Abundances varied typically around 200–300 individuals m<sup>-2</sup>, with a maximum of about 1300 individuals m<sup>-2</sup> (Mumm *et al.*, 1998).

Olli *et al.* (2007) recorded somewhat higher biomass values of about 0.4–0.8 g dw m<sup>-2</sup> for *C. glacialis* in Amundsen Basin at 88–89°N, close to Lomonosov Ridge. The mean abundance was about 1000 individuals m<sup>-2</sup>, dominated by adult females at about 650 m<sup>-2</sup> (Olli *et al.*, 2007). Similar abundance values were recorded by Thibault *et al.* (1999) on the trans-polar Arctic Ocean section, with values of typically 1000–1500 individuals m<sup>-2</sup> (dominated by adult females) and the highest values found in the region of Lomonosov Ridge.

The highest abundance of *C. glacialis* has been reported from the outer Laptev shelf and slope with values up to 10 000–20 000 individuals m<sup>-2</sup> in summer (Kosobokova and Hirche, 2001). This is a region of active reproduction for *C. glacialis*, supported by a relatively high production in the Laptev or Great Siberian Polynya system, and corresponds to the area with the highest recorded biomass for the species (Kosobokova *et al.*, 1998; Kosobokova and Hirche, 2001, 2009; Hirche and Kosobokova, 2007). Young copepodite stages (CI–III) made up a large proportion of the population (up to 50% or more) in the areas of high abundance (Kosobokova and Hirche, 2001; Hirche and Kosobokova, 2007). Farther offshore, in the Laptev region, abundance was lower, typically around 2000–3000 individuals m<sup>-2</sup> and dominated by older copepodite stages CIV–VI (Kosobokova and Hirche, 2001; Hirche and Kosobokova, 2007). Lesser abundances still, typically 200–500 individuals m<sup>-2</sup>, have been recorded in the northern Nansen, Amundsen, and Makarov basins (corresponding to biomass values around 0.3–0.4 g dw m<sup>-2</sup>; Hirche and Mumm, 1992; Mumm *et al.*, 1998; Auel and Hagen, 2002). Abundances in this range were also observed in the western Canada Basin in autumn and winter from the SHEBA ice-drift station (Ashjian *et al.*, 2003). Somewhat higher values, 500–1000 individuals m<sup>-2</sup>, were recorded during summer over Northwind Ridge and Chukchi Plateau due to a higher contribution of younger stages CIII–IV (Ashjian *et al.*, 2003). A mean abundance of *C. glacialis* of about 1000 individuals m<sup>-2</sup> was recorded in the western Canada Basin in summer by Kosobokova and Hopcroft (2010).

The population of *C. glacialis* in the central parts of the Arctic Ocean is composed of older copepodite stages, usually dominated by adult females (Thibault *et al.*, 1999; Kosobokova and Hirche, 2001; Hirche and Kosobokova, 2007; Olli *et al.*, 2007). The body dry weights of CV and adult females of *C. glacialis* are usually around 0.5–1 mg (Slagstad and Tande, 1990; Ashjian *et al.*, 2003). The typical biomass values of 0.3–0.4 g dw m<sup>-2</sup> for abundances of 200–500 individuals m<sup>-2</sup> give a mean individual weight of around 1 mg dw, corresponding to the weight of adult females. The somewhat higher abundances recorded by Thibault *et al.* (1999) in Makarov Basin (about 1000–1500 m<sup>-2</sup>) and by Olli *et al.* (2007) in Amundsen Basin (about 1000 m<sup>-2</sup>) were obtained close to Lomonosov Ridge on the Eurasian side of the North Pole. Olli *et al.* (2007) recorded some CI (about 250 individuals m<sup>-2</sup>) and CII and CIII (<100 individuals m<sup>-2</sup>) copepodites in Amundsen Basin. Hirche and Kosobokova (2007) observed a higher fraction of

CI and CII copepodites (up to about 70%) on a transect across Lomonosov Ridge (at about 81°N), where the total abundance was about 3000 individuals m<sup>-2</sup>.

The seasonal study during the SHEBA ice drift in the western Canada Basin obtained results which suggested *C. glacialis* reproduction, but of limited extent (Ashjian *et al.*, 2003). Eggs and nauplii likely of *C. glacialis* were observed in summer (July–August), and small numbers of copepodites CI and CII were found in late summer and winter. Proportions of CIII and CIV increased in spring and early summer, while CVs dominated in summer (July–September), suggesting some cohort development, although this was not so clear in the data (Ashjian *et al.*, 2003). Grainger (1965) reported results from ice-drift station T-3 north of the Canadian Archipelago (at around 79°N, 120°W), which showed the appearance of CI and CII *C. glacialis* in August and September. Grainger (1965) also showed results from the Russian Sedov expedition (data from Bogorov, 1946) which found CI was the dominant stage in late July, CII in early September, and CIII in October. Geynrikh *et al.* (1983) reported seasonal data on *C. glacialis* from Russian ice-drift stations NP-2 (76–82°N, 1950/1951), NP-22 (83–85°N, 1975/1976), and NP-23 (78–84°N, 1977). Copepodite stages CI and CII occurred in summer in 1950 (July–August; 25–40% of the population), suggesting some reproduction in early summer. Apart from summer, the population was dominated by older copepodite stages CIV–CIV, making up 80–90% of the population (Geynrikh *et al.*, 1983).

Ershova *et al.* (2021) summarized data on *C. glacialis* in the CAO collected on cruises from 1993 to 2016. The results were broadly in agreement with previous results, showing low abundance and biomass in the central part of the CAO (north of 84°N), with dominance of older copepodites CV and adults. Mean abundance, as an average over these cruises, was about 1000 individuals m<sup>-2</sup> (range 100–3000 individuals m<sup>-2</sup>), with a corresponding mean biomass of 0.5 g dw m<sup>-2</sup> (range 0.05–1.2 g dw m<sup>-2</sup>).

Low abundances and dominance of older copepodite stages have been interpreted to reflect that *C. glacialis* is not reproducing to any great extent in the CAO, and that the presence of this species here depends on advective transport from core reproduction areas in peripheral zones around the continental margins (Kosobokova and Hirche, 2000, 2001, 2009; Ashjian *et al.*, 2003; Hirche and Kosobokova, 2007; Olli *et al.*, 2007). The northern Barents and Kara seas and the outer Laptev shelf and slope region are areas with vigorous reproduction and high abundance of *C. glacialis* (Slagstad and Tande, 1990; Kosobokova and Hirche, 2001, 2009; Hirche and Kosobokova, 2007). Maturation and egg production depend on food, and females were all immature and did not spawn in the western Laptev Sea, which has heavy ice cover (Kosobokova and Hirche, 2001). Low or no egg production has also been found at other locations with extensive ice cover (Hirche and Kosobokova, 2007).

The relative proportions of different *Calanus* species, with higher abundances of *C. glacialis* over the outer shelf and slope and of *C. hyperboreus* over the adjacent basin (Kosobokova and Hirche, 2009) suggest that *C. glacialis* is even more dependent than *C. hyperboreus* on advective transport for its occurrence in the CAO. The modelling study of Ji *et al.* (2012) supports this notion. They estimated that the critical development time from egg to first diapause stage (CIV in *C. glacialis*) was somewhat shorter for *C. hyperboreus* than for *C. glacialis* (about 75 days at 0°C). Predicted successful reproduction of *C. glacialis* took place along the edges of the CAO and did not extend as far north as for *C. hyperboreus* (Ji *et al.*, 2012). The Transpolar Drift from off the New Siberian Islands and the reflected flow of Atlantic water beneath it along Lomonosov Ridge are transport mechanisms which can carry *C. glacialis*, including young stages, from the core reproduction area in the Laptev Sea towards the North Pole region (Kosobokova and Hirche, 2000, 2009; Ji *et al.*, 2012; David *et al.*, 2015).

The occasional presence of young copepodites of *C. glacialis* in the ice-covered central part of the CAO (Geynrikh *et al.*, 1983; Olli *et al.*, 2007; Ershova *et al.*, 2021) suggests that spawning may



take place under favorable conditions that allow sufficient growth of algae. This led Ershova *et al.* (2021) to question the notion that *C. glacialis* is a strict shelf species. They suggested that in the future it may extend its reproductive range out over deeper waters of the CAO with reduced ice cover. The relatively low *C. glacialis* abundance in the central part of the CAO, recorded during recent cruises, suggests that reproduction is not yet successful in leading to a build-up of locally produced generations of *C. glacialis*. The issue of whether *C. glacialis* can successfully reproduce in the basins of the CAO is an important question that needs to be addressed in future studies.

### 5.2.5.3 *Calanus finmarchicus*

*Calanus finmarchicus* occurs with a high absolute and relative abundance in the area of inflowing Atlantic water along the slope in the southern Nansen Basin (Jaschnov, 1966, 1970; Hirche and Mumm, 1992; Kosobokova and Hirche, 2000, 2009; Hirche and Kosobokova, 2007; Kosobokova *et al.*, 2011; Ji *et al.*, 2012; Wassmann *et al.*, 2015). In the western part (north of the Barents Sea), it was found with biomass values of around 2 g dry weight  $\text{m}^{-2}$ , contributing about 30–40% of the total mesozooplankton biomass (Hirche and Mumm, 1992; Mumm, 1993; Mumm *et al.*, 1998). Even higher biomass values, of up to 4–8 g dw  $\text{m}^{-2}$ , have been recorded at some stations along the shelf edge of the northern Barents and Kara seas (Kosobokova and Hirche, 2009). Farther east, in the Laptev Sea area, the biomass of *C. finmarchicus* is lower, generally around 0.5 g dw  $\text{m}^{-2}$  or 10% or less of the total mesozooplankton biomass (Hirche and Kosobokova, 2007; Kosobokova and Hirche, 2009). In the northern Nansen Basin, the amount of *C. finmarchicus* decreased markedly north of about 83°N, with a mean biomass of about 0.3 g dw  $\text{m}^{-2}$  (Hirche and Mumm, 1992; Mumm *et al.*, 1998). In the central Amundsen and Makarov basins, biomass was much lower still, at <0.05 g dw  $\text{m}^{-2}$  (Mumm *et al.*, 1998; Kosobokova and Hirche, 2009).

In Laptev Sea, *C. finmarchicus* abundance decreased, in the direction of the flow of Atlantic water, from the western to the eastern area, where the biomass was about 0.1–0.2 g dw  $\text{m}^{-2}$  (Kosobokova and Hirche, 2009). A transect across Lomonosov Ridge, at about 81°N, showed the highest biomass over the ridge, associated with the recirculating branch of Atlantic water (maximum biomass of 0.25 g dw  $\text{m}^{-2}$ ; Kosobokova and Hirche, 2000; Hirche and Kosobokova, 2007). In the Laptev Sea, *C. finmarchicus* is represented almost exclusively by older copepodite stage CV and adult females, and the species is considered an expatriate unable to reproduce under Arctic conditions (Kosobokova and Hirche, 2000, 2009; Hirche and Kosobokova, 2007). Young copepodite stages were found over the slope northeast of Svalbard, reflecting successful reproduction upstream in the WSC (Hirche and Kosobokova, 2007). Studies of gonad maturation and egg production have clearly indicated that *C. finmarchicus* is not reproducing successfully in the Arctic Ocean or in the cold Arctic waters of the northern Barents Sea (Tande *et al.*, 1985; Hirche and Mumm, 1992; Hirche and Kosobokova, 2003, 2007). Hirche and Kosobokova (2007) suggested that late availability of food in the short Arctic production season was the main limiting factor for successful reproduction of *C. finmarchicus* in the Arctic Ocean. Ji *et al.* (2012) estimated that the critical development time from egg to overwintering stage (CV) would be 150–200 days at sub-zero temperatures, which is excessively long for successful recruitment under Arctic conditions.

Average individual weights of CV and adult female *C. finmarchicus* are about 200–300  $\mu\text{g}$  dry weight (Tande, 1982; Tande and Slagstad, 1992). This gives abundances of about 3000–5000 and 600–1000 individuals  $\text{m}^{-2}$ , corresponding to biomass values of 1 and 0.2 g dw  $\text{m}^{-2}$ , respectively, which fits those observed in the Laptev Sea region. Hirche and Mumm (1992) recorded abundances of around 5000 individuals  $\text{m}^{-2}$  for CV copepodites and about 1000–3000 individuals  $\text{m}^{-2}$  for adult females along the slope of the western Nansen Basin northeast of Svalbard. Mumm *et al.* (1998) reported abundances of about 2000–6000 individuals  $\text{m}^{-2}$  in the

southern Nansen Basin, around 1000 individuals  $\text{m}^{-2}$  in the northern Nansen Basin, and up to a few hundred individuals  $\text{m}^{-2}$  in the Amundsen and Makarov basins. Similarly, Auel and Hagen (2002) reported an abundance of  $< 150$  individuals  $\text{m}^{-2}$  in the Amundsen and Makarov basins, while nearly 2000 individuals  $\text{m}^{-2}$  were recorded at one station in Nansen Basin. Minoda (1967) recorded *C. finmarchicus* in very small numbers from ice-drift station Arlis II in the western Amundsen Basin north of Greenland.

While *C. finmarchicus* is recorded in small numbers across Lomonosov Ridge in Makarov Basin, it is not found in Canada Basin (Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). Johnson (1963) recorded a few *C. finmarchicus* collected from ice-drift station Alpha in the region of the Mendeleev–Alpha Ridge (at around  $85^{\circ}\text{N}$ ,  $167^{\circ}\text{W}$ ). Grice (1962), with samples obtained with the submarine Seadragon, recorded *C. finmarchicus* in Makarov Basin, but not Canada Basin.

#### 5.2.5.4 *Metridia longa*

*Metridia longa*, along with *C. glacialis* and after *C. hyperboreus*, is the second most important species of zooplankton in terms of biomass in the CAO (Figure 5.7, panel C). It has a wide distribution all over the Arctic Ocean, but differs from the *Calanus* species by being more mesopelagic and omnivorous in its feeding. In terms of life history, it also differs by belonging to the second type described in Section 5.2.4, with an extended reproduction period that is less dependent on a short seasonal production period in summer than for the mostly herbivorous filter-feeding *Calanus* species (Geynrikh *et al.*, 1983; Ashjian *et al.*, 2003; Campbell *et al.*, 2009).

*M. longa* is often found at its highest abundance in the upper part of the Atlantic layer below the halocline, at 200–500 m depth (Geynrikh *et al.*, 1983; Ashjian *et al.*, 2003; Kosobokova and Hopcroft, 2010). It is reported to have seasonal vertical migration and to move into the upper layer in summer (Geynrikh *et al.*, 1983). Observations from ice-drift stations in the northern Canada Basin showed that adult females and older copepodite stages CIII–V were found at depths of 200–500 m in late spring and early summer, before ascending in late summer and early autumn to upper layers, where they remained until the beginning of the next spring (Geynrikh *et al.*, 1983). In Canada Basin in summer, *M. longa* was found at its highest abundance at 200–500 m depth, reflecting large numbers of young copepodite stages, while maximum biomass was found at 50–100 m, due to predominance of older copepodite stages (Kosobokova and Hopcroft, 2010). In the seasonal study at the SHEBA ice-drift station in the western Canada Basin, the highest abundance was generally found at intermediate depth (200–400 m), even during summer (Ashjian *et al.*, 2003). This was also the case in Nansen Basin, where the highest abundance was found at 200–500 m in summer (Hirche and Mumm, 1992). A similar pattern was found here as in Canada Basin (Kosobokova and Hopcroft, 2010), with the highest abundance of young copepodites (CI–IV) in the deeper layer (200–500 m), while adult females occurred with a maximum in the subsurface layer (25–100 m; Hirche and Mumm, 1992). This pattern was also recorded by Geynrikh *et al.* (1983), who listed median depths of CII–CIII at about 250 m and of CV and adult females at around 80–90 m, based on extensive sampling from Russian ice-drift stations. In a compilation of a large dataset from both the Canada and Eurasian basins, Kosobokova *et al.* (2011) listed *M. longa* as the third most abundant zooplankton species at 200–300 m depth, decreasing in rank to seventh in the surface layer (0–25 m) and to sixth at 500–1000 m.

Horizontally, the distribution of *M. longa* resembles those of *C. hyperboreus* and *C. glacialis*, with highest biomass values in the southern Nansen Basin, which decrease eastward along the flow direction of the Atlantic boundary current and northward into the central parts of the Arctic Ocean (Kosobokova and Hirche, 2009). Along the southern slope of Nansen Basin north of the Barents Sea, the biomass of *M. longa* has been found to be about 0.5–1 g dry weight  $\text{m}^{-2}$  (Hirche

and Mumm, 1992), with a maximum value of 2.9 g dw m<sup>-2</sup> recorded at the slope of the Kara Sea northwest of Severnaya Zemlya (Kosobokova and Hirche, 2009). Similar values of 0.5–1 g dw m<sup>-2</sup> have been found along the outer shelf and slope of the Laptev Sea (Kosobokova *et al.*, 1998; Kosobokova and Hirche, 2009). At the transition to the East Siberian Sea, biomass was about 0.5 g dw m<sup>-2</sup>, as it was on a transect across the base of Lomonosov Ridge (0.2–0.8 g dw m<sup>-2</sup>; Kosobokova and Hirche, 2000, 2009).

In the southern and western Canada Basin, the observed biomass of *M. longa* is around 0.2 g dw m<sup>-2</sup>. Kosobokova and Hopcroft (2010) reported a mean biomass of 0.26 g dw m<sup>-2</sup> in the southwestern Canada Basin (72–76°N, comprising 7% of the total mesozooplankton biomass, and corresponding to a mean abundance of 4200 individuals m<sup>-2</sup>). Campbell *et al.* (2009) recorded mean biomass of 0.15–0.2 g dw m<sup>-2</sup> for the slope and basin habitats in the same general area (72–74°N, contributing 3–5% of the total mesozooplankton biomass). Ashjian *et al.* (2003) recorded low biomass of *M. longa* during the SHEBA ice drift over the basins in the western Canada Basin (5% or less of the mesozooplankton biomass), but they found higher biomass with values up to about 1 g dw m<sup>-2</sup> (about 20% of the total) over Chukchi Plateau. This high biomass corresponded to abundances of 10 000–25 000 individuals m<sup>-2</sup>, with a predominance (about 80%) of younger copepodites CI–IV.

The biomass of *M. longa* in the central parts of the Arctic Ocean has been found to be around 0.1 g dw m<sup>-2</sup> (Kosobokova and Hirche, 2009). Mumm *et al.* (1998) recorded mean biomass of 0.1 g dw m<sup>-2</sup> in the Amundsen, Makarov, and northern Nansen basins at abundances of about 500–1200 individuals m<sup>-2</sup> in the upper 500 m. Hirche and Mumm (1992) and Mumm (1993) found biomass values of 0.1–0.2 g dw m<sup>-2</sup> in the central Nansen Basin, with abundance typically between 500 and 1000 individuals m<sup>-2</sup>. In Amundsen Basin (at 88–89°N), Olli *et al.* (2007) recorded biomass values of 0.04–0.16 g dw m<sup>-2</sup> for *M. longa*, again at similar abundances of 500–1000 individuals m<sup>-2</sup> (upper 200 m; around 5% of the total mesozooplankton biomass). Kosobokova (1982) reported biomass values of about 0.1 g dw m<sup>-2</sup> (range of 0.06–0.13 g dw m<sup>-2</sup>) from ice-drift station NP-22 in the northern Canada Basin (82–85°N), with somewhat higher values around 0.2 g dw m<sup>-2</sup> for NP-23 farther south and west in Canada Basin (*M. longa* made up typically 5–10% of total mesozooplankton biomass).

*M. longa* is generally in a wide range of copepodite stages, including younger ones. This suggests that it is actively reproducing in the central CAO. However, its abundance declines from the peripheral to the central parts of the CAO, indicating that conditions are limiting and that recruitment may not balance mortality on a gradient from south to north towards the centre. Reproduction apparently takes place during winter, as suggested by observations from ice-drift stations (NP-22 and NP-23; Geynrikh *et al.*, 1983). The youngest copepodite stages (CI and CII) have been observed to be most abundant from November to April, suggesting that the most intensive reproduction occurs from October to March when the adult females are distributed in the upper layer (Geynrikh *et al.*, 1983). Brodsky and Pavshchik (1977) had suggested earlier that peak reproduction occurs in summer (June–July), based on maximum numbers of copepodite stage CI in July, although they noted that reproduction took place over an extended period of time. Reproduction in winter is supported by observations from ice-drift station Alpha in the northern Canada Basin (81–85°N) where the highest relative abundances of copepodite stages CI–CIII were found in December and February (when observations ended; Johnson, 1963). In addition, adult males were observed in October–November at ice-station Arlis II in western Amundsen Basin, supporting reproduction in winter (Minoda, 1967).

Observations from ice-drift station SHEBA showed a predominance of adult females and stage CV in winter and autumn, when the station drifted over deep water and the population level of *M. longa* was low (at or below 1000–2000 individuals m<sup>-2</sup>; Ashjian *et al.*, 2003). The proportion of adult males peaked in November (up to 20% of total abundance), which also suggests

reproduction in winter in this case. During late winter and spring (February–June) when the station drifted over Northwind Ridge and Chukchi Plateau, the population abundance was much higher (10 000–25 000 individuals  $\text{m}^{-2}$ ). Young stages CI and CII were relatively abundant in winter and spring (January–May), followed by an increase in stage CIII, suggesting cohort development (Ashjian *et al.*, 2003). The presence of males during spring and summer and of nauplii in late summer and autumn (June–September) indicated continued reproduction during summer.

Observations from the western Nansen Basin showed a high abundance of young copepodite stages CI and CII of *M. longa* in the slope region north of Svalbard in summer (1000–2000  $\text{m}^{-2}$ ; about 35% of all copepodite stages; Hirche and Mumm, 1992). Farther north, in Nansen Basin, where the population was much less abundant, observations showed few of the youngest copepodites and a predominance of stages CIII and CIV along with adult females. These observations are consistent with reproduction in winter and spring, with subsequent cohort development during summer. The gonads of females in Nansen Basin were mostly in stage 3 (developing) or stage 4 (mature; about 30%), and males were present in relatively large numbers (average female: male sex ratio 6:1; Hirche and Mumm, 1992). This suggested that reproduction can continue in summer, although rates of egg production were found to be low ( $< 1$  egg  $\text{female}^{-1} \text{d}^{-1}$ ; Hirche and Mumm, 1992).

#### 5.2.5.5 *Microcalanus pygmaeus*

*Microcalanus pygmaeus* was described by G. O. Sars (1900) from samples from the Fram expedition by Fridtjof Nansen. It is a small calanoid copepod that is among the numerically most important zooplankton species in the Arctic Ocean. In samples from Canada Basin, taken in July 2005, it occurred with a mean abundance of about 30 000 individuals  $\text{m}^{-2}$  and made up about 22% of total zooplankton abundance in numbers (collected with a 150  $\mu\text{m}$  net; Kosobokova and Hopcroft, 2010). In samples across Lomonosov Ridge, between the eastern Amundsen Basin and Makarov Basin, it made up a slightly lower fraction (17–18% of total zooplankton abundance; 150  $\mu\text{m}$  net), while it made up a somewhat larger fraction, of 28% (176  $\mu\text{m}$  net), in the material from the NP-22 ice-drift station in the northern Canada Basin (Kosobokova and Hirche, 2000). In terms of biomass, *M. pygmaeus* has been found to make up 4–6% of the total mesozooplankton abundance (Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010). *M. pygmaeus* is largely a mesopelagic species found predominantly in the Atlantic layer (Kosobokova, 1980). It was the top ranked species in the study from Kosobokova *et al.* (2011) in terms of abundance from 100 to 1000 m depth, while its rank decreased to fourth in the upper 25 m, and to sixth at 1000–2000 m depth.

## 5.3 Invertebrate sea ice fauna

### 5.3.1 Faunistic overview

Sea ice biota is often called sympagic (meaning “with ice”). Melnikov (1997) used the term cryopelagic fauna to denote animals that lived in association with the underside of the sea ice. Autochthonous cryopelagic fauna are those animals that live continually in close contact with the ice and are rarely found in the water column below the ice. The allochthonous cryopelagic fauna is made up of organisms that live only part-time in association with sea ice (Melnikov, 1997). In this latter group there are many zooplankton species that can be found directly under the ice, as well as benthic species, including meroplanktonic larval forms (Gradinger and Bluhm, 2005; Ehrlich *et al.*, 2020). In addition to organisms that live on the underside of the ice, there is also a fauna component that lives within the matrix of the sea ice, the so-called cryointerstitial fauna (Melnikov, 1997) or sea ice meiofauna (Bluhm *et al.*, 2017a, 2017b, 2018).



The number of species of sea-ice invertebrates is difficult to state as an exact number for three main reasons: (i) studies of meiofauna have often been carried out with low taxonomic resolution (not to species level), and there are several undescribed species in this fauna (Bluhm *et al.*, 2017a); (ii) the species number depends on how much of the water layer under the ice is included; and (iii) the species number also depends on the criteria used to count a species of zooplankton as part of the allochthonous ice fauna (e.g. regular vs. rare occurrence). Melnikov (1997) listed 42 species, of which 10 were considered part of the autochthonous faunal group. A large majority were crustaceans (37 species, or 88%), with copepods (18 species) and amphipods (14 species) as the dominant groups. Melnikov did not include the typical groups of meiofauna (nematodes, rotifers, flatworms) in his list, so at least around 20 more species (see below) can be added to this list, giving a total of 60+ species of Arctic sea ice invertebrate fauna. Arndt and Swadling (2006) provided an overview of the species of crustaceans, while Bluhm *et al.* (2017a) summarized information on species of meiofauna.

Sea-ice meiofauna are comprised of a range of different phyla and classes, including copepods, rotifers, nematodes, acoel and other flatworms, cnidarians, and other rarer groups (Bluhm *et al.*, 2017a, 2018). In addition to metazoans, large protists, like ciliates and dinoflagellates, are also sometimes considered part of the meiofauna. Otherwise, protozoans are considered part of the sea-ice microfauna (Bluhm *et al.*, 2017a, 2018). Meroplankton (early life stages of benthic invertebrates) can be a dominant component of meiofauna in landfast ice in shallow waters (Gradinger *et al.*, 2009), but this component is rare or absent in the pack ice of the CAO (Bluhm *et al.*, 2018). Bluhm *et al.* (2018) noted a large-scale, pan-Arctic, pattern in the composition of meiofauna, with rotifers and copepods making up most of the meiofauna in Nansen Basin and the central part of the CAO. Nematodes were an important component in the Makarov and Canada basins, whereas flatworms were the largest component in terms of numbers in Canada Basin. Among copepods, harpacticoids (which are slender, benthic forms) are a characteristic part of the ice meiofauna, but calanoid and cyclopoid copepods also contribute to this faunal component.

Three nematode species have been described and are probably endemic to Arctic sea ice: *Teristus melnikovi*, *Cryonema crissum*, and *C. tenue* (Tchesunov and Riemann, 1995). In addition, there are likely a few more species which are undescribed (Tchesunov and Riemann, 1995). The group of rotifers includes eight species, with *Synchaeta hyperborea* and *S. tamara* as the most common (Friedrich and de Smet, 2000). For flatworms (Acoela and Platyhelminthes), there has been no detailed taxonomic study, but the group is considered present with "at least a handful of species" (Bluhm *et al.*, 2017a). The meiofauna copepods include the harpacticoids *Harpacticus superflexus*, *Halectinosoma* sp., and *Tisbe furcata*, and the cyclopoids *Cyclopina gracilis* and *C. schneideri* (Arndt and Swadling, 2006; Bluhm *et al.*, 2017a). A hydroid species, *Sympagohydra tuuli*, was newly described from land-fast sea ice at Barrow, Alaska (Piraino *et al.*, 2008). The species has also been found in sea ice in the Eurasian Basin of the CAO (Siebert *et al.*, 2009).

True sea-ice macrofauna (the autochthonous component) consists of a limited number of species adapted to living in close association with the underside of sea ice, with amphipods as the dominant group (Bluhm *et al.*, 2017b). Melnikov (1997) listed six amphipods in the group of autochthonous species, while Arndt and Swadling (2006) listed 20 species of Arctic ice amphipods (their Table 1), with most of them being rare. Five species of amphipods are common in the pack ice of the CAO: *Gammarus wilkitzkii*, *Eusirus holmi*, *Apherusa glacialis*, *Onisimus nanseni*, and *Onisimus glacialis* (Figure 5.8; Barnard, 1959; Melnikov and Kulikov, 1980; Melnikov, 1997; Hop and Pavlova, 2008; David *et al.*, 2015). More information on sea ice amphipods is given in [Section 5.3.2](#).

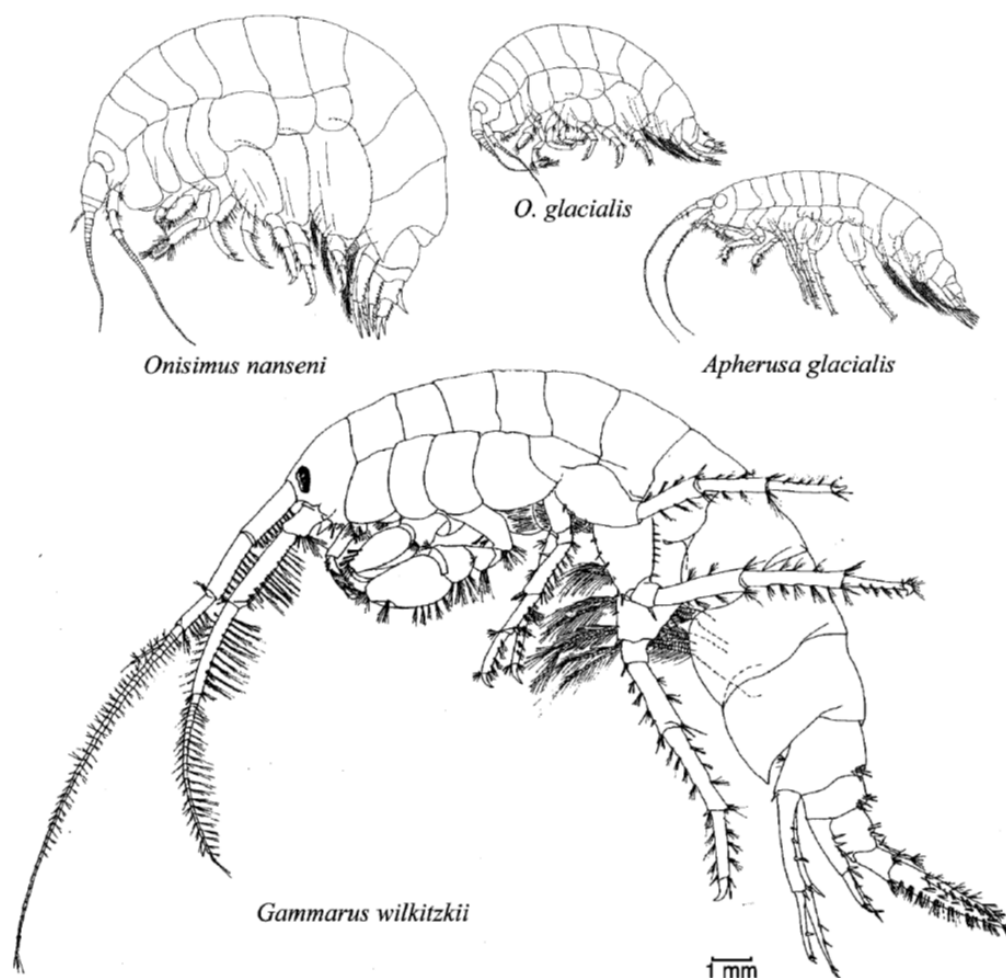


Figure 5.8. Drawings (to same relative scale) of four common species of sea ice amphipods in the CAO. Reproduced with permission from Arndt *et al.* (2005).

The mysid *Mysis polaris* has regularly been found on the underside of sea ice in both summer and winter from Russian drift stations in the CAO (Kulikov, 1980; Melnikov, 1997). This species grows to a size of about 3 cm. The polychaete *Antinoella* (or *Harmothoe*) *sarsi* has been found between crystals on the underside of pack ice (Melnikov, 1997). This is a widespread benthic species with complex taxonomy [the species is now called *Bylgides sarsi* (*Bylgides promamme* for the subspecies *promamme*); World Register of Marine Species<sup>2</sup>].

The two copepods *Tisbe furcata* and *Jaschnovia brevis* (also called *J. johnsoni*, which is now considered a junior synonym; Markhaseva, 1996) were listed as part of the autochthonous fauna by Melnikov (1997). *T. furcata* is a small harpacticoid and is also found as part of the meiofauna in ice. *J. brevis* is a calanoid copepod that is considered a benthopelagic species.

Allochthonous ice fauna includes many of the common epipelagic zooplankton species in the Arctic Ocean. Among the species listed by Melnikov (1997) were the copepods *Calanus glacialis*, *C. hyperboreus*, *Metridia longa*, *Microcalanus pygmeus*, *Pseudocalanus elongatus*, *P. minutus*, and *Oithona similis*, the hyperid amphipods *Themisto abyssorum* and *T. libellula*, the chaetognath *Eukrohnia hamata*, and the appendicularian *Fritillaria borealis*. These zooplankton species come up beneath the sea ice and may be found in the interface layer between ice and water. It is

<sup>2</sup> <https://www.marinespecies.org/>

probably more correct to consider them as part of the under-ice fauna, rather than being strictly a part of the ice fauna.

### 5.3.2 Ice amphipods

Among larger metazoans in the ice fauna, amphipods are the most conspicuous and abundant component. As a group, amphipods are widespread globally in both marine and freshwater environments, and include nearly 7000 species in total. It is perhaps not surprising that it is this group of crustaceans that has come to occupy and dominate the under-ice habitat in the Arctic Ocean. Amphipods that live in association with ice have special physiological adaptations to cope with large variations in salinity and low temperatures at or near the freezing point of seawater (Aarset and Aunaas, 1987a, 1987b; Aarset, 1991). Salinity can vary from very low (brackish water), during ice melt, to high, when brine forms during freezing. Ice amphipods have been shown to be euryhaline osmoregulators, being able to tolerate such variations (Aarset and Aunaas, 1987a, 1990; Aarset 1991). They were found to be freeze-sensitive, and did not tolerate being frozen into solid ice (Aarset and Torres, 1989). However, the increased concentration of osmolytes when exposed to higher-salinity brine, lowered the freezing point of their body fluids. This allows the amphipods to stay in the vicinity of ice during freezing and ice formation (Aarset and Aunaas, 1987b; Aarset, 1991).

Ice amphipods have different feeding strategies, with a wide range and flexibility in their feeding ecology (Poltermann, 2001). Werner (1997a) found that *Apherusa glacialis*, *Onisimus* species, and *Gammarus wilkitzkii* all fed on ice algae, but to varying degree. Juveniles of all species, being generally released in spring, may feed to a large extent on ice algae. Older individuals can also graze on algae and detritus (dead organic matter) in the aggregated mats and filaments on the underside of the ice, but, depending on the species, they may also feed as carnivores on smaller zooplankton (Arndt *et al.*, 2005; Arndt and Swadling, 2006).

Sea-ice amphipods all have a similar reproductive biology, with females carrying their eggs in brood pouches during their development. They have multiannual life cycles, with lifespans of 2–6 years, and are iteroparous (reproduce more than once during their lifespan; Arndt and Swadling, 2006). Reproduction takes place during winter, and females carry their eggs during a long incubation period of up to 6–7 months. Juveniles are released from brood pouches typically in spring, at the start of seasonal production (Melnikov, 1997; Poltermann *et al.*, 2000). However, the release of juveniles may occur over an extended time-period, perhaps as an adaptation to the extreme and variable conditions in the Arctic pack ice (Poltermann *et al.*, 2000). The number of eggs produced (the fecundity) is relatively high for ice amphipods compared to other amphipods, which is seen as an adaptation to counter losses from the population due to ice export and predation (Poltermann *et al.*, 2000).

The life history of sea-ice amphipods, with lifespans of two or more years and reproduction once a year, give population structures with distinct peaks in size frequency diagrams, representing the different cohorts (newly released juveniles, 1-year old, 2-year old, etc.). Therefore, data on length distribution, combined with the abundance of sampled populations under the sea ice, can reveal the basic life histories and population dynamics of the investigated species. This is particularly the case where there has been seasonal sampling throughout the year (Kulikov, 1980; Kunisch *et al.*, 2020).

#### ***Gammarus wilkitzkii***

*G. wilkitzkii* is the largest and most conspicuous species of sea-ice amphipods (Figure 5.9). It grows to a maximum size of about 6 cm for males and 5 cm for females (Poltermann *et al.*, 2000). Individuals reach maturity mostly at 2 years of age and may live 5–6 years (Poltermann, 2000; Poltermann *et al.*, 2000; Beuchel and Lønne, 2002). Females may reproduce repeatedly over 2–3

years. Eggs are fairly large (0.6–0.8 mm in diameter) and relatively few in number (average of about 130 per female, Poltermann *et al.*, 2000). Compared to other gammarid amphipods, fecundity is on the high side, and, through repeated spawning over several seasons, a female may produce a total of 300–500 eggs (Poltermann *et al.*, 2000).

*G. wilkitzkii* is a carnivorous-omnivorous species, with a wide spectrum of food sources (Scott *et al.*, 2001; Arndt, 2002; Arndt *et al.*, 2005; Iken *et al.*, 2005; Kohlbach *et al.*, 2016). It has been found to feed effectively on copepods and other zooplankton prey (Poltermann, 2001; Arndt, 2002; Werner *et al.*, 2002). Antennae and mouthparts are equipped with long, dense setae, which suggests that they also feed by filtration (Arndt *et al.*, 2005). *G. wilkitzkii* can feed on microalgae and detritus, which they can also scrape off from the ice surface (Arndt, 2002; Arndt and Swadling, 2006). Juveniles were able to graze ice algae effectively, whereas larger adult individuals had low specific grazing rates on algae (two orders of magnitude lower than juveniles; Werner, 1997a). *G. wilkitzkii* is associated with holes and cracks in the ice, which they use as hiding places to seek refuge when threatened by predators such as juvenile polar cod (or divers; Lønne and Gulliksen, 1991a). Individuals can sit in the openings in the sea ice with their setose antennae and gnathopods extended out of the hole, presumably to feed (Lønne and Gulliksen, 1991a; Arndt and Swadling, 2006).



Figure 5.9. The large sea ice amphipod *Gammarus wilkitzkii* occurring in crevices on the underside of sea ice. Photo by Kevin Raskoff, Monterey Peninsula College.

#### ***Eusirus holmii***

*E. holmii* was originally considered a bathypelagic species (living deeper than 1000 m), but it has been recorded associated with sea ice, with individuals that are distinctly different from the bathypelagic form in eyes and body coloration (the sympagic form is white and transparent, while the bathypelagic form is red; Macnaughton *et al.*, 2007). *E. holmii* was listed as an allochthonous species by Melnikov (1997). In recent investigations, using a special trawl (Surface and Under-Ice Trawl, SUIT) to sample the underside of sea ice along transects up to 5 km long, the species was found to be a regular member of the under-ice community (David *et al.*, 2015; Ehrlich *et al.*, 2020). *E. holmii* was recorded as more abundant than *G. wilkitzkii* in the Eurasian Basin, where it was present at two thirds of all stations sampled for under-ice fauna (David *et al.*, 2015). It was also recorded in the under-ice habitat in Nansen Basin north of Svalbard (Ehrlich *et al.*, 2020) and in the Beaufort and Chukchi seas (Flores *et al.*, 2020).



### ***Apherusa glacialis***

*A. glacialis* is a smaller species than *G. wilkitzkii*, growing to a length of about 1.7 cm ([Figure 5.10](#)). It reaches maturity after one year and spawns once during its lifespan of two years (Beuchel and Lønne, 2002). Eggs are small (about 0.2 mm), with an average of about 550 eggs per female (Poltermann *et al.*, 2000). *A. glacialis* is predominantly a herbivorous species, feeding largely on ice algae (Scott *et al.*, 1999; Tamelander *et al.*, 2006; Kohlbach *et al.*, 2016). They are commonly found on the smooth undersurface of the ice where they move around, and along vertical floe edges (Lønne and Gulliksen, 1991a).



Figure 5.10. The sea ice amphipod *Apherusa glacialis*. Photo: Hauke Flores.

### ***Onisimus nanseni* and *O. glacialis***

*O. nanseni* (formerly *Pseudalibrotus nanseni*) reaches a maximum length of about 2.5 cm and has an estimated lifespan of 2.5 years (Arndt and Beuchel, 2006). *O. glacialis* is a smaller species (1.7 cm length), but with an estimated longer lifespan of 3.5 years (Arndt and Beuchel, 2006). The two species differ in their life cycles, with *O. glacialis* apparently maturing one year later, in its second year of life, compared to *O. nanseni* (Arndt and Beuchel, 2006). Both species are considered omnivorous scavengers, feeding on detritus, carcasses, and plant material (Poltermann, 2001; Arndt *et al.*, 2005). Of the two species, *O. nanseni* appears to be more carnivorous, whereas *O. glacialis* is more herbivorous (Arndt *et al.*, 2005, Arndt and Swadling, 2006).

### **Other sea-ice amphipods**

In addition to the five, most common, amphipods described above, Melnikov (1997) listed three more autochthonous species that were found under the pack ice from Russian ice-drift stations. They were *Gammaracanthus loricatus*, *Metopa wiesei*, and a *Neopleustes* species. Of these three, *G. loricatus* is a large species (closely related to the freshwater species *Gammaracanthus lacustris*), and has been found occasionally in sea ice around Svalbard (Lønne and Gulliksen, 1991b; Hop and Pavlova, 2008). Another species, *Pleusymtes karsteni* was described from ice-drift station T-3 and collected pelagically under the ice (Barnard, 1959). It was also found associated with sea ice north of Svalbard by Macnaughton *et al.* (2007), who suggested that the species could possibly have a more obligate sympagic lifestyle than previously thought.

Several more gammarid amphipod species with benthic connection have been found associated with sea ice: *Gammarus setosus*, *Onisimus littoralis*, *Anonyx nugax*, and *Weyprechtia pinguis*.



Benthosympagic species are most common for ice over shallow shelf waters, and tend to be rare or absent when ice drifts out over the basins (Carey, 1985; Melnikov, 1997).

### 5.3.3 Distribution

Characteristic features of the distribution of ice fauna are (i) large variability with season, ice type, and geographical position; and (ii) a high degree of patchiness in relation to under-ice topography (Arndt and Swadling, 2006). Interstitial meiofauna are found vertically dispersed within the sea ice, but they mostly concentrate in the lower part, with about two thirds of the individuals generally found in the lower 10 cm of ice (Bluhm *et al.*, 2018). Meiofauna show large-scale patterns in composition, with the meroplankton component found mainly in fast ice in shallow waters and decreasing with increasing distance from land (Bluhm *et al.*, 2018). Some of the typical harpacticoid and cyclopoid ice copepods, which are common in coastal sea ice, are rare or not found in drift ice over deeper water in the CAO basins (Arndt and Swadling, 2006).

A similar trend is found with ice amphipods, with benthosympagic species becoming rare or absent in sea ice that drifts out over deep water (Melnikov, 1997; Arndt and Swadling, 2006). Of the two dominant species of ice amphipods in the CAO, *Gammarus wilkitzkii* appears to be associated mostly with multiyear ice, whereas *Apherusa glacialis* may be associated more with first-year ice. *G. wilkitzkii* has been found to be most abundant on ice ridges, whereas *A. glacialis* is most abundant on the flat underside of ice floes and along floe edges (Hop *et al.*, 2000; Hop and Pavlova, 2008). This difference in distribution potentially reflects a difference in feeding ecology. The carnivorous *G. wilkitzkii* may see an enhanced prey field of zooplankton passing by a ridge compared to flat ice (Poltermann, 2001; Hop and Pavlova, 2008). The herbivorous *A. glacialis* may find better feeding conditions on thinner ice, because it allows more algae growth than thicker ridges. Hop and co-workers observed these patterns for pack ice north of Svalbard and in the northern Barents Sea.

A different pattern was found by Gradinger *et al.* (2010) in the southwestern Canada Basin (72–76°N). In this study, *A. glacialis*, which was the numerically dominant species (87% of amphipod abundance), was found in largest numbers on pressure ridges, as was the case with *G. wilkitzkii* and *Onisimus* spp. One reason for the difference could be that the sea ice in this study (conducted in July 2005) was in a state of rapid melt, with low salinity layer under the ice and low algal biomass (Chl *a* < 0.2 mg m<sup>-3</sup> at most stations).

The results of Gradinger *et al.* (2010) illustrate the high degree of patchiness in the distribution of ice amphipods, with highly skewed frequency distributions of abundance (number of individuals m<sup>-2</sup>) and many outliers with high values in the upper end of the distribution (see their Figure 4). For example, *A. glacialis* was observed several times with high abundance values, of 400–800 individuals m<sup>-2</sup>, when compared to the median abundance of about 15 individuals m<sup>-2</sup>. The data of Hop and Pavlova (2008) also illustrates the high sampling variance and patchiness. In their data from 25 flat-ice floes and 18 ridges (sampled at different times during 2003–2005; their Table 3), the sampling variance at each station (n = 3–7) expressed as a coefficient of variation [standard deviation (s. d.)/mean] was 1.0 and 0.9 for flats and 0.9 and 0.7 for ridges for *G. wilkitzkii* and *A. glacialis*, respectively.

### 5.3.4 Recolonization of sea ice and maintenance of populations

Two important issues for ice amphipods in the CAO are how new ice becomes colonized and how the amphipods maintain their populations. When the seasonal ice melts from the surrounding shelves and the basin margins each summer, ice amphipods lose their substrate and must remain in the water column or at the seabed, or die. For allochthonous species, it is assumed that they recolonize ice from the water column or the seabed when new sea ice forms in autumn. For autochthonous species, this is less clear, because they are assumed (by

definition) to remain with the ice all the time. They can spread horizontally to colonize ice floes within the area of ice extent, but they can presumably not swim hundreds of km to stay with the ice as it recedes seasonally into the CAO. So, how do they then maintain their populations?

This question needs to be addressed against the background of large-scale movements of sea ice in the Beaufort Gyre and with the Transpolar Drift out from the CAO through Fram Strait. Melnikov (1997) distinguished five zones with respect to the biogeography and functional structure of the sympagic or cryopelagic biotope. The Beaufort Gyre was considered a basis for the populations, where residence time was long. The Transpolar Drift, in contrast, was regarded as a zone leading into a zone of expatriation, where populations depended on up-stream sources and where expatriation was inevitable once the ice reached the exit through Fram Strait. Between the Beaufort Gyre and the Transpolar Drift, Melnikov recognized a transitional zone where the fate of the ice could vary between joining each of these features. The fifth was a zone of new ice formation in the Laptev Sea area.

Sea ice that exits through Fram Strait and, to a lesser degree, into the northern Barents Sea, has an associated ice fauna. Transport of ice amphipods with the exiting sea ice has been estimated in several studies (Lønne and Gulliksen, 1991c; Arndt and Lønne, 2002; Hop *et al.*, 2006; Hop and Pavlova, 2008). It was originally estimated to be 3.6–3.8 million tonnes wet weight (ww) per year (Arndt and Lønne, 2002; Hop *et al.*, 2006), but it was adjusted down to about 0.5 million tonnes by Hop and Pavlova (2008), mainly because they used lower mean values for biomass of amphipods (1.6 vs. 5–6 g ww m<sup>-2</sup> for multiyear ice). The fate of these amphipods is not clear, but they presumably represent a biomass input to the ecosystem of the Greenland Sea, where most of the sea ice melts (Werner *et al.*, 1999).

The issue or mystery of how ice amphipods colonize new ice and maintain their populations in the CAO made Arndt and Swadling (2006) question the usefulness of the distinction between allochthonous and autochthonous forms. The Beaufort Gyre offers a mechanism for population retention and maintenance, as pointed out by Melnikov (1997). There are also smaller (cyclonic) gyres that circulate off the East Siberian Sea and in the Laptev Sea and may contribute to population maintenance by prolonging the residence time of sea ice (Gordienko, 1958). Another feature is the tendency of ice to move in loops reflecting eddy circulation (Gordienko, 1958; Treshnikov and Baranov, 1972; Melnikov, 1997). This contributes to dispersal and transport of ice amphipods (and other ice biota) in the opposite direction to net transport, prolonging the mean residence time of sea ice.

Melnikov (1989) suggested another retention mechanism involving seasonal vertical migration between two layers with opposing flow directions: (i) the outflowing top layer with sea ice, and (ii) the deeper inflowing Atlantic layer. He suggested this for two amphipod species *Apherusa glacialis* and *Onisimus nansenii*, which he then characterized as allochthonous. By leaving the sea ice and swimming down into the Atlantic water layer, the amphipods would be transported back into the Arctic Ocean (Figure 5.11). Laybourn-Parry *et al.* (2012) noted a seasonal pattern with a high abundance of *A. glacialis* and *Onisimus* sp. under sea ice in summer, and a low abundance or absence in autumn, which suggested that the amphipods could have left the ice for the water column in late summer or early autumn. This seasonal pattern of low abundance in autumn has also been observed for sea ice in Fram Strait and the Greenland Sea for *A. glacialis* and *Onisimus* spp., but not *Gammarus wilkitzkii* (Werner and Gradinger, 2002; Werner and Auel, 2005; Werner, 2006). The lack of amphipods in autumn was interpreted in two alternative ways: (i) the amphipods left the sea ice to spend time in the water, and are thus not true autochthonous species; or (ii) they left the older ice to recolonize new ice which was forming in late autumn (and was not sampled in the studies).

Amphipods leaving the ice and swimming down into the inflowing Atlantic water layer was also presented as a retention mechanism by Berge *et al.* (2012). This was based on winter

observations of *A. glacialis* in the water column at 200–2000 m depth north of Svalbard. Kunisch *et al.* (2020) reviewed literature to show that *A. glacialis* was consistently found in the water column over both shelves and basins of the Arctic Ocean, demonstrating that the species should be regarded as allochthonous rather than being strictly associated with sea ice as an autochthonous species. The abundance values recorded for the water column were of a similar magnitude to values recorded under-ice (both expressed as individuals  $\text{m}^{-2}$ ). This seems to be a case where listing the species as autochthonous (e.g. Melnikov and Kulikov, 1980; Lønne and Gulliksen, 1991a, 1991b, 1991c; Melnikov, 1997), contrary to Melnikov (1989) who listed it as allochthonous, has confused and constrained interpretations and assumptions regarding ice amphipods. Observations suggest that the two *Onisimus* species (*nanseni* and *glacialis*) should possibly also be regarded as allochthonous rather than autochthonous.

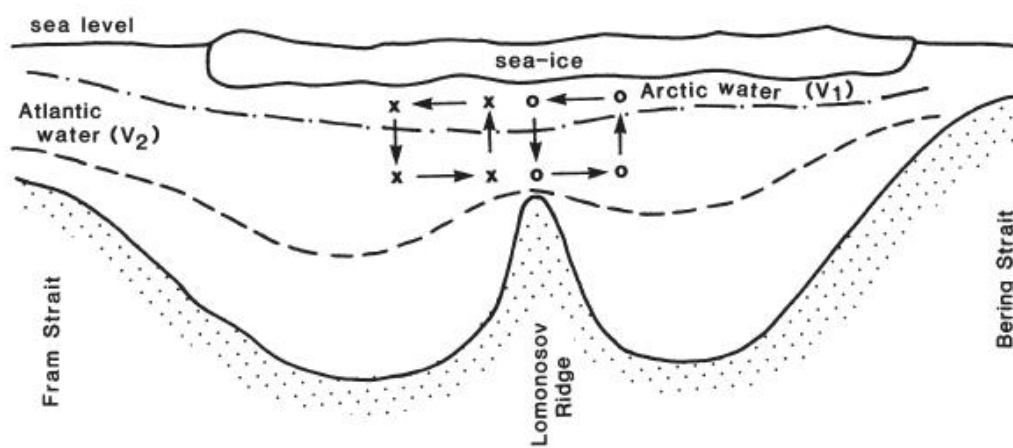


Figure 5.11. A suggested mechanism for population retention of sea-ice amphipods in the CAO. By leaving the sea ice by the end of the productive season, in late summer, and swimming down into the inflowing layer of Atlantic water, the amphipods would be transported back into the CAO, where they later can ascend and recolonize new sea ice. Reproduced with permission from Melnikov (1989).

The species most tightly linked to sea ice seems to be *G. wilkitzkii*. However, this species is also commonly found widespread in the water column in open-water situations, although generally limited to areas that are seasonally ice-covered (Steele and Steele, 1974, 1975). Although *G. wilkitzkii* lives attached to the ice surface most of the time, it is an active swimmer that moves around in the layer just below the ice and makes short excursions to prey on calanoid copepods (Gulliksen and Lønne, 1989; Werner *et al.*, 2002). It is apparently able to feed on copepods and survive in open-water conditions (Scott *et al.*, 2001). Individuals caught in the water column in the Greenland Sea had been eating and were in a good enough energetic state to afford the cost of swimming to maintain their position in the water for some time (Werner *et al.*, 1999). It remains to be clarified, but it is possible that *G. wilkitzkii* should also be regarded as an allochthonous species with a sympagic-pelagic life-history pattern, rather than being strictly autochthonous.

A few decades ago, the export of sea ice was about 1 million  $\text{km}^2$  per year, or roughly 20% of the ice cover in the Arctic Ocean, and was dominated by multiyear ice. This indicates a mean turnover time or residence time of around five years. The situation has now changed to a predominance of first-year ice and a very low fraction (1%) of multiyear ice four years or older. The old multiyear ice, with its extensive deformation and pressure ridges contributing to a complex under-ice topography, has been considered an important habitat for the long-term maintenance of sea ice fauna (Gradinger *et al.*, 2010). With this habitat now substantially reduced, there is more seasonal ice that melts away during summer inside the CAO, and less

ice that is being exported out of the CAO. The annual cycle and population dynamics of sea-ice amphipods (and other sea-ice invertebrates) in relation to the temporal and spatial dynamics of sea ice are important topics that remain to be explored and better understood. The aspect of recolonization of new sea ice is particularly important in order to understand and predict impacts of climate change on the CAO ecosystem.

## 5.4 Abundance and biomass

### 5.4.1 Methodological aspects

The recorded abundance of zooplankton is very sensitive to the mesh size in the nets used for collection. Zooplankton organisms are retained by the net primarily according to their width, and to a lesser degree according to their length. Median retention (50%) occurs when the organism width is about equal to the mesh size. The retention line between no retention (all organisms pass through the mesh) and complete retention is steep (between organism widths of about 0.6- and 1.5-fold the mesh size; Skjoldal *et al.*, 2013). The width of many small copepods, such as older stages of *Oithona* or younger stages of *Pseudocalanus*, is around 0.15–0.2 mm (Skjoldal *et al.*, 2013). Therefore, they will only partially be retained by the commonly used mesh sizes of 150–200  $\mu\text{m}$ . The number of individuals generally increases with decreasing size, whereas smaller zooplankton are less important for biomass (Arashkevich *et al.*, 2002; Hopcroft *et al.*, 2005). Finer-meshed nets catch more small individuals, and give a much higher abundance compared to coarser nets. However, finer-meshed nets do not necessarily give a higher recorded biomass, since they may be less efficient at capturing large individuals, which can be more important for the total biomass than the increased capture of small individuals (Hopcroft *et al.*, 2005; Skjoldal *et al.*, 2013). Hopcroft *et al.* (2005) used the combined taxon-based data from two nets (53 and 236  $\mu\text{m}$ ) to get an improved estimate of the total biomass of zooplankton.

Zooplankton collection in the Arctic Ocean has been done with nets ranging from 50–70  $\mu\text{m}$  (Hopkins, 1969a, 1969b; Hopcroft *et al.*, 2005) to around 600  $\mu\text{m}$  (Johnson, 1963). Most studies have used nets with a mesh size of 150–200  $\mu\text{m}$  (e.g. Thibault *et al.*, 1999; Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Ashjian *et al.*, 2003; Olli *et al.*, 2007; Kosobokova and Hopcroft, 2010), while some studies have used coarser nets with 300- $\mu\text{m}$  mesh (Mumm, 1993; Mumm *et al.*, 1998; David *et al.*, 2015; Ehrlich *et al.*, 2020).

Biomass has been determined by four different methods:

- i) The most common method is to calculate biomass based on counts of species, including stages of copepods and size measurements of individuals in preserved samples (usually formalin-fixed), combined with average weights of species and stages, and taxon-specific length-to-weight relationships (e.g. Kosobokova, 1982; Hirche and Mumm, 1992; Mumm, 1993; Kosobokova *et al.*, 1998; Kosobokova and Hirche 2000, 2009; Hopcroft *et al.*, 2005; Kosobokova and Hopcroft, 2010).
- ii) Biomass is measured directly as a displacement volume and then converted to other units of biomass using empirical relationships (e.g. Ashjian *et al.*, 2003).
- iii) Biomass is measured directly as dry weight on dried samples (e.g. Thibault *et al.*, 1999).
- iv) Individuals in preserved samples are sorted (after counting) into groups that are dried and weighed. The biomass of small copepods is determined based on size-to-weight relationships. This variant of method was used by Hopkins (1969a, 1969b).

Biomass has most commonly been expressed as dry weight (or more correctly dry mass; Postel *et al.*, 2000). Ash-free dry weight has been used in some studies (Hirche and Mumm, 1992; Mumm, 1993; Hopcroft *et al.*, 2005; for copepod-dominated zooplankton, the ash content is typically around 15%, making ash-free dry weight about 15% lower than dry weight; Postel *et al.*, 2000). Biomass estimated as wet weight has been converted to dry weight using a factor of 0.16, empirically determined for Arctic zooplankton (Kosobokova and Hirche, 2000, 2009). Displacement volume has been converted to units of dry weight or C through empirical relationships (Wiebe *et al.*, 1975; Wiebe, 1988; Postel *et al.*, 2000). Zooplankton loses weight during fixation (due to leakage of organic substances), and this loss has, in some cases, been compensated for by applying correction factors (Hirche and Mumm, 1992; Mumm, 1993; Mumm *et al.*, 1998; 37% weight was added to copepod biomass based on Giguère *et al.*, 1989).

Kosobokova *et al.* (1998) compared direct measurements of dry weight (for samples obtained with a Bongo net, mesh size of 200  $\mu\text{m}$ ) with calculated estimates based on counts and individual weights (for samples obtained with Multinet, mesh size of 150  $\mu\text{m}$ ) at 17 stations in the Laptev Sea. The two methods differed by factors of 0.63–2.40 (calculated/measured biomass) at single stations, but the differences were not statistically significant (Kosobokova *et al.*, 1998). Ashjian *et al.* (2003) measured the biomass of zooplankton as displacement volume converted to units of C, and they also calculated the biomass of dominant copepods by counts and mean weights. The two different methods gave broadly comparable results, with biomass values around 1 g C  $\text{m}^{-2}$  during winter and around 3 g C  $\text{m}^{-2}$  during summer (compare their Figures 4 and 9). However, there were also some discrepancies, e.g. a pronounced peak in calculated biomass of nearly 5 g C  $\text{m}^{-2}$  in January that was not reflected in the measured biomass. One reason for such discrepancies can be that the individual weights of copepodite stages can vary quite a lot, by factors of up to five (Ashjian *et al.*, 2003).

## 5.4.2 Zooplankton

### 5.4.2.1 Vertical distribution

Some data on the abundance and biomass of dominant copepods have been summarized in [Section 5.2](#). Overall, the total amount of zooplankton (both as numbers and biomass) decreases more or less exponentially with increasing depth ([Figure 5.12](#); Kosobokova, 1982, 2012; Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011; Bluhm *et al.*, 2015). Abundance in the upper 50 m (corresponding to the upper polar mixed layer) is typically around a thousand to a few thousand individuals  $\text{m}^{-3}$  (1–5 individuals  $\text{l}^{-1}$ ): 500–3000 individuals  $\text{m}^{-3}$  at the Laptev slope (captured with a mesh size of 150  $\mu\text{m}$ ; Kosobokova *et al.*, 1998); 500–5000 individuals  $\text{m}^{-3}$  across Lomonosov Ridge near the base on the Siberian side (mesh size of 150  $\mu\text{m}$ ; Kosobokova and Hirche, 2000); 150–450 individuals  $\text{m}^{-3}$  in the central Nansen, Amundsen, and Makarov basins (mesh size of 200  $\mu\text{m}$ ; Auel and Hagen, 2002); 500–2000 individuals  $\text{m}^{-3}$  in Canada Basin (mesh size of 150  $\mu\text{m}$ ; Kosobokova and Hopcroft, 2010). The abundance in the halocline gradient layer (50–200 m) decreases by nearly an order of magnitude compared to the top layer in summer to about 100–500 individuals  $\text{m}^{-3}$  across Lomonosov Ridge (Kosobokova and Hirche, 2000) and in Canada Basin (Kosobokova and Hopcroft, 2010; Kosobokova, 2012), and about 50–100 individuals  $\text{m}^{-3}$  in the Nansen, Amundsen, and Makarov basins (mesh size of 200  $\mu\text{m}$ ; Auel and Hagen, 2002). The abundance in the Atlantic layer (200–1000 m) is lower still, at about 20–200 individuals  $\text{m}^{-3}$  across Lomonosov Ridge and in Canada Basin (Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010). In the deep water below 1000 m, abundance continues to decline to a level of around five individuals  $\text{m}^{-3}$  below 2000 m in Canada Basin (Kosobokova and Hopcroft, 2010). There is thus an order of magnitude change between the upper polar mixed layer and the top of the Atlantic layer, another order of magnitude change to the upper part of the deep water,



and nearly three orders of magnitude difference between the top layer and the bottom water (Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2010).

The vertical distribution of biomass reflects the pattern of abundance, with a pronounced decrease with increasing depth. Biomass in the upper 50 m has been found to be typically around 10–50 mg dry weight  $\text{m}^{-3}$  (Kosobokova, 1982; Kosobokova *et al.*, 1998; Thibault *et al.*, 1999; Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Bluhm *et al.*, 2015; Flores *et al.*, 2019). The very top layer, the upper 10 m of lower salinity water under the ice, often has low abundance and biomass of zooplankton (Brodsky and Pavshchikov, 1977; Kosobokova, 1982). However, the ice–water interface layer, where cryopelagic fauna concentrate, is usually not sampled by zooplankton nets. A recent comparison of under-ice fauna and epipelagic zooplankton biomass indicated that the volumetric biomass concentration of under-ice fauna accounted for about 20–60% of the epipelagic (0–200 m) zooplankton biomass in the CAO (Flores *et al.*, 2020).

The maximum biomass is commonly found in the subsurface layer, often in the 25–50-m depth layer, instead of at 0–25 m depth (Kosobokova and Hopcroft, 2010). Biomass in the halocline layer (50–200 m) is typically 2–10 mg dw  $\text{m}^{-3}$  (Kosobokova, 1982; Auel and Hagen, 2002; Kosobokova and Hirche, 2009; Kosobokova and Hopcroft, 2010). Higher values in this layer were recorded by Thibault *et al.* (1999) on the transect across the Arctic Ocean, with a mean value of 25 mg dw  $\text{m}^{-3}$  (range of 10–40 mg dw  $\text{m}^{-3}$ ) for the 100–200 m layer. (These high values are one reason for the high biomass values recorded in this study). In the Atlantic layer (200–1000 m), the biomass is typically 1–5 mg dw  $\text{m}^{-3}$  (Kosobokova and Hirche, 2009; Kosobokova and Hopcroft, 2010; Bluhm *et al.*, 2015). Auel and Hagen (2002) recorded lower values ( $< 1$  mg dw  $\text{m}^{-3}$ ) at several stations in the Nansen, Amundsen, and Makarov basins (using a 300- $\mu\text{m}$  mesh size net), whereas Thibault *et al.* (1999) recorded higher values at the transpolar transect (mean of 9 mg dw  $\text{m}^{-3}$ , and range of 5–17 mg dw  $\text{m}^{-3}$ , for the 200–500 m layer). Biomass in the deep water below 1000 m is typically very low, on the order of 0.1–1 mg dw  $\text{m}^{-3}$  (Kosobokova and Hirche, 2009; Kosobokova and Hopcroft, 2010; Bluhm *et al.*, 2015).

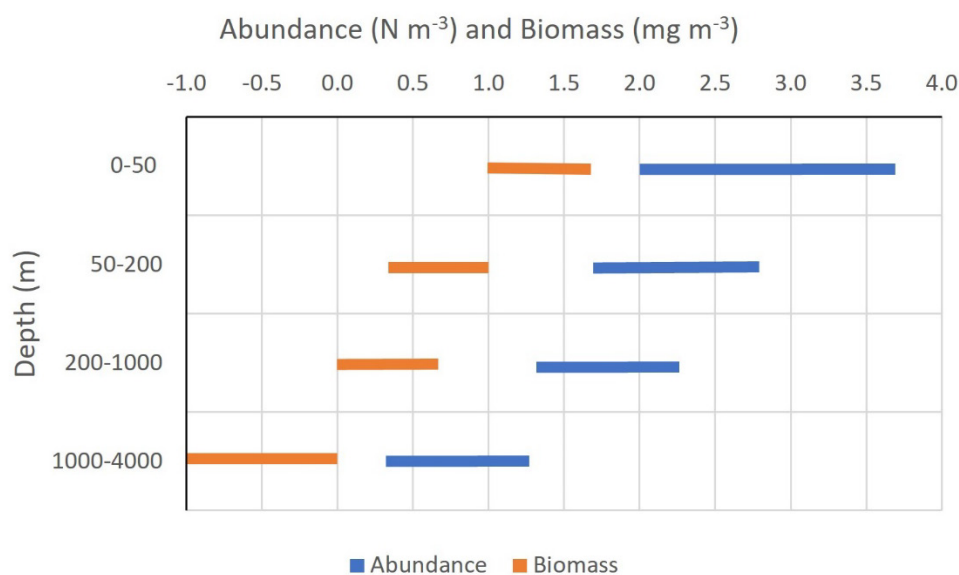


Figure 5.12. Vertical profiles of numerical abundance (number of individuals  $\text{m}^{-3}$ ) and biomass (mg dry weight  $\text{m}^{-3}$ ) in the CAO. Values are given on log-10 scale as typical ranges for the upper polar mixed layer (0–50 m), the halocline layer (50–200 m), the Atlantic water layer (200–1000 m), and deep water (> 1000 m). See the text for more information.

#### 5.4.2.2 Horizontal and geographical distribution

The depth-integrated biomass of zooplankton ranges broadly between 1 and 10 g dw m<sup>-2</sup> over the Arctic Ocean (Kosobokova and Hirche 2000, 2009; Kosobokova, 2012). There is an overall spatial pattern, with high biomass (up to 5–10 g dw m<sup>-2</sup>) in the southern Nansen Basin along the continental rim and continuing into the Laptev Sea region and across the eastern end of Lomonosov Ridge. There is also relatively high biomass in the Chukchi Borderland region in the western Canada Basin (Ershova and Kosobokova, 2019). Biomass is lower by a factor of about three (2–3 g dw m<sup>-2</sup>) in the central parts of the Arctic Ocean, in the Amundsen, Makarov, and northern Canada basins (Kosobokova, 2012). The lowest biomass (around 1 g dw m<sup>-2</sup>) is probably found on the western side of the CAO between Greenland and the North Pole (Figure 5.7, panel D).

In Nansen basin, transects north from the shelf into the basin interior have shown a spatial pattern, with high zooplankton biomass on the outer shelf and along the slope in the region of the inflowing Atlantic water north of the Barents and Kara seas (Mumm, 1993; Mumm *et al.*, 1998; Kosobokova and Hirche, 2009). Kosobokova and Hirche (2009) summarized information from several RV Polarstern cruises which revealed biomass values of typically 5–7 g dw m<sup>-2</sup> along the slope, but with a range of 2–24 g dw m<sup>-2</sup>. The highest value (24 g dw m<sup>-2</sup>, which is comparable to high values in productive ecosystems like the Bering and Norwegian seas) was recorded at the slope of the northeastern Kara Sea (northwest of Severnaya Zemlya) where the Barents and Fram Strait branches of inflowing Atlantic water meet. *Calanus finmarchicus* contributes to the high biomass in the southern Nansen Basin, along with *C. glacialis* and *C. hyperboreus* (Hirche and Mumm, 1992, Hirche and Kosobokova, 2007, Kosobokova and Hirche, 2009). In the western Nansen Basin, there was a sharp drop in biomass north of about 83°N, coinciding with a front between the inflowing fresh and older Atlantic water in the basin (Mumm, 1993).

In the Laptev Sea region, biomass in the slope and adjacent Nansen Basin has been found to be around 4–6 g dw m<sup>-2</sup> (range of 3–8 g dw m<sup>-2</sup>; Kosobokova *et al.*, 1998; Kosobokova and Hirche, 2009). *Calanus glacialis* was the main contributor to the biomass over the outer shelf and slope, while *C. hyperboreus* dominated over the outer slope and basin (Kosobokova and Hirche, 2009). On the shallow Laptev shelf, biomass was fairly low, at or below about 1 g dw m<sup>-2</sup> (Kosobokova *et al.*, 1998). At the transition between the Laptev and East Siberian seas, across the base of Lomonosov Ridge at about 81°N, biomass was also found to be around 4–6 g dw m<sup>-2</sup> in the adjacent Amundsen and Makarov basins, with a peak of 9.5 g dw m<sup>-2</sup> over Lomonosov Ridge (Kosobokova and Hirche, 2000, 2009).

In the western and central Amundsen Basin, including the North Pole region, zooplankton biomass has been found to be about 2 g dw m<sup>-2</sup> (Mumm *et al.*, 1998; Auel and Hagen, 2002; Olli *et al.*, 2007; Kosobokova and Hirche, 2009). Mumm *et al.* (1998) recorded a mean of 1.9 g dw m<sup>-2</sup> (range of 1.3–2.3 g dw m<sup>-2</sup>) in the upper 500 m, Auel and Hagen (2002) found a mean of 2.0 g dw m<sup>-2</sup> in the upper 1500 m (including a station in Makarov Basin), while Olli *et al.* (2007) recorded values of 1.5–2.0 g dw m<sup>-2</sup> in the upper 200 m at six stations at 88–89°N. Similar values about 1.5–2 g dw m<sup>-2</sup> were recorded by Mumm *et al.* (1998) in the upper 500 m in the northern Nansen Basin (mean 1.6 g dw m<sup>-2</sup>), at the central Lomonosov Ridge (mean 1.6 g dw m<sup>-2</sup>), and in the central (northern) Makarov Basin (mean 1.4 g dw m<sup>-2</sup>). Kosobokova and Hirche (2009) calculated a mean of 2.5 g dw m<sup>-2</sup> (s.d. 0.5) over the water column to 3000 m depth for six stations in the Amundsen and Makarov basins north of 85°N.

Zooplankton biomass in Canada Basin has been found to be variable and dependent on location (Kosobokova, 2012). Relatively high values have been recorded in the southwestern area in the region of the Chukchi slope and Chukchi Borderland. Campbell *et al.* (2009) obtained mean values of 4.5 and 3.6 g C m<sup>-2</sup> (corresponding to about 8–9 g dw m<sup>-2</sup>) in summer for the water

column over the slope (200–1000 m depth) and basin (> 1000 m), respectively, in the transition area between the Chukchi and Beaufort seas (71–74°N). In the same general area, but somewhat farther north in the southwestern Canada Basin (72–77°N), Hopcroft *et al.* (2005) recorded a mean biomass of 1.0 g dw m<sup>-2</sup> in the upper 100 m. Sampling deeper over the whole water column, Kosobokova and Hopcroft (2010) obtained a mean biomass of 3.6 g dw m<sup>-2</sup> (range of 3.0–5.3 g dw m<sup>-2</sup>) for stations between 72 and 76°N in the southwestern Canada Basin, with a mean biomass in the upper 100 m of 1.9 g dw m<sup>-2</sup>. Ashjian *et al.* (2003) recorded biomass values of about 3 g dw m<sup>-2</sup> when the SHEBA station drifted over the southwestern Canada Basin (at about 75–76°N) in autumn and winter. Higher values of about 5–9 g dw m<sup>-2</sup> were recorded when the station drifted across Northwind Ridge and Chukchi Plateau through late winter, spring, and summer. The high zooplankton biomass values recorded in the slope region in the southwestern Canada Basin, north of Chukchi Sea, are comparable to the high values observed in the southern Nansen Basin and Laptev region summarized previously.

Zooplankton biomass data from the northern Canada Basin were recorded during the NP-22 ice-drift station in 1975–1976 (82–85°N; Kosobokova, 1982; Kosobokova and Hirche, 2000). Biomass in the upper 1000 m ranged from 1 to 2 g dw m<sup>-2</sup>, with a mean of 1.5 g dw m<sup>-2</sup>, for all stations and covering different seasons. Zooplankton biomass recorded from the NP-23 drift station in Makarov Basin in 1977 (79–83°N) was somewhat higher, with a range of 1–3 g dw m<sup>-2</sup> and a mean of 2.1 g dw m<sup>-2</sup> (Kosobokova, 1982).

Thibault *et al.* (1999) recorded consistently high zooplankton biomass on a transect across the Arctic Ocean, from the Chukchi Sea, via the North Pole, to Fram Strait. The route of the ship went north over Mendeleev Ridge and Makarov Basin to the central Lomonosov Ridge and the North Pole and then further across to the northern Nansen Basin. Biomass in the upper 500 m ranged from 5 to 13 g dw m<sup>-2</sup>, with a mean of 8.7 g dw m<sup>-2</sup>, for 13 stations from the western Canada Basin to the northern Nansen Basin. These values are in the upper range of the high values recorded along the continental rim in the eastern Arctic and in the Chukchi Borderland region, and are considerably higher (by a factor of 3–5) than other biomass values recorded in the northern Makarov, Amundsen, and northern Nansen basins. As noted above, what drives the high biomass values reported by Thibault *et al.* (1999) are high biomass concentrations in the 100–200 m depth layer and, partly, in the 200–500 m layer.

The lowest biomass values recorded are those of Hopkins (1969a, 1969b). He found a mean biomass of 0.3 g dry weight m<sup>-2</sup> for samples obtained from ice-drift station Arlis II in the westernmost Amundsen Basin, north of Greenland and Fram Strait (Hopkins 1969a, 1969b). Samples were collected with a fine-meshed net (73 µm) mainly during winter (March 1964, October 1964–January 1965) to depths of 500–1500 m. Most of the biomass was found in the upper 500 m, or even in the upper 100 m during mid-winter (maximum 1.5–3 mg dw m<sup>-3</sup>; Hopkins 1969a). The biomass values reported by Hopkins (1969a, 1969b) are lower, by almost an order of magnitude, than later measurements in the Amundsen Basin (Mumm *et al.*, 1998; Auel and Hagen, 2002; Olli *et al.*, 2007). Arliss II drifted further west (closer to North Greenland) than most subsequent sampling with icebreakers in the region from the western base of Lomonosov Ridge and across Morris Jesup Plateau [from about 86°N, 50°W in March 1964 to about 83°N, 10°W (just north of Nordaustlandet) in January 1965; Hopkins, 1969a].

It is perhaps significant that some of the lowest recorded biomass values in subsequent studies have been found in the westernmost positions in Amundsen Basin. Mumm *et al.* (1998) recorded a mean biomass of 1.6 g dw m<sup>-2</sup> at Morris Jesup Plateau, while Auel and Hagen (2002) recorded about 1.2 g dw m<sup>-2</sup> in the upper 500 m in the southwestern Amundsen Basin (their station 46). While these values are higher, by a factor of about five, than the low value of 0.3 g dw m<sup>-2</sup> reported by Hopkins (1969a, 1969b), they suggest that there is a very low biomass in waters north of Greenland. Supporting this is the fact that the recorded biomass increased, by over an

order of magnitude to a mean of  $4.5 \text{ g dw m}^{-2}$ , once Arliss II drifted south of Fram Strait with the East Greenland Current from February to April 1965 (Hopkins, 1969a). Two sources of errors that may imply that Hopkins' low value of  $0.3 \text{ g dw m}^{-2}$  is an underestimate, are the fine-meshed net used, assuming 100% filtration efficiency (Hopkins, 1969a), and the weighing of preserved samples (Giguère *et al.*, 1989). Correcting for these factors suggests a true value of around  $0.5 \text{ g dw m}^{-2}$ , or possibly even somewhat higher.

Another dataset recorded from Arliss II in the same period as the samples of Hopkins (1969a, 1969b) was reported by Minoda (1967). This was based on sampling with a larger net (45-cm North Pacific Standard net, with 330- $\mu\text{m}$  mesh size) in the upper 200 m depth layer from June to December 1964. The biomass, recorded as wet weight (after removal of jellyfish, shrimps, and gammarid amphipods), ranged between 0.9 and  $13 \text{ g m}^{-2}$ , with a mean of  $5.8 \text{ g m}^{-2}$  (Minoda, 1967). Using a conversion factor 0.16 (Kosobokova and Hirche, 2000, 2009) gives a mean dry weight of  $0.9 \text{ g m}^{-2}$ , with a range of 0.1– $2.0 \text{ g dw m}^{-2}$ . The biomass of the 200–500 m layer constituted around 20% of the biomass in the upper 500 m in the profiles for the western Amundsen Basin reported by Auel and Hagen (2002), and about 30–40% of the biomass in the profiles reported by Hopkins (1969a, 1969b). Adding 30% for biomass deeper than 200 m would bring the estimate of Minoda (1967) up to about  $1.2 \text{ g dw m}^{-2}$  for the 0–500 m layer, which is comparable to the more recent results of Mumm *et al.* (1998) and Auel and Hagen (2002).

Hopkins (1969b) also reported low biomass values for samples obtained from ice-drift station T-3, drifting in the southern Canada Basin north of Alaska ( $74\text{--}76^\circ\text{N}$ ,  $140\text{--}160^\circ\text{W}$ ) from October 1965 to September 1966. Biomass in the upper 100–200 m was about  $1 \text{ mg dw m}^{-3}$ , similar to the values he obtained at Arliss II (Hopkins, 1969a), but an order of magnitude lower than those found in other studies. Hopkins (1969b) calculated mean values based on the material from T-3 and Arliss II of  $0.62 \text{ mg dw m}^{-3}$  for the upper 200 m,  $0.14 \text{ mg dw m}^{-3}$  for the Atlantic layer (200–900 m), and  $0.04 \text{ mg dw m}^{-3}$  for deep water ( $> 900 \text{ m}$ ). Several of the samples at T-3 were taken with coarser mesh size (215  $\mu\text{m}$ ), with no clear difference from the results obtained with the finer-meshed net (Hopkins, 1969b). The results reported by Hopkins (1969b) stand out as exceptionally low, by about an order of magnitude, when compared to later studies. An open question is whether this represents a temporal change, or whether the very low values of Hopkins are an artefact. Resolving this question may require going back to the original data.

Hopkins (1969b) reported mean abundances of 56, 13, and 3–4 individuals  $\text{m}^{-3}$  for the 0–200 m, 200–900 m, and  $> 900 \text{ m}$  depth layers, respectively. Grainger (1989) noted that these abundances were similar to those reported by Pavshchik (1971) from near the North Pole, with about 200 individuals  $\text{m}^{-3}$  in the upper 200 m, about 15 individuals  $\text{m}^{-3}$  in the Atlantic layer, and usually  $< 2$  individuals  $\text{m}^{-3}$  in the bottom water. Kosobokova and Hopcroft (2010) recorded mean abundances of about 450, 55, and 12 individuals  $\text{m}^{-3}$  for the same depth intervals in Canada Basin. These abundance values are roughly fivefold higher than those recorded by Hopkins (1969b). The mean weight per individual collected (mean biomass/mean abundance) was about  $11 \text{ } \mu\text{g individual}^{-1}$  in the samples of Hopkins (1969b) compared to 20–30  $\mu\text{g individual}^{-1}$  in the samples of Kosobokova and Hopcroft (2010). This may largely be an effect of the finer mesh size used by Hopkins (60–70 vs.  $150 \text{ } \mu\text{m}$ ). Thus, the low biomass values reported by Hopkins (1969b) reflected both smaller numbers and smaller individuals in the samples.

### 5.4.3 Sea ice invertebrates

#### 5.4.3.1 Meiofauna

The interstitial meiofauna are moderately abundant, but their biomass is very low due to their small size. Bluhm *et al.* (2018) summarized information on abundance from available datasets

from the Arctic (23 datasets with a total of 721 ice cores). Mean abundances of the main groups of meiofauna (flatworms, rotifers, nematodes, copepods, and meroplankton) were each 2000–4000 individuals  $\text{m}^{-2}$ . While the maximum recorded abundance for total meiofauna is about 400 000 individuals  $\text{m}^{-2}$  for nearshore fast ice, the abundance in the pack ice of the basins is typically low, at 2000–20 000 individuals  $\text{m}^{-2}$  (Gradinger *et al.*, 2005, 2010; Bluhm *et al.*, 2018).

The biomass of meiofauna copepods and nauplii was summarized by Arndt and Swadling (2006). Typical values for copepodites were 1–2 mg C  $\text{m}^{-2}$  (corresponding to abundance values around 2000–3000 individuals  $\text{m}^{-2}$ ), with maximum values of up to 20 mg C  $\text{m}^{-2}$ . Using a dw-to-C ratio conversion factor of 2, these values correspond to 2–4 mg dw  $\text{m}^{-2}$ . For nauplii, the biomass values were much lower (typically by an order of magnitude or more), around or below 0.1 mg C  $\text{m}^{-2}$  (0.2 mg dw  $\text{m}^{-2}$ ). The biomass values of meiofauna copepodites are three orders of magnitude lower than the typical biomass of mesozooplankton in the CAO (2–5 g dw  $\text{m}^{-2}$ ).

#### 5.4.3.2 Macrofauna – sea ice amphipods

The abundance of sea ice amphipods is typically 5–100 individuals  $\text{m}^{-2}$  (Arndt and Swadling, 2006; Hop and Pavlova, 2008; Bluhm *et al.*, 2017a, 2017b). *Gammarus wilkitzkii* is a large species (up to 5–6 cm in length) and is often dominant in terms of biomass, while the smaller *Apherusa glacialis* (up to 1.5 cm) can be dominant in terms of numbers (Melnikov, 1997; Arndt and Swadling, 2005; Hop and Pavlova, 2008; David *et al.*, 2015; Bluhm *et al.*, 2017b). *Onisimus nanseni* and *O. glacialis* are typically less abundant and make up a small fraction of ice amphipod biomass (Bluhm *et al.*, 2017b). *G. wilkitzkii* was found in relatively high abundance in the northern Barents Sea and the waters north of Svalbard in the 1980s and 1990s, with mean values of 20–90 individuals  $\text{m}^{-2}$  (Lønne and Gulliksen, 1991b; Hop *et al.*, 2000). The corresponding biomass values were 1–6 g ww  $\text{m}^{-2}$ , corresponding to about 0.3–1.8 g dw  $\text{m}^{-2}$  (using a conversion factor of 0.3 for ice amphipods; Hop *et al.*, 2006). These high values were found mostly in multiyear ice in the northernmost part of the Barents Sea (78–81.5°N). Much lower values (by 1–2 orders of magnitude) were found in first-year ice in the Barents Sea by Lønne and Gulliksen (1991a). They explained this as being caused by the distance to the multiyear ice, which was believed to be the source of colonization of new first-year ice. Values of 10–30 individuals  $\text{m}^{-2}$  and 0.2–0.7 g ww  $\text{m}^{-2}$  (0.06–0.2 g dw  $\text{m}^{-2}$ ) were found north of Svalbard in 1998 and 2000 (Beuchel *et al.*, 1998 and Arndt *et al.*, 2000, cited in Arndt and Swadling, 2006).

Hop and Pavlova (2008) reported on an extensive dataset from the northern Barents Sea and the waters north of Svalbard, collected in 2003–2005. Mean values for the ridges and flats of the under-ice topography were 2–144 and 0–36 individuals  $\text{m}^{-2}$ , respectively. Biomass values were 0.03–6.3 g ww  $\text{m}^{-2}$  for ridges and 0.01–0.9 g ww  $\text{m}^{-2}$  for flats. Mean values over all stations were 4 and 29 individuals  $\text{m}^{-2}$  and 0.15 and 1.6 g ww  $\text{m}^{-2}$  (0.05 and 0.5 g dw  $\text{m}^{-2}$ ) for flats and ridges, respectively. Weighted average values (with 40/60 division between multiyear ice and first-year ice, representing ridges and flats; Hop and Pavlova, 2008) were 14 individuals  $\text{m}^{-2}$  and 0.7 g ww  $\text{m}^{-2}$  (0.2 g dw  $\text{m}^{-2}$ ). For waters around Svalbard, there appears to have been a substantial decline in the numbers and biomass of *G. wilkitzkii* since the 1980s (Barber *et al.*, 2015; Bluhm *et al.*, 2017b). The abundance of *G. wilkitzkii* was found to be very low in the Eurasian Basin in recent studies, probably due to the almost complete loss of multiyear ice in this region (David *et al.*, 2015; Ehrlich *et al.*, 2020).

*A. glacialis* was found in abundances (5 to >100 individuals  $\text{m}^{-2}$ ) comparable to those of *G. wilkitzkii* in multiyear ice in the northern Barents Sea and north of Svalbard in the studies of Lønne and Gulliksen (1991a) and Hop *et al.* (2000). However, biomass values were lower (<0.1–0.9 g ww  $\text{m}^{-2}$ ), due to the smaller size of *A. glacialis*. Hop and Pavlova (2008) found a higher abundance of *A. glacialis* on flats (0.2–75 individuals  $\text{m}^{-2}$ ) than on ridges (0.3–27 individuals  $\text{m}^{-2}$ ), which is opposite to the pattern found for *G. wilkitzkii*. Mean values



were 14 and 7 individuals  $\text{m}^{-2}$  for flats and ridges, respectively, with a weighted mean of 11 individuals  $\text{m}^{-2}$  for both types of ice habitats. Corresponding mean values for biomass were 0.11 and 0.08 g ww  $\text{m}^{-2}$  for flats and ridges, respectively, and 0.10 g ww  $\text{m}^{-2}$  for both combined.

In studies in the northern Barents Sea and north of Svalbard, the abundance of the *Onisimus* species has been much lower and more variable than for *A. glacialis* and *G. wilkitzkii*. Typical values were around 1 individual  $\text{m}^{-2}$ , with biomass values around 0.1 g ww  $\text{m}^{-2}$  (Hop *et al.*, 2000; Arndt and Swadling, 2006). Hop and Pavlova (2008) found overall mean values of 1.2 and 0.5 individuals  $\text{m}^{-2}$  for *O. nansenii* and *O. glacialis*, respectively, with *O. nansenii* more abundant on ridges (2.2 vs. 0.1 individuals  $\text{m}^{-2}$ ) and *O. glacialis* more abundant on flats (0.8 vs. 0.1 individuals  $\text{m}^{-2}$ ). The mean biomass was 0.06 and 0.01 g ww  $\text{m}^{-2}$  for *O. nansenii* and *O. glacialis*, respectively.

*A. glacialis* was recorded as the dominant ice amphipod in the southwestern Canada Basin, where it made up 87% of the total number of individuals, followed by *Onisimus* spp. (7%) and *G. wilkitzkii* (6%) (Gradinger *et al.*, 2010). The median abundance of *A. glacialis* varied from < 1 to 106 individuals  $\text{m}^{-2}$  for different locations, with the highest abundance in ridges (median values up to 172 individuals  $\text{m}^{-2}$ ). The median abundance at different locations was up to 8 individuals  $\text{m}^{-2}$  for *G. wilkitzkii* and up to 10 individuals  $\text{m}^{-2}$  for *Onisimus* spp. Some individual sample values had much higher abundance, with up to 760 individuals  $\text{m}^{-2}$  for *A. glacialis*, 448 individuals  $\text{m}^{-2}$  for *Onisimus* spp., and 96 individuals  $\text{m}^{-2}$  for *G. wilkitzkii*. These occasional high values reflected the highly patchy distribution of the sea ice amphipods. One consequence of the highly skewed frequency distribution, with a tail-end of high values, is that the median is much lower than the mean. In the dataset reported by Hop and Pavlova (2008, their Table 3), the mean abundance was about threefold higher than the median for *A. glacialis* and *G. wilkitzkii*.

The total abundance of ice amphipods (all species combined) is driven by the two most abundant species, *A. glacialis* and *G. wilkitzkii*. Hop *et al.* (2001) found mean values of 16–110 individuals  $\text{m}^{-2}$  for different ice structures in the northern Barents Sea, with the highest values for ridges. Corresponding biomass values were 0.3–4.2 g ww  $\text{m}^{-2}$  (or 0.1–1.4 g dw  $\text{m}^{-2}$ ). Hop and Pavlova (2008) found mean values of 20 and 42 individuals  $\text{m}^{-2}$  for flats and ridges, with an overall mean of 28 individuals  $\text{m}^{-2}$ . The biomass values were 0.3 and 1.8 g ww  $\text{m}^{-2}$  for flats and ridges, with an overall mean of 0.9 g ww  $\text{m}^{-2}$ . In units of dry weight, these biomass values would be 0.1 (flats), 0.6 (ridges), and 0.3 g dw  $\text{m}^{-2}$  (combined).

The abundance and biomass of ice amphipods at Franz Josef Land in 1981–1982 were found to be 16–32 individuals  $\text{m}^{-2}$  and 0.5–2.1 g ww  $\text{m}^{-2}$  for first-year ice and 48–490 individuals  $\text{m}^{-2}$  and 2.5–4.5 g ww  $\text{m}^{-2}$  for multiyear ice [ranges of mean values for different sampling periods (one high value for multiyear ice of 21.1 g ww  $\text{m}^{-2}$  for a number of 81 individuals  $\text{m}^{-2}$  is unrealistically high); Averintzev, 1993 (values summarized by Arndt and Lønne, 2002 and Arndt and Swadling, 2006)]. Poltermann (1998) reported high mean values of 420 individuals  $\text{m}^{-2}$  and 10.6 g ww  $\text{m}^{-2}$  for ice amphipods at a nearshore location at Franz Josef Land in summer 1994. The high values were driven by *G. wilkitzkii*, which made up 88% of the numbers and 93% of the biomass. Poltermann explained that the high occurrence of this species was caused by the influx of multiyear ice through tidal currents combined with a benthic lifestyle during part of the year (Weslawski, 1994).

Werner (1997b) found a high biomass of ice amphipods in a multiyear ice pack in the Greenland Sea, with a mean of 14.7 g ww  $\text{m}^{-2}$  for a mean abundance of 171 individuals  $\text{m}^{-2}$ . The biomass was dominated by *G. wilkitzkii*, while *A. glacialis* dominated in terms of numbers (100 individuals  $\text{m}^{-2}$ ). In first-year ice in the Laptev Sea, she found lower mean values, 17 individuals  $\text{m}^{-2}$  and 2.6 g ww  $\text{m}^{-2}$ . Arndt and Lønne (2002) cite a value of 12 individuals  $\text{m}^{-2}$  for *G. wilkitzkii*, found by Melnikov (1997), for ice-drift stations in the CAO. If we assume that they were a mixture of 2–4 year-old individuals with mean length of 3 cm and mean weight of

0.15 g (Kulikov, 1980; Poltermann, 2000), the corresponding biomass would be about 2 g ww m<sup>-2</sup>. This is probably an overestimate since the average individual weight in the studies summarized by Arndt and Swadling (2006) is generally much lower than 0.15 g. Mean values of biomass and abundance found by Hop and Pavlova (2008) for *G. wilkitzkii* give a mean of 0.04 g per individual (which would give a biomass of 0.5 g ww m<sup>-2</sup>).

We note that most of the reported ice amphipod abundances were derived from selectively chosen dive transects over short distances (several to hundreds of meters). Abundances derived with a Surface and Under-Ice Trawl (Figure 5.13) that operates at a larger scale (kilometers of under-ice habitat) are often much lower (e.g. *A. glacialis*, 0.003–2 individuals m<sup>-2</sup>; David *et al.*, 2015; Ehrlich *et al.*, 2020). This may, in part, reflect a lower catch efficiency by the trawl for amphipods that live on the ice surface and can seek cover in holes and cracks.

To summarize, the biomass of ice amphipods is typically 0.5–2 g ww m<sup>-2</sup> on average. Some higher values have been recorded in some ice types, with high-end values of up to 10–15 g ww m<sup>-2</sup> (e.g. Werner, 1997b; Poltermann, 1998). Due to patchy distribution, individual samples may show even higher values in the high end of the statistical range. There is a scarcity of quantitative studies in the pack ice in the CAO, but available information suggests that the range of 0.5–2 g ww m<sup>-2</sup> may also be representative for this area. Data from north of Svalbard suggest that there has been a decline in sea ice amphipods over the last two decades (Barber *et al.*, 2015; Bluhm *et al.*, 2017b). There are also indications from Canada Basin and the central part of the CAO that ice amphipods have become less abundant (Melnikov *et al.*, 2002; Melnikov, 2009; Melnikov and Semenova, 2013).

The range of 0.5–2 g ww m<sup>-2</sup> is equivalent to 0.15–0.6 g dw m<sup>-2</sup> (using a conversion factor of 0.3; Hop and Pavlova, 2008). This is an order of magnitude lower than the biomass of zooplankton, which is typically 2–5 g dw m<sup>-2</sup> in the CAO (Section 5.4.2).



Figure 5.13. Operation of the Surface and Under-Ice Trawl (SUIT) used to collect ice amphipods, polar cod, and other ice fauna from the underside of sea ice. Photo: Benjamin Lange.

## 5.5 Trophic links and interactions

The zooplankton and invertebrate sea ice fauna considered in this section are the intermediate steps in the foodweb of the CAO, linking primary producers with higher-trophic-level consumers in the ecosystem. Phytoplankton and ice algae are the primary producers in the CAO. Among the zooplankton and ice biota are herbivores, omnivores, and carnivores that, in turn, constitute the food for fish, birds, and marine mammals that utilize the production in the CAO.

We have seen in Section 4 that the overall PP is low in the CAO, in the order of  $10 \text{ g C m}^{-2} \text{ year}^{-1}$ . The relative roles of phytoplankton and ice algae are unclear, although most of the PP is by phytoplankton. Annual PP is relatively high in the peripheral parts of the CAO that open up through ice melt each season ( $20\text{--}30 \text{ g C m}^{-2}$ ), whereas it is low in the central part of the CAO with permanent ice cover ( $< 5 \text{ g C m}^{-2}$ ). In this latter area, PP by ice algae may be of the same magnitude as that of phytoplankton, whereas the higher production in the peripheral areas is driven mainly by increased phytoplankton production. Characteristic features of the primary producers are that a considerable fraction of the PP, perhaps about  $1/3$  (Gosselin *et al.*, 1997), is released as DOM, and that small algal cells, in the picoplankton size class, constitute a relatively large part of the algal community (Lovejoy *et al.*, 2007; Metfies *et al.*, 2016). A consequence of these features is that the microbial loop comes into play, lowering the overall transfer efficiency from primary producers to higher trophic levels, due to the intermediary steps involving bacteria, heterotrophic flagellates, and protozoans. However, the ability to switch to a heterotrophic mode of the foodweb may enhance the resilience of the high-Arctic ecosystem during periods of low PP due to nutrient limitation (Flores *et al.*, 2019).

Diversity and flexibility are characteristic features of the feeding ecology for both zooplankton and invertebrate ice biota. The dominant large calanoid copepods, notably *Calanus hyperboreus*, *C. glacialis*, and *C. finmarchicus*, are non-selective filter-feeders considered to be mainly herbivores. They depend primarily on phytoplankton during the short summer season for their growth and development, although *C. glacialis* and *C. hyperboreus* can also use ice algae (Søreide *et al.*, 2010; Daase *et al.*, 2013; Kohlbach *et al.*, 2016). The short productive period and low temperature (close to freezing) are the main limiting factors for the *Calanus* species in the CAO (Ji *et al.*, 2012).

While they are predominantly herbivores, the *Calanus* species, with their filter feeding foraging mode, will also collect and eat heterotrophic nano- and microplankton. As such, they should more appropriately be considered omnivores. One important aspect is that their filters (made up of bristles on their feeding appendages) are relatively coarse, and *Calanus* species generally do not retain algae smaller than about  $5 \mu\text{m}$  in size (Frost, 1972; Harris, 1996). Therefore, they do not feed effectively on picoplankton and the smallest nanoplankton, including the heterotrophic components, among the smallest organisms in the CAO. *Calanus* species can feed on larger heterotrophic plankton such as copepod eggs and nauplii, including those of their own species (Bonnet *et al.*, 2004). The fourth large copepod in the CAO, *Metridia longa*, is also a filter-feeder, but it is regarded as more omnivorous when compared to the *Calanus* species (Haq, 1967; Hopkins *et al.*, 1985). Small copepods such as the numerically dominant *Oithona similis*, are considered generalist omnivores, eating a variety of food including algae, small zooplankton prey, and detritus (Paffenhöfer, 1993). The pteropod *Limacina helicina* is a filter-feeder and mainly a herbivore, whereas the larvaceans (*Oikopleura vanhoeffeni* and *Fritillaria borealis*) feed on the low end of the prey size spectrum with a very fine-meshed filter that collects even bacteria.

Among the zooplankton, there are important carnivorous species. The chaetognaths (*Eukrohnia hamata* and *Parasagitta elegans*) are specialized predators on copepods, which they select by size

(Feigenbaum and Maris, 1984). The large pteropod *Clione limacina* is a specialized predator on *Limacina* species (Conover and Lalli, 1972; Böer *et al.*, 2005). Various species of medusae and siphonophores live in the deeper layers of the CAO, where they feed as predators on other zooplankton (Purcell *et al.*, 2010; Raskoff *et al.*, 2010). Ctenophores are predators on copepods and other zooplankton prey, and they are found both in the epipelagic layer and deeper down in the basins. Experimental work and diet analysis in Canada Basin suggest that ctenophores in under-ice habitats can consume substantial amounts of large lipid-rich copepod prey in a short amount of time (Purcell *et al.*, 2010).

The pelagic hyperiid amphipod *Themisto libellula* is mainly a carnivorous species feeding on the large *Calanus* copepods and other prey (Wing, 1976; Scott *et al.*, 1999; Auel and Hagen, 2002; Dalpadado *et al.*, 2008). They can also feed on ice amphipods, as observed by Lønne and Gulliksen (1991a). In addition to animal prey, *T. libellula* also feeds on detritus and ice algae, as shown by stomach contents and lipid composition (Dunbar, 1946; Bradstreet and Cross, 1982; Scott *et al.*, 1999). Dunbar (1957) considered *T. libellula* to be a key species in Arctic marine ecosystems, comparing its dominant role there to that of lemmings on the Arctic tundra, and to Antarctic krill. While it is difficult to evaluate if this is true, it suggests that *T. libellula* could play a very important role in the CAO. It is part of the under-ice or autochthonous fauna and has been seen to form large unisex swarms (either males or females) on the lee side of ridges or "bummocks" (Melnikov, 1997). Unfortunately, we know very little about the life history and spatial ecology of this species. It has also been seen to form swarms close to the bottom in the Norwegian Sea, at depths of about 1000 m, where individuals were observed to pick up particles from the seabed (Vinogradov, 1999).

The gammarid amphipods that dominate the ice fauna, are generalist feeders with a broad range in their diet, including ice algae, detritus, zooplankton, and other animal prey (Arndt and Swadling, 2006). Of the two dominant species, *Gammarus wilkitzkii* is predominantly a carnivore and *Apherusa glacialis* is predominantly a herbivore (Arndt *et al.*, 2005; Arndt and Swadling, 2006). The next two species in importance are considered detritivores, with *Onisimus nanseni* tending towards being a scavenger, and *O. glacialis* a herbivore (Arndt *et al.*, 2005). Ice algae, and the detritus stemming from their production, are important food for the ice amphipods (Kohlbach *et al.*, 2016). This is especially the case for the young individuals released by females in early spring so that they can utilize the ice algae bloom (Melnikov, 1997; Arndt and Swadling, 2006). Ice amphipods may also feed on plankton and detritus in the water column, as well as on or near the seabed. The larger *G. wilkitzkii* may feed on sub-ice copepods, such as the *Calanus* species, when they are directly under the ice (Hop and Pavlova, 2008).

The biomass of ice amphipods is about an order of magnitude lower than zooplankton biomass when integrated per m<sup>2</sup> (0.15–0.6 vs. 2–5 g dw m<sup>-2</sup>). The biomass of sea ice meiofauna (2–5 × 10<sup>-3</sup> g dw m<sup>-2</sup>) is three orders of magnitude lower than that of zooplankton. Much of the biomass of zooplankton is made up of large copepods (*C. hyperboreus* makes up about 50% in the central part of the CAO) and small copepods. Small copepods may have 1–2 generations per year (Norrbín, 1991), whereas *C. hyperboreus* may take four years to complete its life cycle (Hirche, 1997). Rates of metabolism and production are generally size-dependent, and increase with decreasing body size (Banse and Mosher, 1980). The ratio between annual production and average population biomass (the so-called P/B ratio) is about five for *C. finmarchicus* with an annual life cycle at higher temperatures (5–10°C; Skjoldal *et al.*, 2004). An empirical relationship (Banse and Mosher, 1980) predicts a P/B ratio of about one for the larger *T. libellula* (Skjoldal *et al.*, 2004). Poltermann (1998) estimated a P/B ratio of 0.4 for *G. wilkitzkii* based on data from Franz Josef Land. We can assume that the P/B ratio and biomass turnover is higher for zooplankton because they are generally smaller organisms than ice amphipods. However, Kosobokova (1986) estimated annual P/B ratios of < 1 (0.3–0.9) for *C. hyperboreus* and *C. glacialis* based on samples collected from Russian ice-drift stations in the CAO.

An annual PP of  $10 \text{ g C m}^{-2}$  is equivalent to about  $20 \text{ g dw m}^{-2}$  (considering the C content as 50% of dw). If we assume a growth efficiency of 20% (80% respiration; Skjoldal *et al.*, 2004), this level of PP allows a secondary production by herbivores of  $4 \text{ g dw m}^{-2}$ , which is similar in magnitude to the standing stock biomass of zooplankton ( $2\text{--}5 \text{ g m}^{-2}$ ). Similar values for secondary production have been estimated in field studies (Forest *et al.*, 2011; Flores *et al.*, 2019). However, the calculation builds on assumptions and should be taken only as a rough indication that PP can support the observed level of zooplankton biomass with a P/B ratio of about one. It does not take into account the microbial loop (which burns off much of the production as respiration), nor that many of the zooplankton forms are omnivores and carnivores. With the same assumption of 20% growth efficiency, the tertiary level of production would be  $0.8 \text{ g dw m}^{-2}$  (this is the production by organisms feeding on herbivorous zooplankton, the so-called primary carnivores). This category includes planktivorous fishes.

If scaled up to the CAO area of 3 million  $\text{km}^2$ , a production rate of  $0.8 \text{ g dw m}^{-2}$  is equivalent to  $2.4 \times 10^{12} \text{ g}$ , or 2.4 million t. This estimation is provided as an illustration of the production potential for primary carnivores, including planktivorous fish. However, other organisms need to be recognized among the carnivores, such as the protozoans of the microbial loop, and invertebrate predators such as *T. libellula*, chaetognaths, ctenophores, medusae, and siphonophores. If accounted for, the production potential for planktivorous fish would be considerably lower, probably well below 1 million t.

*C. hyperboreus*, which dominates the zooplankton biomass in the CAO, requires several years to complete its life cycle in the CAO (Dawson, 1978; Rudyakov, 1983). The fact that it persists in relatively large numbers and biomass, despite limited reproduction, suggests that mortality must be relatively low. It is present in the upper water layer during summer, where it grazes on phytoplankton and possibly ice algae, and where it would be seen by visually feeding fish such as polar cod (*Boreogadus saida*; Langbehn and Varpe, 2017). The apparently low mortality of *C. hyperboreus* indicates that predation from visually feeding fish is low in the CAO.

The order of magnitude lower biomass of sea ice amphipods, compared to zooplankton, shows that they have an overall much lower role for the energy flow in the CAO ecosystem. However, this could be deceptive when considering their roles in the ecosystem. We know they are important prey for seabirds, such as the little auk (*Alle alle*) and thick-billed murre (*Uria lomvia*) in ice-covered waters (Lønne and Gabrielsen, 1992), for polar cod (Kohlbach *et al.*, 2017), and for ringed seal (*Pusa hispida*; Labansen *et al.*, 2007). Kohlbach *et al.* (2017) estimated that the observed densities of ice amphipods and *Calanus* spp. in the ice–water interface layer in the CAO could provide sufficient food for polar cod residing under ice in the same area. The role of the sea ice amphipods as prey is partly because they occur concentrated in a layer on the underside of the ice. With their demography of a long lifespan and a relatively low fecundity, they are vulnerable to predation, and antipredation adaptations are no doubt important aspects of their biology. This includes camouflage coloration. For example, Lønne and Gulliksen (1991a) noted that *Onisimus* spp., found along with floating algal clumps in small holes on the ice undersurface, attained the same colour as the algae. The largest species, *G. wilkitzkii*, seeks refuge inside holes and cracks where they can attach themselves using spiny appendages on the legs (Lønne and Gulliksen, 1991a). In multiyear ice north of Svalbard, juvenile polar cod living on the underside of the ice were feeding on *Apherusa glacialis*, *Onisimus* spp., and *Themisto libellula*, but they took few and only small *G. wilkitzkii*, despite this species being dominant in terms of biomass (Lønne and Gulliksen, 1989, 1991b). This was thought to be due to its "spiny morphology" and large size (Lønne and Gulliksen, 1991b).

The fact that many amphipods appear to leave the sea ice in late summer, in addition to the spatial aspect of retention by moving down into the Atlantic layer (Kunisch *et al.*, 2020), may also be beneficial in terms of predator avoidance. Ice algae, as food, is present mainly in the first



part of the summer before it is washed off due to ice melt (Gradinger *et al.*, 2010). Seasonal bird and mammal visitors move into the ice of the CAO primarily in late summer, when the ice has opened up due to the melt. Leaving the ice at this time may be advantageous from a nutritional point of view since the amphipods may feed as predators on zooplankton or as detritivores in the deeper Atlantic water layer.

The ice meiofauna are a unique biodiversity feature of the Arctic sea ice, but they appear to play a small role in the overall functioning of the ecosystem. Their biomass is lower by two orders of magnitude when compared to ice amphipods, and by three orders when compared to zooplankton. While solely considering biomass may not properly reflect their roles in production and energy flow (due to their smaller size), they are still likely to channel only a small fraction of PP in the ecosystem of ice-covered waters. Ice meiofauna are diverse in their feeding biology, and can eat bacteria and detritus (and use DOM) in addition to ice algae (Bluhm *et al.*, 2018). They graze on ice algae in the interior ice matrix, but their grazing impact appears to be limited (< 10% of ice algal biomass; Gradinger *et al.*, 1999; Michel *et al.*, 2002), which may be related to limited access in the narrow brine channels (Krembs *et al.*, 2000; Bluhm *et al.*, 2018).

Ice algae growing on the underside of sea ice or along floe edges, in the form of mats, tufts, clumps, or filaments, is a layer of concentrated food. The colonial forms, such as *Melosira arctica*, can be attached together by excreted mucous material (Poulin *et al.*, 2014). Similar to the colonial prymnesiophyte *Phaeocystis pouchetti* (Verity *et al.*, 2007), one would assume that the colonial ice algae have evolved mechanisms that would protect the extracellular mucus against bacterial degradation or deter grazing. The very fact that the long strands of *M. arctica* can develop in the presence of ice amphipods eager to eat ice algae is indirect evidence of an antigrazing mechanism. However, this is an issue which requires more research. Large aggregates of *M. arctica* have been found to sink to the seabed in the Eurasian Basin, where they represent a considerable organic input to the deep-sea benthos (Boetius *et al.*, 2013). This suggests that a considerable part of the ice algal production bypasses use by ice fauna and zooplankton and goes directly to the benthos at depth in the CAO.

## 6 Sympagic and pelagic bacterial communities

*Pauline Snoeijs-Leijonmalm*

### 6.1 Lack of data

A recent survey of the global ocean microbiome excluded only one major oceanic region due to absence of data – the Arctic Ocean (Sunagawa *et al.*, 2015). This illustrates that the Arctic Ocean is very undersampled, particularly the CAO. Although the CAO is less productive than other oligotrophic oceanic regions not covered by ice, it is not a biological desert (Gosselin *et al.*, 1997; Fernández-Méndez *et al.*, 2016). Heterotrophic bacteria and the rest of the microbial loop are active components of the biological communities in the CAO, and bacterial production is high relative to primary production (PP; Wheeler *et al.*, 1996; Rich *et al.*, 1997).

Only six papers have been published (at the time of preparation of this section) with detailed studies of bacterial community structure in the sympagic and pelagic systems of the CAO, targeting the 16S rRNA gene or the metagenome. Three of these studies address sympagic habitats, including melt ponds, melted ice cores, brackish summer brine, and surface seawater under the ice (Bowman *et al.*, 2012; Rapp, 2014; Fernández-Gómez *et al.*, 2019). The other three studies address the pelagic habitat at different depths in the water column (Bano and Hollibaugh, 2002; Galand *et al.*, 2010; Li *et al.*, 2016). Altogether, these six studies include only 18 samples from the sympagic habitat and 27 samples from the pelagic habitat in the 3.3 million km<sup>2</sup> of the CAO. Similar ice and seawater studies carried out in the more nutrient-rich Arctic shelf LMEs, mainly from coastal sites in the Pacific Arctic region and around Svalbard, are about sixfold more numerous (Pedrós-Alió *et al.*, 2015; Deming and Collins, 2017).

### 6.2 Expanding freshwater and brackish-water habitats with climate warming

Today, most of the CAO is still ice-covered in summer, but the entire area is subject to increased melting, and the melt season is being prolonged (Stroeve *et al.*, 2014a, 2014b). Melt ponds on the ice and open-water areas between ice sheets are increasing in abundance and size (Wang *et al.*, 2016), and thick perennial ice is being replaced by annual ice (Maslanik *et al.*, 2011; see [Section 3.4.3](#)). Seasonal differences in sea-ice extent from ice melt in summer, and in the associated habitat of sympagic microbes in the CAO, are becoming more pronounced with global warming (Haine and Martin, 2017). When sea ice melts, the brine volume increases dramatically (Stoecker *et al.*, 2000), pathways open up for brine drainage, the exchange of matter and gases between air, ice cover, and seawater, and brine salinity drops from hypersaline to low-salinity brackish. Especially brackish brine (fed by meltwater inside the ice) is an expanding sympagic habitat for microbes in summer all over the CAO, and the flux of sympagic bacteria and their metabolic products from sea ice to the pelagic zone is enhanced as well. The brine is brackish through the mixing of meltwater with saline winter brine, and/or the diffusion of salts from the underlying seawater through increased porosity (permeability) of the solid ice (Petrich and Eicken, 2017). These processes are expected to reach a maximum if the North Pole area becomes ice-free in summer, as predicted in climate scenarios (Screen and Williamson, 2017).

### 6.3 Global patterns in bacterial community structure also found in the CAO

Known global patterns of pelagic bacterial distributions at the class level are also valid for the CAO, as shown by a meta-analysis performed by Fernández-Gómez *et al.* (2019; [Figure 6.1](#)). Alphaproteobacteria and Gammaproteobacteria are the two dominant bacterial classes in the

pelagic zone (Zinger *et al.*, 2011; Ladau *et al.*, 2013; Sunagawa *et al.*, 2015; Marteinsson *et al.*, 2016). Other abundant classes are Flavobacteriia (phylum Bacteroidetes) in the photic zone and Deltaproteobacteria in deeper waters (Zinger *et al.*, 2011; Ghiglione *et al.*, 2012; Sunagawa *et al.*, 2015). Sea ice habitats are typically dominated by Gammaproteobacteria and Flavobacteriia (Boetius *et al.*, 2015; Bowman, 2015; Pedrós-Alió *et al.*, 2015).

Many psychrophilic bacteria occurring in the Arctic Ocean are > 97% identical with Antarctic ones, and thus display bipolar distributions (Brinkmeyer *et al.*, 2004; Ghiglione *et al.*, 2012; Sul *et al.*, 2013). This is especially true for sympagic bacteria (e.g. *Colwellia*, *Flavobacterium*, *Glaciecola*, *Polaribacter*, *Polaromonas*, *Pseudoalteromonas*, and *Psychromonas*), but can also be seen for some seawater bacteria (e.g. *Sphingomonas*, and *Sulfitobacter*).

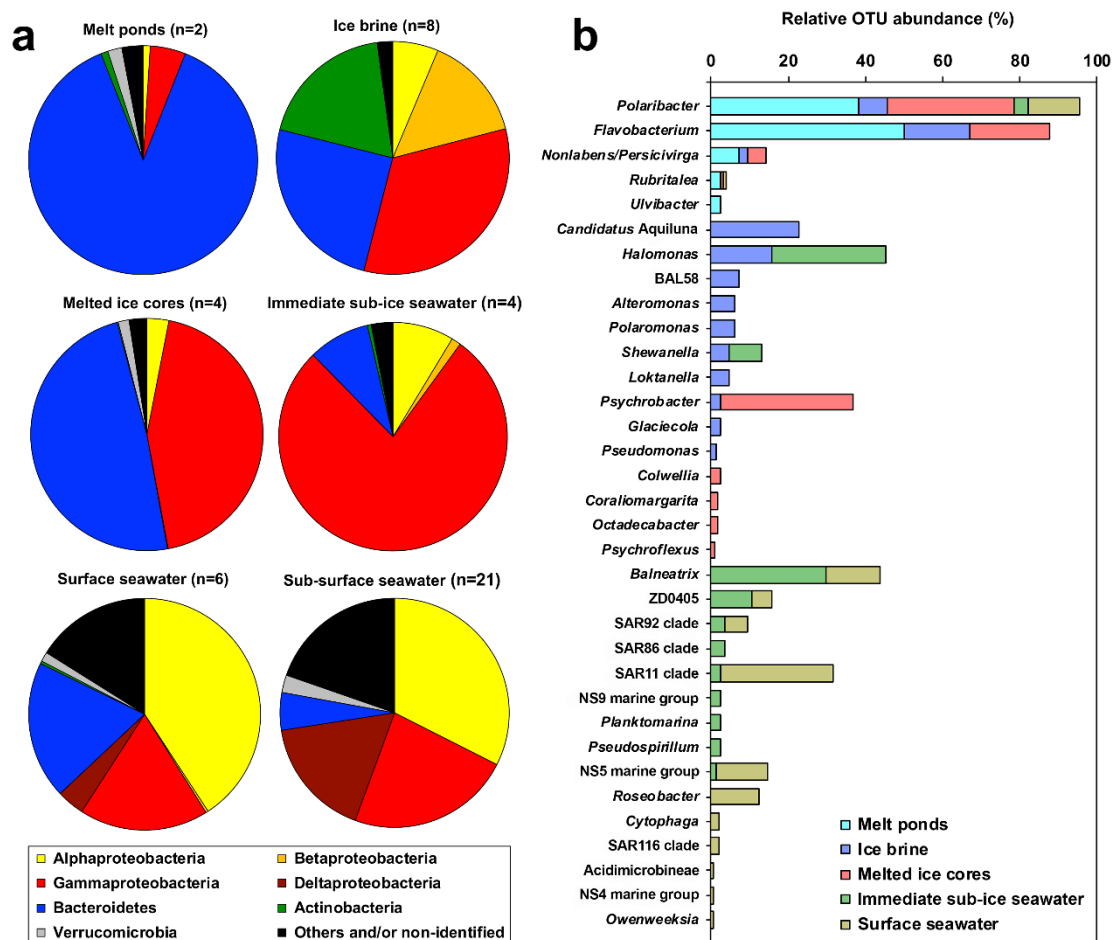


Figure 6.1. Meta-analysis of bacterial community structure in sympagic and pelagic habitats in the Central Arctic Ocean (CAO). (a) Relative abundances of the dominant bacterial classes. The Bacteroidetes consisted mainly of *Flavobacteriia*. (b) Overlap of the dominant bacterial genera/clades. The operational taxonomic units (OTUs) that were identified to the genus level and with relative abundance  $\geq 1.0\%$  were selected, normalized to 100% for each habitat, and plotted together. Figure reproduced with permission from Fernández-Gómez *et al.* (2019).

## 6.4 Different bacterial community structure with ice melt in the CAO

The brackish brine contains a high diversity (OTU richness) and a high abundance of Actinobacteria (19%) and Betaproteobacteria (15%). These two bacterial classes are very rare or absent from melt ponds, ice cores, and seawater (Figure 6.1), and have not been reported as

abundant in the more nutrient-rich Arctic shelf LMEs (Malmström *et al.*, 2007; Deming and Collins, 2017). Thus, Actinobacteria and Betaproteobacteria can be considered indicators of melting sea ice as they are generally more abundant in fresh- than in marine waters (Kirchman *et al.*, 2005; Herlemann *et al.*, 2011), and they have been reported in a few studies from the Arctic marginal ice zone, in melt ponds, the upper ice layer, and surface seawater mixed with meltwater (Brinkmeyer *et al.*, 2004; Larose *et al.*, 2010; Zeng *et al.*, 2013; Hatam *et al.*, 2016).

## 6.5 General pattern of bacterial community structure in the CAO

The general pattern that can be extracted from the few available studies when following the flux of meltwater through the ice down to the immediate sub-ice seawater is typical for the oligotrophic CAO ([Figure 6.1](#)). Dominating classes are Flavobacteriia in melt ponds, Flavobacteriia and Gammaproteobacteria in ice cores, Flavobacteriia, Gamma-, Betaproteo-, and Actinobacteria in brackish ice brine, and Alphaproteobacteria in seawater. Salinity is the principal environmental driver for the microbial community structure in aquatic environments (Herlemann *et al.*, 2011, 2016; Dupont *et al.*, 2014; Lozupone and Knight, 2007). This is also the case in the CAO, but the spatial salinity gradient is never so short and steep as at the ice–seawater interface of a deep ocean basin.

## 6.6 Differences between the CAO and the Arctic shelf seas

In contrast to the CAO, the dominant bacterial classes in sea ice habitats in the Arctic shelf LMEs are highly variable. This variability is probably related to differences in the nutritional status of the parent water, which determines the bacterial community composition in the ice cover when the ice forms (Eronen-Rasimus *et al.*, 2014). For example, Chukchi Sea is one of the most productive seas on earth (Sambrotto *et al.*, 1984), in stark contrast to the strongly oligotrophic CAO (see [Section 4.5.11](#)). Some ice-core studies in the Arctic shelf LMEs report dominance of Gammaproteobacteria (Eronen-Rasimus *et al.*, 2016; Yergeau *et al.*, 2017), while others report dominance of Alphaproteobacteria (Han *et al.*, 2014; Hatam *et al.*, 2014) or more or less equal abundances of Gammaproteobacteria, Alphaproteobacteria, and Flavobacteriia (Hatam *et al.*, 2014, 2016). This variability seems to be independent of the age of the ice (perennial or annual), and related to the proximity of land, which strongly influences trophic state.

## 6.7 Possible functional changes with further climate warming

It is expected that the roles of freshwater and brackish psychrophilic Actinobacteria, Betaproteobacteria, and Flavobacteriia in the upper zone of the CAO ecosystem will increase in concert with global warming. This may have unexpected consequences that range from altered metabolic functions, such as increased photoheterotrophy by *Candidatus Aquiluna* sp. and its relatives (Kang *et al.*, 2012), to increased use of DOM from brine drainage as a substrate by *Polaromonas* sp. and its relatives (Gawor *et al.*, 2016), and to emerging ice-associated fish infections by *Flavobacterium* spp., and *Polaribacter* spp. and their relatives (Loch and Faisal, 2015), e. g. to polar cod (*Boreogadus saida*) (David *et al.*, 2016).

To achieve a better understanding of the consequences of the rapid ecosystem changes in the CAO, future studies should concentrate on identifying the many still unknown metabolic functions of the psychrophilic microbial communities, how they are related to biogeochemical cycles, and how they are affected by the changing environment.

## 7 Arctic benthos

*Jacqueline Grebmeier and Lis Lindahl Jørgensen*

The advective-influenced inflow shelves of the northern Bering and adjoining Chukchi seas in the Amerasian Arctic, and the Barents Sea in the Eurasian Arctic, experience seasonally productive waters. This leads to a high deposition of fresh Chl to the sediments coinciding with the spring bloom, as sea ice retreats. The earlier spring sea ice retreat and later autumn sea ice formation are changing the phenology of primary production (PP), which directly affects benthic community production. Benthic macrofauna (e.g. clams, worms, and amphipods) and more mobile megafaunal invertebrates (e.g. sea stars, and crabs) are tightly linked to regions of high biological productivity (Link *et al.*, 2013; Grebmeier *et al.*, 2015a). Benthic biomass decreases sharply in the deep Arctic Basin where only limited sampling has occurred (Bluhm *et al.*, 2005, 2015). The biodiversity of benthic fauna in these Arctic regions is an important ecosystem service. Thus, understanding the status and change of benthic organisms over continental shelves (Piepenburg *et al.*, 2011), slope regions (Bluhm *et al.*, 2011, 2020; Grebmeier, 2012), and the high Arctic deep basins (Bluhm *et al.*, 2015) are priority areas for evaluating climate change impacts on marine ecosystem function.

### 7.1 Evidence of changes in benthic populations due to changing climate drivers

In the northern Bering and Chukchi seas in the Pacific Arctic, persistent biological hot spots of macroinvertebrates (bivalves, polychaetes, and amphipods) are supported by both *in situ* production and advection of phytodetritus from upstream areas with high PP. These hot spots connect benthic prey to upper trophic benthivores (Grebmeier *et al.*, 2015a, 2018). Between St Lawrence Island and Bering Strait, and northwards into the Chukchi Sea, the persistence of seasonal sea ice has significantly declined over the past decade (Frey *et al.*, 2015, 2019). This phenomenon, along with continuing warming seawater temperatures (Woodgate, 2018), have ramifications for benthic fauna and the overall benthic ecosystem structure. In the Barents Sea in the Atlantic Arctic, benthic composition is being affected by factors directly related to climate change, such as sea ice dynamics, ocean mixing, bottom-water temperature change, ocean acidification, and river/glacier freshwater discharge (Birchenough *et al.*, 2015). In addition, other human-influenced activities, such as commercial bottom trawling and the introduction of non-indigenous species, are regarded as major drivers of observed and expected changes in benthic community structure (Jørgensen *et al.*, 2016, 2017, 2019).

There is evidence of declining benthic biomass in the decadal benthic time-series data in both the northern Bering Sea (Grebmeier, 2012; Grebmeier and Cooper, 2016; Grebmeier *et al.*, 2018) and downstream, through Bering Strait, in the southern Chukchi Sea (Grebmeier *et al.*, 2015b, 2018). In addition, over the last decade, a northward shift in dominant macrofaunal biomass has been observed in the persistent northern Bering Sea hot spot south of St Lawrence Island, related to varying current patterns (Grebmeier and Cooper, 2016; Goethel *et al.*, 2018; Grebmeier *et al.*, 2018). This northward shift in the distributional pattern of benthic species, and the subsequent changes in community composition, have also been recorded in places in the eastern Arctic (e.g. Svalbard Archipelago and Barents Sea; Kortsch *et al.*, 2015; Jørgensen *et al.*, 2017), including for commercial crab species (Fossheim *et al.*, 2015).

There are still uncertainties related to key drivers for Arctic benthic system change. They can vary depending on the location due to shifts in the factors that drive seasonal PP (e.g. sea ice



extent, nutrients, temperature, and pelagic grazing) and the associated export of C to the underlying sediments. Ongoing regional modelling efforts are evaluating key drivers influencing the biological ecosystem response. This developing section will highlight select time-series of benthic data to evaluate benthic response to changing environmental conditions, including the evaluation of uncertainties related to the observed trends over time.

Finally, the Distributed Biological Observatory (DBO), an international network of time-series transects that is developing as a biologically driven observing network, is providing a framework to evaluate the status and trends on a latitudinal basis for the tracking of Subarctic and Arctic benthic species, and their potential expansion northward in the Arctic. The DBO was initially developed in the Pacific Arctic and is recently expanding to the Atlantic Arctic (Moore and Grebmeier, 2018). Subsequent reports will include the status and trends of sentinel benthic faunal community composition and biomass, which are responding to changing climate conditions regionally in the Arctic, both in the Pacific Arctic Gateway and the Atlantic sector.

## 7.2 Ridges and shelves of the CAO

Macrofauna dominates the benthic biomass on the Chukchi and Barents Sea shelves and slope areas and Lomonosov Ridge, but bacterial biomass was equally or relatively even more important on Gakkel Ridge and in the deep basins. Although PP is low, recent foraminiferal investigations have revealed that benthic communities in the CAO are driven by the sedimentation of fresh organic material. Lateral transport of organic material from the Siberian and Chukchi shelves likely provide additional food. The various benthic compartments compete either for fresh organic matter or for refractory material that is transferred to higher levels of the food chain by bacterial mineralization (Kröncke *et al.*, 2000). Up to 42 species of macrofauna were found at water depths of 1018–4478 m along a transect extending between northern Svalbard and Makarov Basin, where species numbers, abundance, and biomass were extremely low. The amphipod *Jassa marmorata* was the most common species. Suspension-feeding species increased towards Lomonosov Ridge, probably due to lateral transport of organic material by deep currents along the ridge (Kröncke, 1994).

Benthic communities are clustered by depth ranges across the slope and basin, with the maximum diversity of macrofauna at the shelf edge at depths of 100–300 m (Grebmeier and Barry, 2007; CAFF, 2017). The limited availability of standardized benthos data makes it difficult to assess if and how the significant sea ice loss observed in the past decade has affected benthic community composition (Vedenin *et al.*, 2018).

At hydrothermal vent systems, chemosynthesis can play a large role in providing nutrients to deep-sea benthic communities (Sweetman *et al.*, 2013). Submarine hydrothermal venting along mid-ocean ridges is an important contributor to ridge thermal structure, and the global distribution of such vents has implications for e.g. the biogeography of vent-endemic organisms. At vent sites on Gakkel ridge, a 1100-km rift valley, abundant macrofauna were observed, but the composition of the chemosynthetic faunal communities is unknown (Edmonds *et al.*, 2003). It is likely that new species of Arctic vent biota will be discovered at hydrothermal sites on Gakkel ridge, which have evolved in isolation from those in other oceans, (Edmonds *et al.*, 2003). These communities remain a knowledge gap for Arctic biodiversity.

## 7.3 Deep basin

Much of the Arctic deep-sea bed has until now experienced only a weak human footprint, but the predicted ice-free summer in the Arctic in the near future may change that situation. Thus, an up-to-date inventory is urgently needed of deep-basin biodiversity (Bluhm *et al.*, 2011, 2020).

The Arctic deep sea is an oligotrophic area with steep gradients in faunal abundance and biomass from the slopes to the basins, primarily driven by food availability, but with an overall density and biomass broadly similar to other deep-sea areas. As in other soft sediment habitats, foraminiferans and nematodes generally dominate the meiofauna; annelids, crustaceans, and bivalves dominate the macrofauna; and echinoderms dominate the megafauna. In total, just over 700 benthic species were catalogued from the central basins a decade ago (Sirenko, 2001; Sirenko *et al.*, 2010).

The benthic biomass in the Amerasian Basin at depths of 1000–2000 m is extremely low ( $0.04 \text{ g m}^{-2}$ ). Benthic foraminiferans account for about 53% of the total biomass, bivalves for 27%, sponges for 7%, and polychaetes for 5%, with other groups making up the remaining 8% (Paul and Menzies, 1974). Paul and Menzies (1974) called the High Arctic biocoenoses a *Thenaea abyssorum* (sponge) and *Spirorbis granulatus* (polychaeta) community. There is growing evidence that increased Pacific water transport into the Arctic affects the marine ecosystem. Higher biomass values for the benthic compartments, as well as higher total organic C, were observed on the upper slopes of the Pacific Arctic (Grebmeier *et al.*, 2006; Grebmeier and Barry, 2007). An increasing current transport northward into the Pacific Arctic region might contribute to the expansion of subarctic taxa into the Arctic, which could have a strong influence in restructuring the benthic ecosystem in this region in future (Waga *et al.*, 2020).

The Eurasian Basin is one of the most oligotrophic regions in the world oceans (Kröncke *et al.*, 2000). This statement was based on findings showing that higher biomass values for the benthic compartments, as well as higher total organic C and total hydrolysable amino acids, were recorded for the Barents Sea slope than for the deeper stations in the basins and ridge slopes. Faunal abundance and bacterial and macrofaunal biomass decreased significantly with increasing latitude, with faunal size classes reflecting a distinct food chain typical of oligotrophic systems.

The standing stocks of meiobenthic organisms were observed to be extremely low in the deep Makarov Basin (3170 m) and on Alpha Ridge (1470 m), while being significantly higher on Lomonosov Ridge (Schewe, 2001). Meiobenthic abundances were up to tenfold lower than those reported from non-ice-covered deep-sea regions. However, a significant decrease in meiobenthic abundance with increasing water depth was still detectable (Schewe, 2001).

## 8 Fish

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### 8.1 Introduction

The CAO is undersampled and understudied when it comes to fish fauna. There are two obvious and related reasons for this. The first is that the extensive sea ice cover is an obstacle for collecting fish using trawls, which is a standard capture method for fish investigations. The other has been a general lack of interest in fish in this area, since the CAO is far north of areas with active fisheries, and, therefore, does not require fish stock investigations to support fisheries management. This is changing with global warming and loss of sea ice, and there is now a growing interest in knowing whether there are fish at fishable concentrations in the CAO (van Pelt *et al.*, 2017).

Fish were observed and collected from under the sea ice from Soviet and US ice-drift stations in the mid-20<sup>th</sup> century (Walters, 1961; Andriyashev *et al.*, 1980). These early studies recorded two small cod species, polar cod (*Boreogadus saida*) and Arctic cod (*Arctogadus glacialis*), as common elements of the sea-ice biota (Melnikov, 1997). Use of icebreakers as research platforms increased in the last decades of the 20<sup>th</sup> century, although investigations of fish were generally not a high priority. The German icebreaker RV Polarstern used a small trawl (Agassiz) to sample fish from stations in the Laptev Sea in 1993 (Chernova and Neyelov, 1995). RV Polarstern has also operated a special trawl to sample the underside of sea ice (David *et al.*, 2016). In the last ten years or so, there have been a growing number of investigations on fish in the two gateway areas: the Chukchi and Beaufort seas on the Pacific side (Mecklenburg and Steinke, 2015), and slope waters north of the Barents Sea on the Atlantic side (Haug *et al.*, 2017).

Modern research icebreakers are equipped with scientific echosounders which can be used to detect fish in the water column below the vessels, as well as demersal fish that swim some distance above the seabed. There is now an increased awareness of the opportunity to use acoustic tools to obtain information on fish in the CAO. An example is acoustic data collected by the Swedish icebreaker RV Oden during an expedition to the North Pole in summer 2016, which are now being prepared for publication (Snoeijs-Leijonmalm, *et al.*, 2021).

An agreement to prevent unregulated fishing in the CAO was reached in 2018 among the five coastal states as well as the European Union (EU) and four distant-water fishing countries. In the process leading up to the agreement, a group of experts compiled and summarized information on the occurrence of fish in the CAO (Anon., 2017; Mundy *et al.*, 2017). As part of the agreement, a programme for a joint scientific research and monitoring plan is being developed (Anon., 2017, 2018).

This Section summarizes information known about fish in the CAO, building on the information collected by the group of experts under the fisheries agreement process. One aspect covered is the number and types of fish species found in the CAO. Species found on adjacent Arctic shelves are included, to permit discrimination between species found only on the shelves and those also found on the slopes of the CAO basins or restricted to the basins. Special emphasis is given to the two small cod species (polar cod and Arctic cod), which are probably the most important components for the energy flow in the foodwebs of the CAO. Two particularly important issues are: (i) to what extent do these two species occur pelagically in the CAO, and (ii) to what extent

do they provide connectivity between the shelf and basin parts of the CAO through drift of larvae and juveniles and active migrations by adult fish.

## 8.2 Taxonomy and biogeography

### 8.2.1 Arctic and Arctic-boreal species

Around 720 species of fish have been recorded in the wider Arctic area, which includes the Bering Sea and the Aleutian Islands on the Pacific side, and the Nordic Seas south to the Faroe Isles on the Northeast Atlantic side (Mecklenburg *et al.*, 2002, 2011, 2018; Møller *et al.*, 2010; Skjoldal, 2022). Most of them are boreal species (371 or 51%), temperate or more southern species (132 or 18%), and widely distributed species (122 or 17%; Skjoldal, 2022). A smaller number of species are biogeographically classified as Arctic (59 species) and Arctic-boreal (40 species). Note that this number of species is approximate due to taxonomic uncertainties and uncertainties in biogeographic classification. The ca. 100 Arctic and Arctic-boreal species account for 14% of the fish in the wider Arctic area. Arctic, in a biogeographical sense, means species able to live in Arctic water at subzero temperatures, which may require special physiological adaptations for species that come in contact with sea ice (e.g. antifreeze agents in body fluids). Arctic-boreal species are distributed across biogeographical regions, with many of them occurring in the northern part of the boreal zone and extending their distribution into the true Arctic region (ice-covered waters).

Arctic and Arctic-boreal fish species are distributed primarily on the shelves and slopes surrounding the Central Arctic Ocean LME. About 100 species of fish have been recorded in the Beaufort Sea LME, while a slightly smaller number (80+) have been recorded in the Chukchi Sea portion of the Northern Bering–Chukchi Sea LME. More than 200 species have been recorded in the Barents Sea LME, with about 100 species considered common (Dolgov *et al.*, 2011; Wienerroither *et al.*, 2011). A larger number of species (269) were listed for Greenland waters, but many of them were deep-water forms in the Labrador and Irminger seas (Møller *et al.*, 2010). The number of Arctic and Arctic-boreal species found on the northern Barents Sea shelf adjacent to the CAO is nearly 60. With recent warming, several boreal species have extended their distribution onto the northern Barents Sea shelf [e.g. Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*)], increasing the total number of species in this region (Fossheim *et al.*, 2015). The number of fish species on the Siberian shelf LMEs (Kara, Laptev, and East Siberian seas) is similar, at about 50–80 species (Dolgov, 2013; Karamushko, 2013; Dolgov *et al.*, 2018). The number of species recorded in the Canadian High Arctic–North Greenland LME is somewhat lower, at about 30.

### 8.2.2 Fish families and species

The majority of the 99 species of fish which are classified as Arctic and Arctic-boreal, 66 species (or 67%), belong to two taxonomic orders: Scorpaeniformes (scorpionfishes and flatheads) and Perciformes (perch-like fishes). Within the Scorpaeniformes, the most species-rich fish families in the Arctic Ocean are sculpins (family Cottidae) and snailfishes (Liparidae). Other families of sculpins [sailfin sculpins (Hemipteridae), fatheads (Psychrolutidae), and poachers (Agonidae)] and lumpsuckers (Cyclopteridae) also contribute to the Arctic fish fauna. Within the Perciformes, eelpouts (Zoarcidae) and pricklybacks (Stichaeidae) are represented by numerous species. Eight of the species classified as Arctic or Arctic-boreal are not found in the CAO or in the Nordic Seas adjacent to the CAO. In contrast, 15 species classified as mainly boreal by Mecklenburg *et al.* (2018) are found in the wider CAO area, including the adjacent Arctic shelves. Removing the eight species not found, and adding the 15 mainly boreal species, brings the total number of fish recorded from the wider CAO to 106 species. These 106 species are

listed in [Table 8.1](#), along with information on biogeographical classification, habitat association, depth range, and maximum size. [Figure 8.1](#) illustrates some of the types of Arctic fish species. In the following paragraphs, an overview is provided of the fish species by families found in the basins and on the adjacent shelves of the CAO.

Eelpouts (Zoarcidae)	The most species-rich family in the Arctic Ocean, with 26 species recorded in the wider CAO (including the adjacent Arctic shelves; <a href="#">Figure 8.2</a> ). Common and widespread species include polar eelpout ( <i>Lycodes polaris</i> ), longear eelpout ( <i>L. seminudus</i> ), glacial eelpout ( <i>L. frigidus</i> ), and shulupaoluk ( <i>L. jugoricus</i> ). Eelpouts are elongated benthic fishes, most of which are relatively small, with lengths of 20–40 cm. The largest species is the greater eelpout ( <i>L. esmarkii</i> ), which can grow to a maximum length of up to 1 m and is found in the Atlantic gateway area. Eelpouts are predominantly found on Arctic slopes, and they range from shallow water species, such as the shulupaoluk, to deep-water species, such as the glacial eelpout.
Sculpins (Cottidae)	The second most species-rich group, with 11 species in the wider CAO. They are small benthic species that, in contrast to the eelpouts, are found mainly on Arctic shelves ( <a href="#">Table 8.1</a> ).
Poachers (Agonidae)	Small benthic fishes with elongated, sculpin-like body shape. Three species are found in the wider CAO, including Arctic alligatorfish ( <i>Aspidophoroides olrikii</i> ) and Atlantic poacher ( <i>Leptagonus decagonus</i> ).
Fathead sculpins (Psychrolutidae)	Small benthic fishes with one species, polar sculpin ( <i>Cottunculus microps</i> ), in the CAO.
Lumpsuckers (Cyclopteridae)	Small benthic fishes with round body shape. Four species are found in the wider CAO ( <a href="#">Figure 8.2</a> ), including leatherfin lumpsucker ( <i>Eumicrotremus derjugini</i> ) and Atlantic spiny lumpsucker ( <i>E. spinosus</i> ).
Snailfishes (Liparidae)	A group of small and mostly benthic species. Eight species are found in the wider CAO ( <a href="#">Figure 8.2</a> ), including black seasnail ( <i>Paraliparis bathybius</i> ) and threadfin seasnail ( <i>Rhodichthys regina</i> ), which are characteristic deep-water species in the CAO basins.
Pricklebacks (Stichaeidae)	Elongated small fishes that occur with six species in the wider CAO, most of them on the shelves ( <a href="#">Figure 8.2</a> ).
Salmonids (Salmonidae)	The family includes 11 species in the Arctic: seven species of coregonid whitefish (sub-family Coregoninae), two species of Pacific salmon [chum ( <i>Oncorhynchus keta</i> ) and pink ( <i>O. gorbuscha</i> )], and two species of chars [Arctic char ( <i>Salvelinus alpinus</i> ) and Dolly Varden ( <i>S. malma</i> )]. The salmonids are anadromous or amphidromous species that feed in coastal and marine waters and migrate into freshwater rivers and lakes to overwinter and/or spawn.
Cod (Gadidae)	Occurs with five Arctic species: polar cod ( <i>Boreogadus saida</i> ), Arctic cod ( <i>Arctogadus glacialis</i> ), saffron cod ( <i>Eleginus gracilis</i> ), navaga ( <i>Eleginus nawaga</i> ), and Pacific cod ( <i>Gadus macrocephalus</i> ). Greenland cod ( <i>Gadus ogac</i> )



is of uncertain taxonomic status and has been classified as a subspecies of Pacific cod (Mecklenburg *et al.*, 2011). The East Siberian cod (*Arctogadus borisovi*) is not considered a valid species, but rather a synonym of Arctic cod (Jordan *et al.*, 2003; Mecklenburg *et al.*, 2011). The first four species spawn under sea ice in winter. We have included walleye pollock (*Gadus chalcogrammus*; originally *Theragra chalcogramma*) as an additional species of cod that is likely to occur in the CAO. Atlantic cod (*Gadus morhua*) was recently recorded pelagically in the Amundsen Basin of the CAO (Snoeijs-Leijonmalm *et al.*, 2022).

Lings and rocklings (Lotidae)	Occurs with one relatively small rockling species, Arctic rockling ( <i>Gaidropsarus argentatus</i> ), classified as arctic-boreal and found in the Atlantic sector of the Arctic. Arctic rockling was video recorded on Lomonosov Ridge by Yngve Kristoffersen (identified by Andrey Dolgov, PINRO) representing the first documented record from the CAO.
Smelts (Osmeridae)	Occurs with four species in the Arctic: Atlantic capelin ( <i>Mallotus villosus</i> ), Pacific capelin ( <i>Mallotus catervarius</i> ), Arctic rainbow smelt ( <i>Osmerus dentex</i> ), and pond smelt ( <i>Hypomesus olidus</i> ). They are found on Subarctic and Arctic shelves. Capelin was recently split into two species: Atlantic capelin ( <i>M. villosus</i> ) and Pacific capelin ( <i>M. catervarius</i> ; Mecklenburg <i>et al.</i> , 2018). The two smelt species are amphidromous and are found in brackish coastal waters in summer.
Myctophids (Myctophidae)	Found with one small mesopelagic species on the Atlantic side: glacial lanternfish ( <i>Benthoosema glaciale</i> ).
Barracudinas (Paralepididae)	Found with one mesopelagic species on the Atlantic side: white barracudina ( <i>Arctozenus risso</i> ).
Wolffishes (Anarhichadidae)	Found with three species in the wider CAO: northern wolffish ( <i>Anarhichas denticulatus</i> ) and spotted wolffish ( <i>A. minor</i> ) in the Atlantic gateway area, and Bering wolffish ( <i>Anarhichas orientalis</i> ) in the Pacific Arctic.
Flatfish or right-eye flounders (Pleuronectidae)	Represented by five Arctic species. Greenland halibut ( <i>Reinhardtius hippoglossoides</i> ) has a circumpolar distribution and is found along slopes and outer shelves in the Arctic Ocean north of the Barents and Kara shelves and in the eastern Beaufort Sea. Arctic flounder ( <i>Pleuronectes glacialis</i> ; or <i>Liopsetta glacialis</i> ) and starry flounder ( <i>Platichthys stellatus</i> ) are mainly coastal species, while Bering flounder ( <i>Hippoglossoides robustus</i> ) is found in cold water on the Bering and Chukchi shelves. American plaice or long rough dab ( <i>Hippoglossoides platessoides</i> ) is found in the Atlantic gateway area on the shelf and slope north of the Barents Sea. We have included four additional species classified as mainly boreal, bringing the total to nine species of flounders in the wider CAO ( <a href="#">Table 8.1</a> and <a href="#">Figure 8.2</a> ).
Skates (Rajidae)	Found with two species in the wider CAO. Arctic skate ( <i>Amblyraja hyperborea</i> ) has a wide Arctic distribution assumed to be circumpolar (Mecklenburg <i>et al.</i> 2018). Starry ray ( <i>Amblyraja radiata</i> ) is an Arctic-boreal species found in the Atlantic gateway area.

The remaining fish families contain only one species each with arctic or arctic-boreal distribution: Arctic lamprey (*Lethenteron camtschaticum*; family Petromyzontidae), Greenland shark (*Somniosus microcephalus*; Somniosidae), Pacific herring (*Clupea pallasii*; Clupeidae), and Pacific sandlance (*Ammodytes hexapterus*; Ammodytidae).

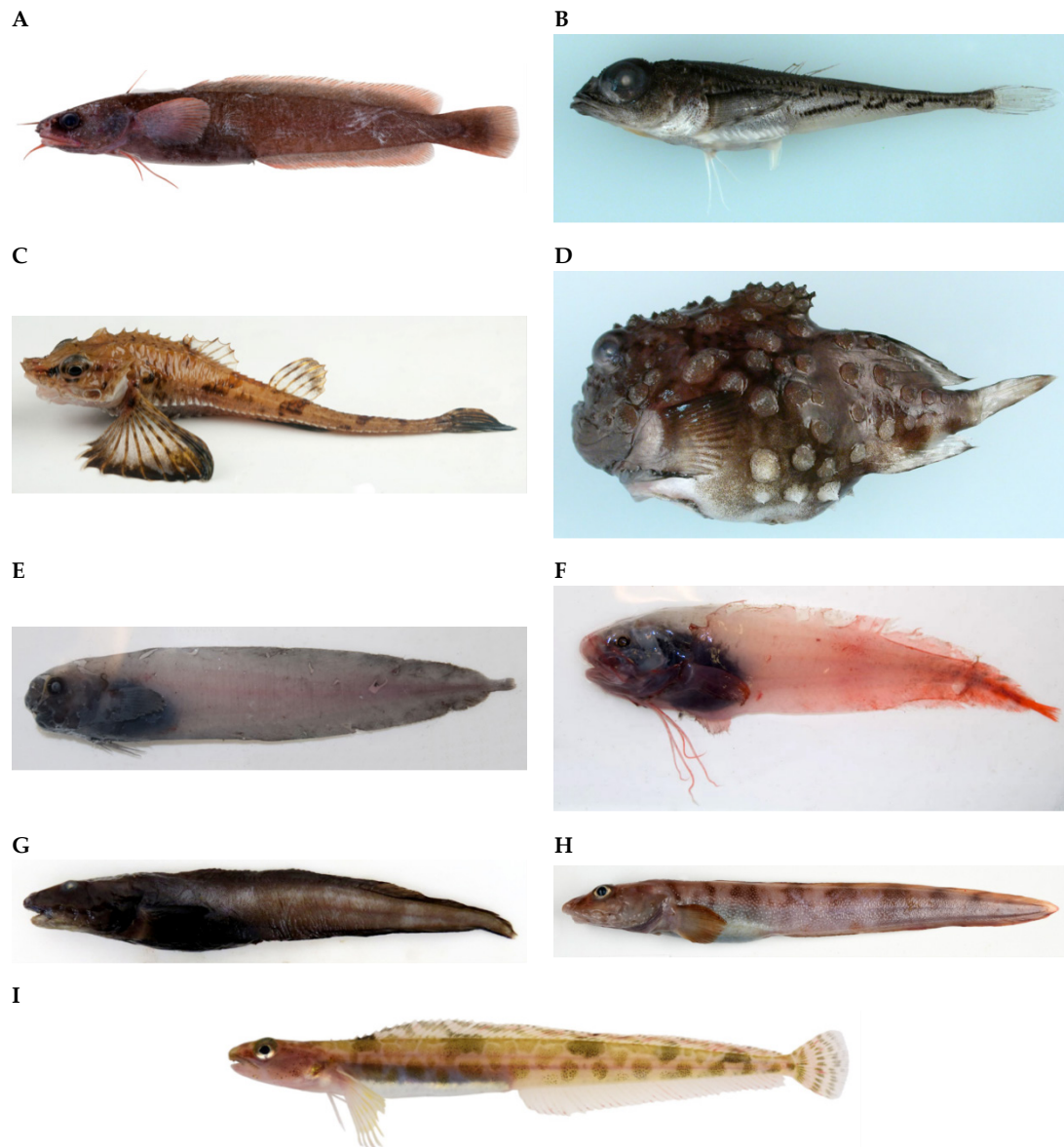


Figure 8.1. Some of the small Arctic fishes found in the CAO. A: Arctic rockling (*Gaidropsarus argentatus*); B: bigeye sculpin (*Triglops nybelini*); C: Atlantic poacher (*Leptagonus decagonus*); D: leatherfin lumpsucker (*Eumicrotremus derjugini*); E: black seasnail (*Paraliparis bathybius*); F: threadfin seasnail (*Rhodichthys regina*); G: glacial eelpout (*Lycodes frigidus*); H: pale eelpout (*Lycodes pallidus*); I: daubed shanny (*Leptoclinus maculatus*). From Mecklenburg *et al.*, (2018). Photos: Ingvar Byrkjedal, Samuel P. Iglesias, Arve Lynghammar, and Catherine W. Mecklenburg.

Table 8.1. Arctic fish species classified biogeographically as Arctic or Arctic-boreal (based on Mecklenburg *et al.*, 2011, 2018; Andriyashev and Chernova, 1995). The list includes also some species that are classified as predominantly or mainly boreal with a range extending into the subarctic zone. The list is arranged taxonomically by fish families. The last column provides information whether the species is found in the CAO (basins beyond the shelf edge) and in the CAO LME (basins excluding the upper slope; see [Figure 1.1](#)). Species present in the CAO are identified by footnotes. Under Max length, if there are two values, the smaller one is the common length of adult individuals. The depth range for anadromous and amphidromous species is not shown. Abbreviations: ssp – subspecies; Arc – Arctic; Bor – boreal; pre – predominantly; Atl – Atlantic; Pac – Pacific; cp – circumpolar; ncp – nearly circumpolar; pcp – probably circumpolar; amp – amphi-, both in Atlantic and Pacific sectors; est – estuarine; brack – brackish; w – western; bent – benthic; dem – demersal; pel – pelagic; lit – littoral; p – probably; ? - uncertain.

Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Petromyzontidae							
Arctic lamprey	<i>Lethenteron camtschaticum</i>	63/32	Arc-Bor	Coastal, Est	Anadromous		
Somniosidae							
Greenland shark <sup>b</sup>	<i>Somniosus microcephalus</i>	7.3 m	Arc-Bor Atl	Shelf, Slope	Dem; mesobenthopel	0–1200	yes/p
Rajidae							
Arctic skate <sup>b</sup>	<i>Amblyraja hyperborea</i>	106	Arc Atl; assumed cp	Slope	Meso/bathybent	100–3000	yes/yes
Starry ray (Thorny skate)	<i>Amblyraja radiata</i>	105	preBor Atl	Slope	Bent	50–100	
Clupeidae							
Pacific herring	<i>Clupea pallasii</i> (ssp.)	46/25	Arc-Bor Pac	Shelf, Brack	Epipel	0–150/250	
Osmeridae							
Atlantic capelin	<i>Mallotus villosus</i>	25/15	Arc-Bor Atl	Shelf, Coastal	Epipel	0–300	?
Pacific capelin	<i>Mallotus catervarius</i>	22	Arc-Bor Pac	Shelf, Coastal	Epipel	0–200	?

Table 8.1 (cont.)							
Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Osmeridae (cont.)							
Arctic rainbow smelt	<i>Osmerus dentex</i>	34	Arc-Bor Pac	Coastal, Est	Anadromous		
Pond smelt	<i>Hypomesus olidus</i>	20	Arc-Bor Pac	Coastal, Est	Anadromous		
Salmonidae							
Coregoninae							
Arctic cisco	<i>Coregonus autumnalis</i>	64/47	Arc	Coastal, Est	Amphidromous		
Least (sardine) cisco	<i>Coregonus sardinella</i>	47/23	preArc Pac	Coastal, Est	Amphidromous		
Bering cisco	<i>Coregonus laurettae</i>	48/30	preArc Pac	Coastal, Est	Amphidromous		
Broad whitefish	<i>Coregonus nasus</i>	61/46	preArc	Coastal, Est	Amphidromous		
Humpback whitefish	<i>Coregonus pidschian</i>	50/33	preArc Pac	Coastal, Est	Amphidromous		
Muksun	<i>Coregonus muksun</i>	90	Arc	Coastal, Est	Amphidromous		
Inconnu (sheefish)	<i>Stenodus leucichthys</i>	150/61	Arc-Bor	Coastal, Est	Amphidromous		
Salmoninae							
Chum salmon	<i>Oncorhynchus keta</i>	100/58	Arc-Bor Pac	Coastal, Shelf, Est	Anadromous		
Pink salmon	<i>Oncorhynchus gorbuscha</i>	76/50	Arc-Bor Pac	Coastal, Shelf, Est	Anadromous		
Arctic char	<i>Salvelinus alpinus</i> (spp.)	107/40	Arc	Coastal, Shelf, Est	Ana- /amphidromous		

Table 8.1 (cont.)								
Family/subfamily and species			Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Salmonidae – Salmoninae (cont.)								
Dolly Varden	<i>Salvelinus malma</i> (ssp.)	127/38	Arc-Bor Pac	Coastal, Shelf, Est	Ana- /amphidromous			
Paralepididae								
White barracudina <sup>b</sup>	<i>Arctozenus risso</i>	30	Wide	Basin	Meso/bathypel	0–2200	Yes?/p	
Myctophidae								
Glacier lanternfish <sup>b</sup>	<i>Benthosema glaciale</i>	10	Arc-Bor Atl	Basin	Mesopel	0/300–850	Yes/p	
Macrouridae								
Roughhead grenadier	<i>Macrourus berglax</i>	110	preBor Atl	Slope	Benthopel	100–1000		
Gadidae								
Arctic cod <sup>a b</sup>	<i>Arctogadus glacialis</i>	60	Arc	Basin	Benthopel	0–930	Yes/yes	
Polar cod <sup>a b</sup>	<i>Boreogadus saida</i>	40/32	Arc cp	Shelf	Benthopel	0–700	Yes/yes	
Saffron cod	<i>Eleginus gracilis</i>	55	Arc-Bor Pac	Coast Shelf Est	Dem, sub/eulitt	0–200/300		
Navaga	<i>Eleginus nawaga</i>	42	Arc Atl	Coastal Shelf	Dem, eulitt	0–15		
Walleye pollock <sup>b</sup>	<i>Gadus (Theragra) chalcogrammus</i>	91	Bor-Pac		Dem, pel	0– > 500	Yes/p	
Pacific cod	<i>Gadus macrocephalus</i>	119	Arc-Bor Pac	Shelf	Dem, pel	0–500		
Atlantic cod <sup>b</sup>	<i>Gadus morhua</i>	200/100	preBor Atl	Shelf	Dem	0–600	Yes/yes	



**Table 8.1 (cont.)**

Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Lotidae							
Arctic rockling <sup>b</sup>	<i>Gaidropsarus argentatus</i>	35	Arc-Bor Atl	Slope	Benthopel	100/500–2260	Yes/yes
Sebastidae							
Deepwater (beaked) redfish <sup>b</sup>	<i>Sebastes mentella</i>	55	Bor-Atl		Mesobent/pel	200–> 1000	Yes/p
Cottidae							
Atlantic hookear sculpin <sup>a b</sup>	<i>Artediellus atlanticus</i>	17	Arc-Bor Atl	Shelf Slope	Mesobent	10–1500	Yes/?
Hamecon	<i>Artediellus scaber</i>	9	Arc ncp	Shelf	Bent, sublitt	0–55	
Arctic staghorn sculpin	<i>Gymnocanthus tricuspis</i>	30	Arc (Atl) cp	Shelf Upper slope	Bent, eulitt	0–100/240	
Twohorn sculpin <sup>b</sup>	<i>Icelus bicornis</i>	17	preArc Atl cp	Shelf Slope	Bent, eulitt	10/50–600	p/-
Spatulate sculpin <sup>b</sup>	<i>Icelus spatula</i>	21/12	Arc-Bor cp	Shelf Slope	Bent, eulitt	10–250/900	p/?
Fourhorn sculpin	<i>Myoxocephalus quadricornis</i>	37	Arc cp	Coastal Shelf Brack	Bent, sublitt	0–20	
Arctic sculpin	<i>Myoxocephalus scorpioides</i>	27/30/20	Arc w	Shelf	Bent, sublitt	0–25	
Shorthorn sculpin <sup>b</sup>	<i>Myoxocephalus scorpius</i>	60	Arc-Bor cp	Shelf Upper slope	Bent, eulitt	0–70/550	p/-
Moustache sculpin <sup>b</sup>	<i>Triglops murrayi</i>	20	Arc-Bor Atl	Shelf Upper slope	Bent	10/100–200/500	p/-

**Table 8.1 (cont.)**

Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Cottidae (cont.)							
Bigeye sculpin <sup>b</sup>	<i>Triglops nybelini</i>	20	Arc Atl pcp	Slope	Mesobent	200–600/1350	Yes/p
Ribbed sculpin <sup>b</sup>	<i>Triglops pingelii</i>	20	Arc-Bor cp	Shelf	Bent, sub/eulit	5–200/500	Yes?/?
Psychrolutidae							
Polar sculpin <sup>a b</sup>	<i>Cottunculus microps</i>	30/14	Arc-Bor Atl	Shelf Slope	Mesobent	160–1 500	Yes/p
Agonidae							
Arctic alligatorfish <sup>b</sup>	<i>Aspidophoroides olrikii</i>	8.6	preArc ncp	Shelf Slope	Bent, eulit	3–200/500	Yes?/?
Atlantic poacher <sup>b</sup>	<i>Leptagonus decagonus</i>	21	Arc-Bor pcp	Shelf	Bent, eulit	120–350/600	Yes/?
Veteran poacher	<i>Podothecus veterinus</i>	28	Arc-Bor Pac	Shelf	Bent, eulit	0–100/240	?
Cyclopteridae							
Arctic lumpsucker	<i>Cyclopteropsis mcalpini</i>	7.5	Arc (Atl)	Shelf	Bent, sub/eulit	18–174	?
Pimpled lumpsucker	<i>Eumicrotremus andriashevi</i>	5	Arc-Bor Pac	Shelf	Bent, sublit	20–90	
Leatherfin lumpsucker <sup>b</sup>	<i>Eumicrotremus derjugini</i>	10	Arc pcp	Shelf Slope	Bent	40–275/900	p/-
Atlantic spiny lumpsucker <sup>b</sup>	<i>Eumicrotremus spinosus</i>	13	preArc Atl	Shelf Slope	Bent, eulit	5–200/900	p/?

Table 8.1 (cont.)

Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/habitat association	Depth range (m)	Present in CAO/LME
Liparidae							
Smalleye tadpole <sup>b</sup>	<i>Careproctus micropus</i>	10.5	Arc Atl	Slope	Mesobent	250/1 000–1800	Yes/p (yes?)
Sea tadpole <sup>a b</sup>	<i>Careproctus reinhardtii</i>	30	Arc Atl pcp	Slope	Mesobent; juv pel	100–1800	Yes/p
Nebulous snailfish <sup>b</sup>	<i>Liparis bathyartcticus</i>	27	preArc cp	Shelf	Bent, eulit	0–600	p/?
Gelatinous snailfish <sup>a b</sup>	<i>Liparis fabricii</i>	21	Arc cp	Shelf Slope	Bent, eulit	0–300/500	Yes/yes
Variegated snailfish	<i>Liparis gibbus</i>	52	Arc-Bor Pac	Shelf	Bent, eulit	0–200/600	?
Kelp snailfish	<i>Liparis tunicatus</i>	14	Arc cp	Coastal Shelf	Bent, lit-eulit	0–50/150	?
Black seasnail <sup>b</sup>	<i>Paraliparis bathybius</i>	26	Arc cp	Lower slope	Meso/bathy-benthopel	600–2 800	Yes/yes
Threadfin seasnail <sup>b</sup>	<i>Rhodichthys regina</i>	32	Arc cp	Lower slope	Meso/bathy-benthopel	400/1000–2 400	Yes/yes
Zoarcidae							
Gymnelinae							
Halfbarred pout	<i>Gymnelus hemifasciatus</i>	18	Arc-Bor ncp	Shelf	Bent, eulit	0–80/200	?
Aurora pout <sup>b</sup>	<i>Gymnelus retrodorsalis</i>	15	Arc Atl	Shelf Slope	Bent	5/60–300/500	p/?
Fish doctor	<i>Gymnelus viridis</i>	30	preArc Pac, wAtl	Coastal Shelf	Bent, eulit	0–50/100	

**Table 8.1 (cont.)**

Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Zoarcidae (cont.)							
Lycodinae							
Checkered wolf eel <sup>b</sup>	<i>Lycenchelys kolthoffi</i>	29	Arc Atl	Slope	Mesobent	200–900	Yes/p
Moray wolf eel <sup>b</sup>	<i>Lycenchelys muraena</i>	23	Arc Atl	Slope	Mesobent	200–1400	Yes/p (yes?)
Naked wolf eel <sup>b</sup>	<i>Lycenchelys platyrhina</i>	15	Arc Atl	Slope	Bathybent	1600–2500	p/p
Adolf's eelpout <sup>a b</sup>	<i>Lycodes adolfi</i>	24	Arc ncp	Lower slope	Mesobent	400–2200	Yes/yes
Greater eelpout <sup>b</sup>	<i>Lycodes esmarkii</i>	102/75	preBor Atl	Slope	Mesobent	150–1100	Yes/p
Doubleline eelpout <sup>b</sup>	<i>Lycodes eudipleurostictus</i>	45	Arc-Atl pcp	Slope	Mesobent	50–1300	Yes/p
Glacial eelpout <sup>b</sup>	<i>Lycodes frigidus</i>	69	Arc (Atl)	Lower slope	Bathybent	500/1000–3 600	Yes/yes
Gracile eelpout <sup>b</sup>	<i>Lycodes gracilis</i>	56	preBor-Atl	Shelf Slope	Epi/mesobent	50–500	Yes?/?
Shulupaoluk	<i>Lycodes jugoricus</i>	51	Arc	Coastal	Bent, lit-eulit	0–20/90	
Lütken's eelpout <sup>b</sup>	<i>Lycodes luetkenii</i>	63	Arc Atl	Lower slope	Mesobent	100–1500	Yes/p
White Sea eelpout	<i>Lycodes marisalbi</i>	23	Arc amp	Shelf	Bent, sublit	0–300	?
Saddled eelpout	<i>Lycodes mucosus</i>	20	Arc Pac, wAtl	Shelf	Bent, sublit	0–90/180	?
Paamiut eelpout <sup>b</sup>	<i>Lycodes paamiuti</i>	29	Arc Atl	Slope	Mesobent	350–1500	Yes/yes?
Pale eelpout <sup>b</sup>	<i>Lycodes pallidus</i> (ssp)	29	Arc Atl/ncp	Slope	Epi/meso/bathybent	10–2 000	Yes/yes
Polar eelpout <sup>a b</sup>	<i>Lycodes polaris</i>	33	Arc ncp	Shelf	Bent, eulit	5–150/300	p/?
Marbled eelpout <sup>b</sup>	<i>Lycodes raridens</i>	86	Arc-Bor Pac	Shelf	Bent, eulit	5–150/500	p/?

**Table 8.1 (cont.)**

Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Zoarcidae – Lycodinae (cont.)							
Arctic eelpout <sup>b</sup>	<i>Lycodes reticulatus</i>	65	Arc Atl	Shelf Slope	Epi/mesobent	5/100–400/900	Yes?/p
Threespot eelpout <sup>b</sup>	<i>Lycodes rossi</i>	31/38	Arc ncp	Shelf Slope	Bent, eulit	40/130–365	p/?
Archer eelpout <sup>a b</sup>	<i>Lycodes sagittarius</i>	43	Arc	Upper slope	Meso/bathybent	120–2200	Yes/yes
Longear eelpout <sup>a b</sup>	<i>Lycodes seminudus</i>	57	Arc ncp	Slope	Mesobent	50/200–1400	Yes/yes
Scalebelly eelpout <sup>b</sup>	<i>Lycodes squamiventer</i>	37	Arc amp/Atl	Slope	Bathybent	200–1800	p/p
Estuarine eelpout	<i>Lycodes turneri</i>	85	preArc Pac	Coastal Shelf	Bent, sublit	0–50/125	
Whiptail scutepout <sup>b</sup>	<i>Lycodon flagellicauda</i>	29	Arc Atl	Lower slope	Meso/bathybent	350–2000	Yes/yes?
Stichaeidae							
Blackline prickleback	<i>Acantholumpenus mackayi</i>	70/40	preBor Pac	Coastal Shelf	Bent, sublit	0–70/150	
Stout eelblenny <sup>a</sup>	<i>Anisarchus medius</i>	29/20	Arc-Bor amp-cp	Shelf	Bent, eulit	0–100/265	?
Fourline snakeblenny <sup>b</sup>	<i>Eumesogrammus praecisus</i>	23	Arc-Bor Pac, wAtl	Shelf Slope	Bent, eulit	5–70/400	p/?
Daubed shanny <sup>b</sup>	<i>Leptoclinus maculatus</i>	22	Arc-Bor amp	Shelf Slope	Bent, eulit	2–200/800	Yes/p
Slender eelblenny	<i>Lumpenus fabricii</i>	37	Arc-Bor amp	Shelf	Bent, sublit	0–50	



Table 8.1 (cont.)								
Family/subfamily and species			Max length (cm)	Distribution	Habitat	Lifestyle/ habitat association	Depth range (m)	Present in CAO/LME
Stichaeidae (cont.)								
	Snakeblenny	<i>Lumpenus lampretaeformis</i>	50	preBor Atl	Shelf	Bent	40–100	
	Arctic shanny	<i>Stichaeus punctatus</i>	22	Arc-Bor amp, wAtl	Coastal Shelf	Bent, sublit	0–50/100	
Pholidae								
	Banded gunnel	<i>Pholis fasciata</i>	30	Arc-Bor amp-Pac, wAtl	Coastal	Bent, sublit	0–50/100	
Anarhichadidae								
	Northern wolffish <sup>b</sup>	<i>Anarhichas denticulatus</i>	180	Arc-Bor Atl	Shelf Slope	Dem, benthopel	150–600/1700	Yes?/p
	Spotted wolffish	<i>Anarhichas minor</i>	180/120	preBor Atl	Shelf	Dem	100–400	
	Bering wolffish	<i>Anarhichas orientalis</i>	124	preBor Pac	Shelf	Dem; juv pel	0–100	?
Ammodytidae								
	Arctic sand lance	<i>Ammodytes hexapterus</i>	28	Arc-Bor Pac, wAtl	Shelf	Dem, eulit	0–100/275	?
Pleuronectidae								
	Flathead sole (Bering flounder)	<i>Hippoglossoides elassodon</i>	52	Arc-Bor Pac	Shelf	Bent, eulit	0–150/400	?
	American plaice <sup>b</sup>	<i>Hippoglossoides platessoides</i>	83/54	Arc-Bor Atl	Shelf Slope	Bent, epi/meso	10–400/1200	Yes/p
	Yellowfin sole	<i>Limanda aspera</i>	48	preBor Pac	Shelf	Bent, eulit	0–150/600	?
	Longhead dab	<i>Limanda proboscidea</i>	41	preBor Pac	Shelf	Bent, sublit	0–100/125	

**Table 8.1 (cont.)**

Family/subfamily and species		Max length (cm)	Distribution	Habitat	Lifestyle/habitat association	Depth range (m)	Present in CAO/LME
Pleuronectidae (cont.)							
Sakhalin sole	<i>Limanda sakhalinensis</i>	35	preBor Pac	Shelf	Bent, eulit	10–200/360	?
Arctic flounder	<i>Liopsetta glacialis</i>	44	Arc-Bor Pac	Coastal Shelf Brack	Bent, sublit	0–20/90	
Starry flounder	<i>Platichthys stellatus</i>	91/35	Arc-Bor Pac	Coastal Shelf Brack	Bent, sublit	0–50/150	
Alaska plaice	<i>Pleuronectes quadrituberculatus</i>	66	preBor Pac	Shelf	Bent, eulit	0–100/450	?
Greenland halibut <sup>a b</sup>	<i>Reinhardtius hippoglossoides</i>	130	Arc-Bor ncp	Shelf Slope	Dem, benthopel	200–2000	Yes/p(yes?)

<sup>a</sup>Species listed by Mundy *et al.* (2017) as recorded in the high seas portion of the Arctic Ocean

<sup>b</sup>Species found or assessed in this report as likely to be found in the CAO basins beyond the shelf break

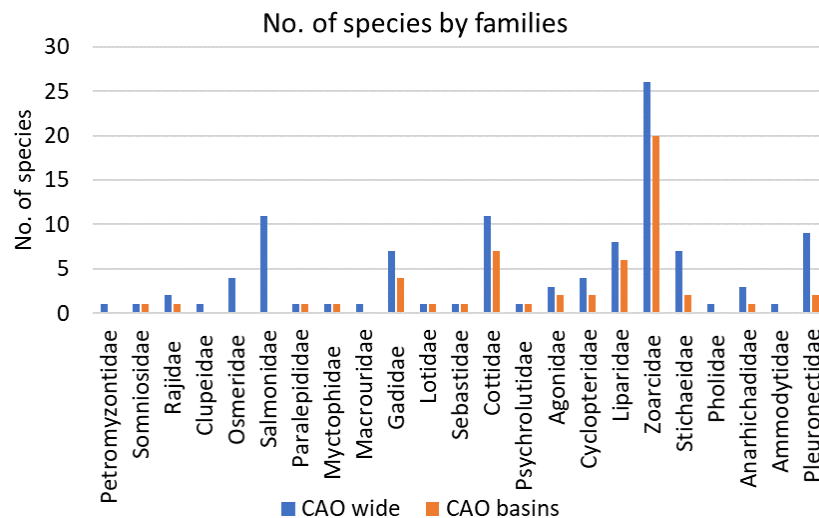


Figure 8.2. Number of fish species by families found in the Central Arctic Ocean, including the adjacent Arctic shelves (CAO wide; 106 species), and in the basin parts of the CAO beyond the shelf breaks (53 species). See [Table 8.1](#) for a list of the species.

## 8.3 Fish distribution in relation to habitats

### 8.3.1 Fish habitats

The wider Arctic Ocean (the basins and surrounding shelves) can be divided into five main habitats or zones: estuarine, coastal marine, shelf, slope, and deep water. A further distinction can be made between benthic and pelagic habitats, with the latter subdivided into epi-, meso-, and bathypelagic according to depth (traditionally 0–200 m, 200–1000 m, and > 1000 m, respectively). This division is based on the penetration of light down into the water column, which may be different in the CAO due to sea ice, when compared to open water at lower latitudes. In the Arctic Ocean, the three pelagic layers correspond to the upper polar mixed and halocline layers, the Atlantic layer, and the deep-water layer, respectively. A similar division is used for benthic species, with epibenthic, mesobenthic, and bathybenthic distributions (Mecklenburg *et al.*, 2018).

Fish species exhibit different lifestyles and habitat associations, which can be classified into benthic, demersal, pelagic, and sympagic types. Some fish, such as many sculpins, snailfishes, and flatfish, have a benthic lifestyle. They sit or rest on the seabed, or make burrows in soft sediments like many eelpouts do. Other fishes, such as e.g. Atlantic cod and haddock, have demersal lifestyles, swimming close to the seabed. Demersal species can make foraging excursions upward in the water column, blurring the distinction between demersal and pelagic lifestyles. An example of a benthic-pelagic-sympagic lifestyle is provided by polar cod, which can be found demersally close to the seabed, pelagically in the water column, and sympagically under sea ice (Hop and Gjørseter, 2013; Melnikov and Chernova, 2013; David *et al.*, 2016; Geoffroy *et al.*, 2016). Conversely, Atlantic herring (*Clupea harengus*) and Pacific herring (*Clupea pallasii*) are considered pelagic species, but are commonly found near the seabed in coastal environments.

The vast majority of the 100 Arctic and Arctic-boreal species are benthic or demersal, with few species considered pelagic or predominantly pelagic (polar cod, Arctic cod, Atlantic and Pacific capelin, Pacific herring, Pacific sandlance, and glacier lanternfish). The dominance of benthic

and demersal species reflects the taxonomic composition with high species richness of sculpins, snailfishes, and eelpouts (see [Figure 8.2](#)).

### 8.3.2 Distribution patterns of fish species by habitats

The fish species in the wider CAO, including adjacent shelves and coasts, have been grouped according to whether they are found mainly on the lower slope and in deep water (> 1000 m), on the slope (mostly upper slope < 1000 m), on the upper slope and outer shelf (typically to a depth of about 500 m), on the shelf, and in coastal waters ([Figure 8.3](#)). The two first groups (deep-water and slope) are described together in [Section 8.3.2.1](#).

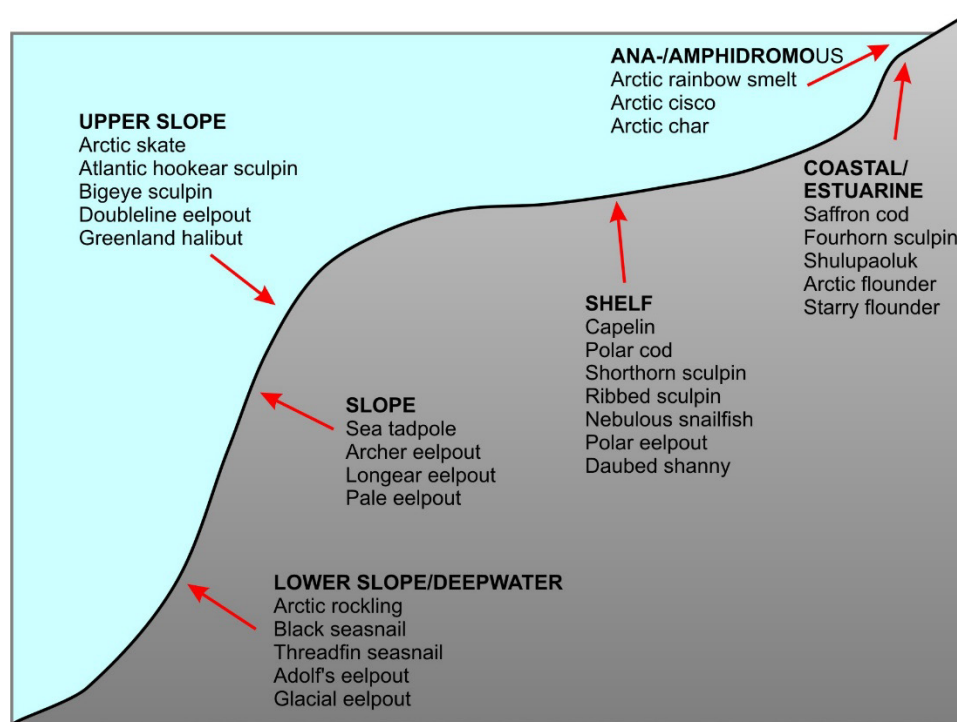


Figure 8.3. Schematic representation of a transect from the coast across the shelf and slope into the deep basin of the CAO, showing common fish species in depth-related habitats.

#### 8.3.2.1 Deep-water and slope species

Three species of fish are found in the deep water in the CAO, where they are assumed to have wide distributions: glacial eelpout (*Lycodes frigidus*), black seasnail (*Paraliparis bathybius*), and threadfin seasnail (*Rhodichthys regina*). They are meso- to bathybenthic species found on muddy bottoms deeper than 500 m and down to depths of 2000–3000 m or more (Mecklenburg *et al.*, 2018). The three species form an assemblage that is common in the cold deep water in the Norwegian Sea (Bergstad *et al.*, 1999; Bjelland and Holst, 2004).

Many species of eelpouts are found along the slopes of the CAO, classified as mesobenthic or meso- to bathybenthic (Mecklenburg *et al.*, 2018; [figures 8.3](#) and [8.4](#)). These include six species of *Lycodes* eelpouts and whiptail scutepout (*Lycodon flagellicauda*). The latter species, along with pale eelpout (*Lycodes pallidus*) and Arctic skate (*Amblyraja hyperborea*), are characteristic of the upper slope cold species assemblage in the Norwegian Sea (Bergstad *et al.*, 1999; Bjelland *et al.*, 2000). Adolf's eelpout (*Lycodes adolfi*), doubleline eelpout (*L. eudipleurostictus*), pale eelpout (*L. pallidus*), longear eelpout (*L. seminudus*), and archer eelpout (*L. sagittarius*) have wide distributions, possibly circumpolar or nearly circumpolar along the slopes around the CAO (Mecklenburg *et al.*, 2018). Arctic skate is assumed to be circumpolar, although this is not

verified for all slope regions (Mecklenburg *et al.*, 2018). Bigeye sculpin (*Triglops nybelini*) and sea tadpole (*Careproctus reinhardti*) are mesobenthic species with wide, possibly circumpolar distributions (Mecklenburg *et al.*, 2018).

### 8.3.2.2 Upper slope and outer shelf

Species distributed along the upper slope and outer shelf include several sculpins, lumpsuckers, snailfishes, and pricklebacks (figures 8.3 and 8.5). Twohorn sculpin (*Icelus bicornis*), spatulate sculpin (*I. spatula*), and leatherfin lumpsucker (*Eumicrotremus derjugini*) have wide circumpolar (or probably circumpolar) distributions on Arctic shelves, extending deeper along the upper slopes (Mecklenburg *et al.*, 2018). The gelatinous sea snail (*Liparis fabricii*) also has a wide circumpolar distribution on shelves and upper slopes, and is also found pelagically in the Atlantic layer over deep water (Mecklenburg *et al.*, 2007, 2018). Daubed shanny (*Leptoclinus maculatus*) is found on Arctic shelves (possibly circumpolar), recorded to depths of over 200 m on the Chukchi and Beaufort slopes (Mecklenburg *et al.*, 2018). Greenland halibut (*Reinhardtius hippoglossoides*) is a much larger species and is found on slopes and deeper shelves, with a nearly circumpolar distribution around the CAO (Chiperzak *et al.*, 1995; Chernova, 2015, 2017; Mecklenburg *et al.*, 2018). Arctic eelpout (*Lycodes reticulatus*) is a medium-sized fish (grows to maximum length of about 60 cm), which is also found on shelves and upper slopes (Wienerroither *et al.*, 2011; Mecklenburg *et al.*, 2018).

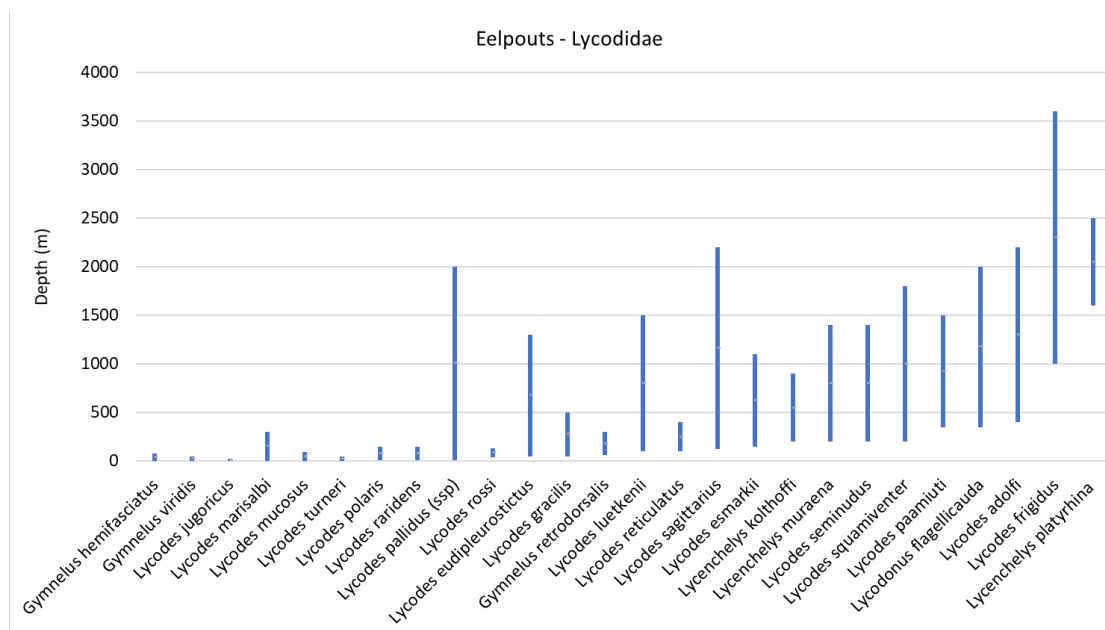


Figure 8.4. Depth distribution of eelpout species (family Zoarcidae) found in the CAO, arranged from shallow-water species (left) to deep-water species (right). The vertical bars denote the depth range from upper to lower depth of occurrence.

### 8.3.2.3 Shelves

Sculpins are an important group of fish on Arctic shelves, and include Arctic staghorn sculpin (*Gymnocanthus tricuspis*), shorthorn sculpin (*Myoxocephalus scorpius*), and ribbed sculpin (*Triglops pingelii*). These are common species with wide circumpolar distributions (Mecklenburg *et al.*, 2018; Figure 8.5). Nebulous (or Arctic) snailfish (*Liparis bathyarcticus*) has a similar wide distribution on Arctic shelves, while kelp snailfish (*L. tunicatus*) is found mainly in shallow coastal waters (Figure 8.3). Polar eelpout (*Lycodes polaris*) is another common species with nearly



circumpolar distribution on the shelves surrounding the CAO. Finally, another eelpout species, shulupaoluk (*Lycodes jugoricus*), is found in shallow estuarine waters (Mecklenburg *et al.*, 2018).

Atlantic capelin (*Mallotus villosus*) and Pacific capelin (*Mallotus catervarius*) are found on Arctic shelves on the Atlantic and Pacific sides of the Arctic Ocean (Mecklenburg *et al.*, 2018). They are pelagic schooling species that rarely venture out over deeper waters in core distribution areas, such as the Barents Sea and the East Bering Sea (Hop and Gjørseter, 2013; Mecklenburg *et al.*, 2018). Pacific capelin is found in the Chukchi and Beaufort seas east to Amundsen Gulf (Mecklenburg *et al.*, 2002, 2011, 2016, 2018). Specimens of capelin collected in the East Siberian and Laptev seas are probably this species (Mecklenburg *et al.*, 2018). Atlantic capelin is found on the northern Barents shelf and in adjacent parts of the northern Kara Sea (Dolgov, 2013; Hop and Gjørseter, 2013; Mecklenburg *et al.*, 2018).

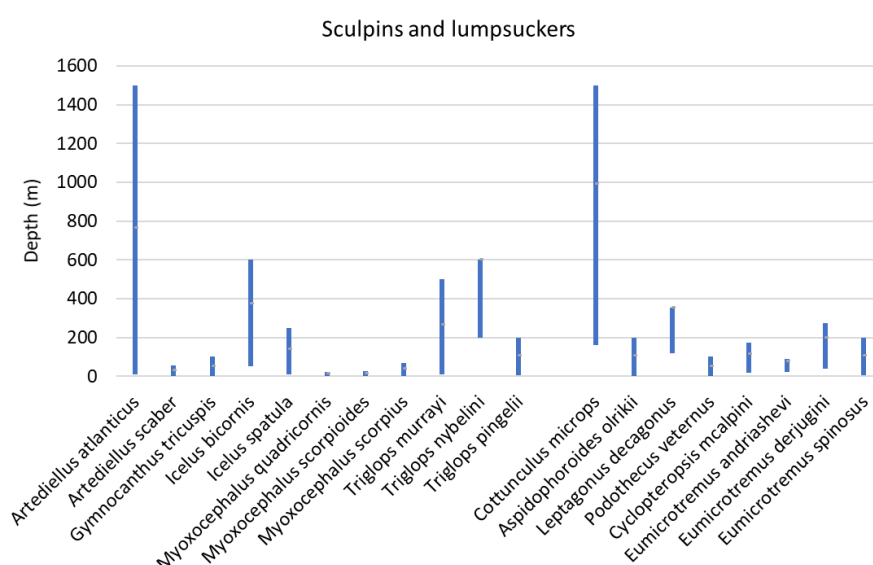


Figure 8.5. Depth distribution of sculpin species (family Cottidae, 11 species), fathead sculpins (family Psychrolutidae, one species), poachers (family Agonidae, three species), and lumpfishes (family Cyclopteridae, four species) found in the CAO. The vertical bars denote the depth range from upper to lower depth of occurrence.

#### 8.3.2.4 Coastal waters

Saffron cod (*Eleginus gracilis*) is found as a mainly coastal species (Figure 8.3) in the Beaufort, Chukchi, and East Siberian seas, with a distribution extending out on the shelves to a depth of usually < 100 m (Mecklenburg *et al.*, 2018). The related navaga (*Eleginus nawaga*) is found in shallow coastal waters in the southeastern Barents Sea and southwestern Kara Sea, separated by a long distance from the shelf edge to the CAO. Pacific herring (*Clupea pallasii*) can also be regarded as a mostly coastal species, found around the rim of the Arctic Ocean from Bathurst Inlet in the Canadian Arctic (at 107°W) to the White Sea region in the southeastern Barents Sea (Mecklenburg *et al.*, 2016, 2018). Arctic flounder (*Liopsetta glacialis*) is another coastal species with a distribution around the rim of the Arctic Ocean very similar to Pacific herring. It is rarely found deeper than 20 m and is commonly associated with brackish waters in estuaries and bays, and even moves into freshwater in rivers (Mecklenburg *et al.*, 2018). Saffron cod, navaga, and Pacific herring are also found in brackish waters. The fourhorn sculpin (*Myoxocephalus quadricornis*) is a characteristic species in brackish Arctic waters, with a circumpolar distribution (Mecklenburg *et al.*, 2018).

Other common coastal species already mentioned are kelp snailfish (*Liparis tunicatus*) and shulupaoluk (*Lycodes jugoricus*).

### 8.3.2.5 Wide distribution from coasts to basins

Two small gadids, polar cod (*Boreogadus saida*) and Arctic cod (*Arctogadus glacialis*), are probably the most abundant fish species in the CAO. They are both sympagic, occurring under sea ice, and their distribution spans from nearshore waters to the basins (Andriyashev *et al.*, 1980; Jordan *et al.*, 2003; Hop and Gjørseter, 2013; Mecklenburg *et al.*, 2018). The largest portions of their populations are benthic-pelagic, often found near the seabed down to a depth of about 800 m (Jordan *et al.*, 2003; Karamushko, 2012). However, the extent to which they occur pelagically in the water column of the CAO is not well known. Due to their importance in the ecosystem of the CAO, both in terms of abundance and ecological significance, the present knowledge of their distribution and their mode of life are described in more detail in [Section 8.5](#).

## 8.4 Number of fish species in the CAO

Twelve fish species were reported in the high seas portion of the CAO by Mundy *et al.*, (2017; Anon., 2017). Most of the high seas area lies well within the Central Arctic Ocean LME, with the 200-nautical-mile EEZ limits of Norway (Svalbard), Russia, Canada, and Denmark (Greenland) extending beyond the slopes and into the deep basins of the Arctic Ocean. There is a noticeable exception on the Pacific side, where the high seas include the Chukchi Borderland and part of the shelf in the East Siberian Sea (see [Figure 1.1](#)). The Central Arctic Ocean LME is defined to include the lower continental slopes (deeper than 1000 m), except in the Beaufort Sea area, where the Beaufort Sea LME includes the lower slope and part of the Canada Basin (north to 76°N).

The number of species in the Central Arctic Ocean LME is higher than the 12 species reported from the high seas portion, due to the inclusion of the lower slope. If the upper slope is also included, i.e. for the CAO basins beyond the shelf break, the number of species is higher still. As there is a general lack of data on fish distributions in the CAO, an overview is provided here of all Arctic and Arctic-boreal fish species reported from the Arctic Ocean and adjacent shelves, in order to assess which fish species could occur in the CAO basins.

Of the 99 fish species classified as Arctic or Arctic-boreal, eight have not been reported from the Arctic shelves and slopes surrounding the CAO. They include species which are found in the Baffin Bay area, but not in the Nordic Seas adjacent to the CAO [threadfin rockling (*Gaidropsarus ensis*), Kido's snailfish (*Careproctus kidoi*), McAllister's eelpout (*Lycodes mcallisteri*), and Arctic hook-ear sculpin (*Artediellus uncinatus*)]. [Table 8.1](#) provides a list of 106 fish species that have been found in the wider CAO area, including the adjacent shelves surrounding the basins. In addition to the 91 Arctic and Arctic-boreal species, the list in [Table 8.1](#) includes 15 species classified as mainly boreal by Mecklenburg *et al.* (2018):

- a) blackline prickleback (*Acantholumpenus mackayi*), Bering wolffish (*Anarhichas orientalis*), and longhead dab (*Limanda proboscidea*), recorded from the Beaufort Sea;
- b) Alaska plaice (*Pleuronectes quadrituberculatus*), yellowfin sole (*Limanda aspera*), and Sakhalin sole (*L. sakhalensis*), recorded from the northern Chukchi Sea;
- c) walleye pollock (*Gadus chalcogrammus* or *Theragra chalcogramma*), recorded in slope waters in the Chukchi and Beaufort seas (Mecklenburg *et al.*, 2018);

- d) on the Atlantic side, white barracudina (*Arctozenus risso*), deep-water redfish (*Sebastes mentella*) and greater eelpout (*Lycodes esmarkii*) have been recorded north of Franz Josef Land;
- e) starry ray (*Amblyraja radiata*), roughhead grenadier (*Macrourus berglax*), gracile eelpout (*L. gracilis*), and spotted wolffish (*Anarhichas minor*) have been recorded north of Svalbard; and
- f) Atlantic cod (*Gadus morhua*) has been recorded pelagically in the Fram Strait (Ingvaldsen *et al.*, 2018) and recently also over deep water in the Amundsen Basin (Snoeijs-Leijonmalm *et al.*, 2022).

Many of the species listed in [Table 8.1](#) are estuarine, coastal, or shelf species, and are thus not likely to spread into the Central Arctic Ocean LME other than as incidental spillover. Half of the species, 53 in total, have not been recorded in the basin part of the CAO beyond the shelf break. The information in records on habitat association and depth range has been used here to assess which species are likely or not to be found in the CAO basins. For some of the species, uncertainty is indicated (by "?") in [Table 8.1](#). This includes the two species of capelin that have not been recorded beyond the shelf edge, but that might possibly move there to forage in summer.

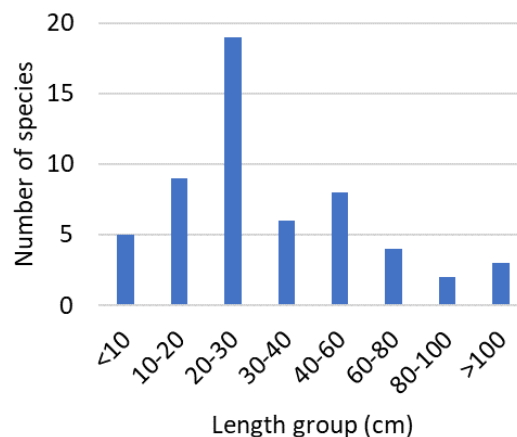
The remaining 53 species in [Table 8.1](#) (identified with <sup>b</sup>) are either found (39 species) or have been assessed as likely to be found (14 species) in the CAO basins beyond the shelf break. Eelpouts, which are, to a large extent, slope species ([Figure 8.4](#)), are the dominant fish family, with 20 species in the CAO basins (14 species recorded, and 6 likely to be found; [Figure 8.2](#)). Sculpins are the second largest group, with seven species in the CAO (three have been recorded, four are likely to be found). Sculpins, as a group, are predominantly shelf species, and they generally occur in the CAO on the upper slope when their distributions extend beyond the shelf break. The next largest group is snailfishes with six species (five recorded, one likely to occur; [Table 8.1](#)).

The number of fish species in the CAO LME is lower, with 14 species recorded and another 22 species potentially occurring there ([Table 8.1](#)). Of the 12 species listed by Mundy *et al.* (2017) as recorded in the high seas portion of the Arctic Ocean (identified with <sup>a</sup> in [Table 8.1](#)), two are unlikely to occur in the CAO LME since they are predominantly shelf species [stout eelblenny (*Anisarchus medius*) and Canadian eelpout (*Lycodes polaris*)]. They are included in the list from Mundy *et al.* (2017) because they are found in the shelf portions of the high seas in the Chukchi and East Siberian seas (see [Figure 1.1](#)). Stout eelblenny has not been identified in the CAO beyond the shelf edge. Of the remaining 11 species on Mundy's list, 10 have been recorded from the CAO basins (beyond the shelf edge), while one species (*Lycodes polaris*) is likely to be found there. Six of the 12 species have been recorded in the CAO LME (*Arctogadus glacialis*, *Boreogadus saida*, *Liparis fabricii*, *Lycodes adolfi*, *Lycodes sagittarius*, and *Lycodes seminudus*), while three more are potentially found there (*Cottunculus microps*, *Careproctus reinhardtii*, and *Reinhardtius hippoglossoides*). In addition, we have listed nine species as recorded in the CAO LME that were not on the list of 12 species by Mundy *et al.* (2017): Arctic skate (*Amblyraja hyperborea*), Arctic rockling (*Gaidropsarus argentatus*), Atlantic cod (*Gadus morhua*), black seasnail (*Paraliparis bathybius*), threadfin seasnail (*Rhodichthys regina*), glacial eelpout (*Lycodes frigidus*), paamiut eelpout (*L. paamiuti*), pale eelpout (*L. pallidus*), and whiptail scutepout (*Lycodon flagellicauda*; [Table 8.1](#); see Mecklenburg *et al.*, 2018 for information on distribution in the CAO).

The reason for the larger number of species reported here for the CAO basins when compared to the 12 species listed by Mundy *et al.* (2017), is that general information on distribution from the literature is used here, while Mundy *et al.* (2017) required information on exact location of

sampling (latitude and longitude). Many studies are reported without such details, but do provide information on study area and sampling depth.

In addition to the 14 species recorded from the CAO LME, 21 species are listed here that could be found there based on the depth range of their general distributions ([Table 8.1](#)): Greenland shark (*Somniosus microcephalus*), glacier lanternfish (*Benthoosema glaciale*), walleye pollock (*Gadus chalcogrammus*), northern wolffish (*Anarhichas denticulatus*), Greenland halibut (*Reinhardtius hippoglossoides*), eight species of eelpouts, and a few more.



**Figure 8.6.** Number of fish species by length groups (cm) in the CAO basins beyond the shelf break. The length is maximum length attained by the species (see [Table 8.1](#)).

The two small cod species, polar cod (*Boreogadus saida*) and Arctic cod (*Arctogadus glacialis*), are probably the two most important species in the CAO (see species accounts in [Section 8.5](#)). Greenland halibut is found along the slope from the northern Barents and Kara seas into the Nansen Basin east to the Laptev and East Siberian seas (Chernova, 2017; Haug *et al.*, 2017). While it is found mainly on the upper slope (above 1000 m depth), it likely also occurs in the CAO LME. The fish in the CAO are generally small species, most of them being smaller than 30 cm in maximum length ([Figure 8.6](#)). Some of the eelpouts can grow to a size of more than 30 cm, the largest being the greater eelpout (*Lycodes esmarkii*) that can grow up to 1 m in length. Two larger species that are likely to occur in the CAO LME are Arctic skate (*Amblyraja hyperborea*), which is a deep-water species found along slopes commonly to a depth of 1500 m or deeper, and Greenland shark (*Somniosus microcephalus*).

## 8.5 Two important cod species

### 8.5.1 Polar cod (*Boreogadus saida*)

Polar cod ([Figure 8.7](#); note that the species is called Arctic cod in North America; Scott and Scott, 1988; Page *et al.*, 2013) is a key species in Arctic marine foodwebs, acting as a major link between lower and higher trophic levels (Welch *et al.*, 1992; Hop and Gjørseter, 2013). It has a wide circumpolar distribution in all parts of the contiguous Arctic with seasonal or permanent sea-ice cover (excluding the Baltic Sea and Sea of Okhotsk). It is associated with sea ice, possibly all over the Arctic Ocean (David *et al.*, 2016; Mecklenburg *et al.*, 2018). Polar cod was collected and recorded from Russian ice-drift stations in the 1950s–1970s, including observations near the North Pole at about 88.5°N (Andriyashev *et al.*, 1980). It has been found associated with sea ice, living or hiding in crevices and wedges along edges of melting sea ice (Bradstreet *et al.*, 1986; Lønne and Gulliksen, 1989; Gradinger and Bluhm, 2004).



Figure 8.7. (Upper) Polar cod (*Boreogadus saida*) and (lower) Arctic cod (*Arctogadus glacialis*). Note the relatively large eyes which indicate that the species live in low-light environments. Photos: Samuel P. Iglesias and Catherine W. Mecklenburg.

Using a trawl designed for sampling the underside of sea ice (SUIT – Surface and Under Ice Trawl; see [Figure 5.13](#)), David *et al.* (2016) reported the distribution and abundance of polar cod in Eurasian Basin in late summer 2012. Polar cod were mainly juveniles (52–140 mm in length), dominated by 1-year-old individuals. The median abundance was 5000 individuals  $\text{km}^{-2}$ , representing a median biomass of 19  $\text{kg km}^{-2}$  (ranging from 0 to 66  $\text{kg km}^{-2}$  at 13 stations). Scaled up, this would constitute a total biomass of about 19 000 t for Eurasian Basin (with an area of roughly 1 million  $\text{km}^2$ ), and about 57 000 t for the entire CAO, if a similar abundance is assumed for Amerasian Basin. While this estimate is uncertain, it provides an indication of the biomass of polar cod associated with the underside of sea ice in the CAO.

The sea ice at the sampling stations in the CAO were backtracked, using satellite data on ice drift, and were found to have originated from ice formation on the Laptev Sea and Kara Sea shelves during the previous winter (October–January), with mean drift time of about 300 days (David *et al.*, 2016). A sea-ice drift hypothesis was suggested as a possible mechanism for the occurrence of juvenile polar cod under sea ice in Eurasian Basin (David *et al.*, 2016). According to this hypothesis, post-larvae, stemming from spawning in winter and development through the ice-free period in summer (Graham and Hop, 1995; Bouchard and Fortier, 2011), might seek refuge under the forming sea ice in early winter and be transported with the ice out into the CAO. The Laptev Sea may hold a population of polar cod (Ponomarenko, 1968), and may be a particularly important source area of sympagic juvenile polar cod in the CAO. The average density of polar cod was about fourfold higher under sea ice originating from the Laptev Sea compared to ice originating from the Kara Sea (ca. 10 000 and 2500 individuals  $\text{km}^{-2}$ , respectively; David *et al.*, 2016). The Laptev Sea is an important source for sea ice that feeds into



the Transpolar Drift, which may be the main mechanism and route for transporting juvenile polar cod from spawning areas on the shelf and into the CAO. During the drift, the fish largely rely on sympagic resources, which were shown to be sufficiently abundant to sustain the observed abundance of polar cod under sea ice (Kohlbach *et al.*, 2017).

The fate of the juvenile sympagic polar cod in Eurasian Basin is unknown. Whether, and to what extent, they leave the sea ice to live pelagically deeper in the water column has not been investigated. The strong predominance of 1-year-old juveniles recorded by David *et al.* (2016), suggests that older and larger individuals may either die (because they are eaten) or seek safety farther down in the water column. Predator avoidance by polar cod has been observed in Amundsen Gulf, Arctic Canada (Benoit *et al.*, 2010). Andriyashev *et al.* (1980) reported, from observations and collections of polar cod from an ice-drift station (NP-16) in Canada Basin (at about 80°N, 177°E), that individuals were relatively small in early winter (November–December; range 85–190 mm, most individuals were smaller than 150 mm). Melnikov and Chernova (2013) reported what appeared to be large aggregations of polar cod on the underside of the ice in winter, from a more recent ice-drift station (NP-37 in 2009–2010) in the central part of Canada Basin. The fish were mostly immature juveniles of similar size, with length 75–169 mm and an age of 1–4 years. The dominant age group was 2-year-olds (86–94% of total abundance).

The population structure of polar cod on the shelves surrounding the CAO is not well described and understood. There is a migratory population in the Barents Sea which is relatively well studied (Hop and Gjøsæter, 2013), and Ponomarenko (1968) suggested that there are also migratory populations in the Laptev and Chukchi seas ([Figure 8.8](#)). There is also a large population in the Amundsen Gulf region that has been investigated in recent years (Benoit *et al.*, 2008, 2010, 2014; Geoffroy *et al.*, 2011, 2016; Majewski *et al.*, 2016). Polar cod are also abundant in the Canadian Arctic Archipelago (Welch *et al.*, 1993; Crawford and Jorgenson, 1996; Hop *et al.*, 1997), in coastal regions of the Beaufort and Chukchi seas (Crawford *et al.*, 2012a; Mueter *et al.*, 2017), and on the East Greenland shelf in the Greenland Sea (Boertmann *et al.*, 2020a).

The Barents Sea is home to two stocks (or stock components) of polar cod. The largest of the two is the East Barents Sea stock, which spawns under ice in winter in the Pechora region in the southeastern Barents Sea (Moskalenko, 1964; Ponomarenko, 1968; Rass, 1968; Boitsov *et al.*, 2013; Eriksen *et al.*, 2015, 2019). After spawning, the polar cod migrate north through the eastern Barents Sea to feed in the northern Barents Sea and adjacent parts of the northern Kara Sea (Ponomarenko, 1968; Boitsov *et al.*, 2013). In late autumn, they migrate south again to wintering and spawning areas in the southeastern Barents Sea. There is also a Svalbard stock (or stock component) of polar cod that is believed to spawn on the east side of the Svalbard archipelago (Ajiad *et al.*, 2011; Boitsov *et al.*, 2013; Hop and Gjøsæter, 2013; Eriksen *et al.*, 2019). Evidence of this is seen in bimodal and often disjunct distributions of 0-group polar cod juveniles in autumn (Gjøsæter, 1995; Eriksen *et al.*, 2015). The biomass of polar cod in the Barents Sea has been around 1–2 million t in recent decades, but the eastern stock appears to have declined considerably in the most recent and warm years (Ajiad *et al.*, 2011; Boitsov *et al.*, 2013; Hop and Gjøsæter, 2013; Eriksen *et al.*, 2015, 2017, 2019; Huserbråten *et al.*, 2019) and to have shifted its distribution northeast.

Polar cod are found in the Kara Sea (Orlov *et al.*, 2020a). However, most of these fish are believed to belong to the East Barents stock, with individuals moving into the northern Kara Sea to feed and some of them returning to the spawning area through the Kara Sea and Kara Gate (Ponomarenko, 1968). There is also spawning of polar cod in the Kara Sea, but it is not well known if there are additional stocks or stock components (Borkin *et al.*, 2008; Dolgov, 2013).

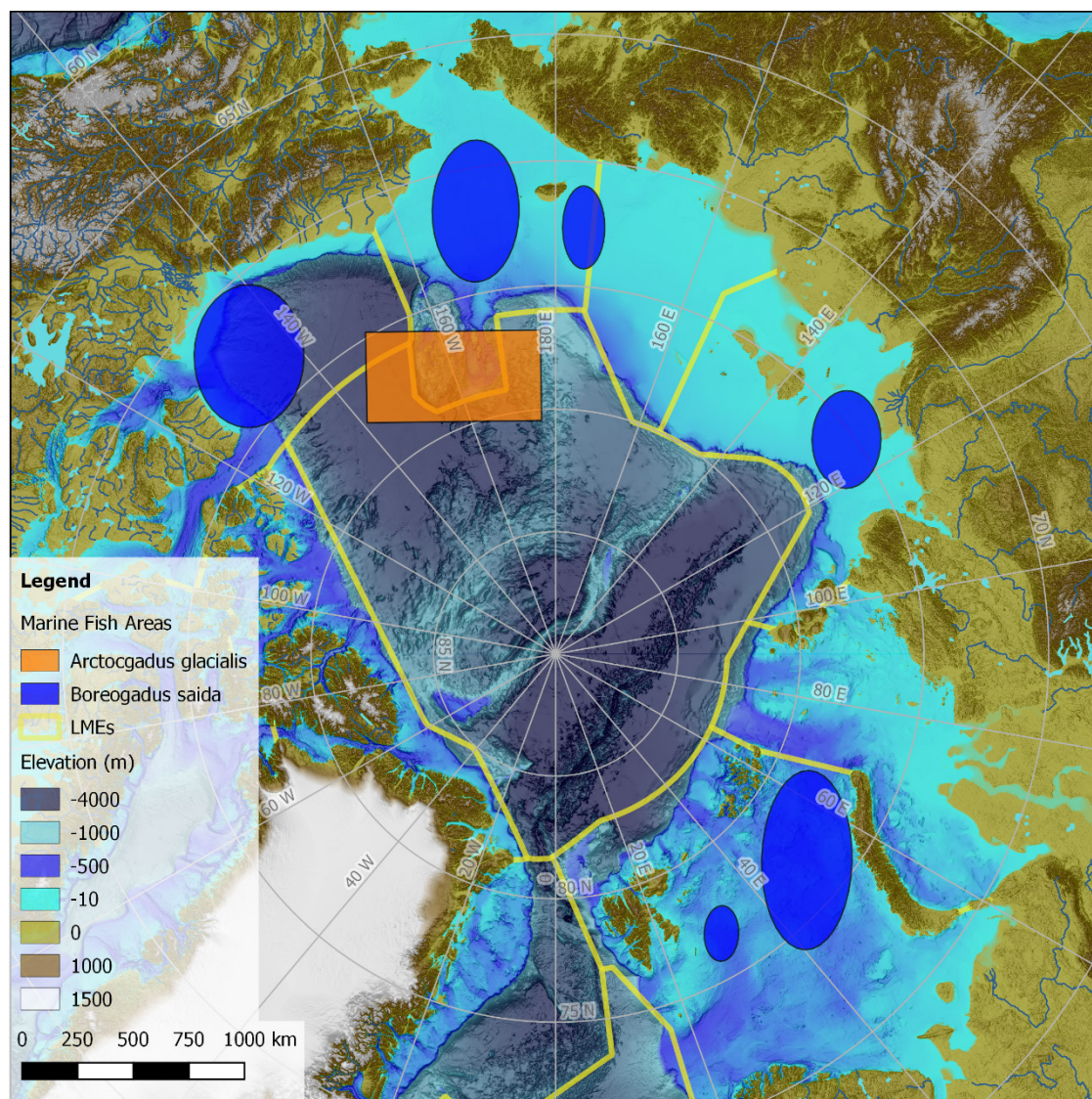


Figure 8.8. Known and tentative migratory populations or stocks of polar cod (*Boreogadus saida*) on the shelves surrounding the CAO. See the text for more information and sources for the geographical stocks or potential stocks. Also indicated is the location of a potential spawning area for Arctic cod (*Arctogadus glacialis*).

Polar cod is the most important fish in the Laptev Sea (Glebov *et al.*, 2016a; Orlov *et al.*, 2020b), where there is probably a relatively large migratory population (Ponomarenko, 1968). Several morphological forms of polar cod have been reported from the Laptev and East-Siberian seas (Chernova, 2018). The fish can feed in summer on the relatively rich zooplankton on the outer Laptev shelf (e.g. *Calanus glacialis* and *C. hyperboreus*; Kosobokova *et al.*, 1998; Kosobokova and Hirche, 2001) and move to coastal waters to spawn in winter. Khatanga Bay, at the base of the Taimyr Peninsula, has been identified as a wintering area and potential spawning area for polar cod (Ponomarenko, 1968, citing Moskalenko, 1960). Sampling of post-larvae in September (2003 and 2005) showed relatively high abundance (up to 0.2 larvae m<sup>-3</sup>) over the slope region of the eastern Laptev Sea (between about 120 and 150°E; Bouchard and Fortier, 2008). The post-larvae ranged from 15 to 60 mm, with mean length of 26 and 37 mm during the two years of study, respectively. Larvae hatching time was calculated, from otoliths and age-length regression, to be from January to June (into early July), with a better survival in 2005 due to an earlier and more frequent opening of the system of flaw polynyas (Great Siberian Polynya; Bouchard and Fortier, 2008). Early access to open water in polynya areas has been suggested as important for

successful recruitment of polar cod populations (Fortier *et al.*, 2006; Bouchard and Fortier, 2008, 2011; Bouchard *et al.*, 2017). The high abundance of post-larvae recorded in the outer Laptev Sea in September, shortly before freeze-up starts, suggests that this is an important source area for colonization of newly forming sea ice, which is in agreement with the sea ice drift hypothesis of David *et al.* (2016). It is of interest to note that the contribution of *Arctogadus glacialis* larvae was low, making up 0 and 11% of the total in the two years of study (Bouchard and Fortier, 2011).

Polar cod is found in the East Siberian Sea, and larvae have also been observed there (Rass, 1945; Ponomarenko, 1968; Glebov, 2016b; Orlov *et al.*, 2020c). However, it is not known if this reflects local spawning, or whether larvae have been advected from spawning areas elsewhere (Ponomarenko 1968). Ponomarenko (1968) described great schools of polar cod migrating past coastal sites in the eastern East Siberian Sea and along Wrangel Island and the coast of Chukotka into the western and southern Chukchi Sea. Ponomarenko corresponded with scientists at polar stations in the Russian Arctic, and his accounts and interpretations of migratory patterns of stocks were based on more than 150 reports that he received from these stations from 1959 to 1961.

Ponomarenko (1968) recognized a stock of polar cod living in the Chukchi Sea and the cold waters of the northern Bering Sea. He depicted a seasonal pattern of southward migration to wintering and spawning areas in the southern Chukchi Sea and northern Bering Sea in autumn, and migration back north in spring and summer. Abundance was suggested to increase in winter in the southern Chukchi Sea and the northern Bering Sea, and decrease in summer due to migration of the fish northward. Such seasonal migrations of polar cod, northward in spring and summer and southward in autumn, was also suggested by Lowry and Frost (1981). Based on what is now known about currents and water circulation in the Chukchi Sea, southern-spawned larvae would be transported north through the Chukchi Sea to nursery areas in the northern Chukchi Sea. Surveys of larvae and juveniles (0-group, or young of the year) have revealed that polar cod is usually the dominant species with a wide distribution in the Chukchi Sea (Norcross *et al.*, 2010). Quast (1974) obtained an average density of juvenile polar cod (modal size 44 mm in length) of 28 individuals per 1000 m<sup>3</sup> (or 0.03 individuals m<sup>-3</sup>) in the eastern central Chukchi Sea (between Point Hope and Icy Cape). Wyllie-Echeverria *et al.* (1997) sampled fish larvae and juveniles in late summer and early autumn in 1989–1991 and found polar cod to be the dominant species, being widely distributed in different water masses in the surveyed area of the northeastern Chukchi Sea. The size range of polar cod larvae and juveniles was 27–52 mm in early September 1989, and 12–51 mm in August–September 1990 (Wyllie-Echeverria *et al.*, 1997). Larvae as small as 6.3 mm (which is close to the size at hatching) were found in July, indicating that hatching extended well into the summer period.

An acoustic-trawl survey of USA waters in the northern Bering and Chukchi seas in 2012 and 2013 showed polar cod to be the dominant species, with a total estimated abundance of about 10<sup>11</sup> (100 billion) individuals (de Robertis *et al.*, 2017). The mean length was 35 mm, and they were 0-group fish. Larger individuals (100–150 mm) were observed in lesser abundance and mainly in the northern Bering Sea (de Robertis *et al.*, 2017). Other surveys in the Chukchi Sea have shown the presence of 0-group polar cod (30–40 mm in length), but also larger polar cod, collected using a demersal trawl on the shelf (up to 260 mm; Gallaway and Norcross, 2011; Logerwell *et al.*, 2015; Norcross *et al.*, 2015). Polar cod was the most abundant fish species (by an order of magnitude) collected with bottom-trawl gear on the adjacent western Beaufort shelf and slope, with the highest catches from 100–500 m depth (Rand and Logerwell, 2011). The collected fish were 50–230 mm in length, with a median length of 100–120 mm. More recent Russian acoustic surveys in the Chukchi Sea have indicated the presence of quite a high biomass of polar cod (Nikolayev *et al.*, 2008; Orlov *et al.*, 2020d).



Data from the Chukchi Sea are consistent with the suggestion of Ponomarenko (1968) of a large migratory population spawning in the northern Bering Sea or southern Chukchi Sea and residing in the northern Chukchi Sea during summer. However, it remains to be verified, along with more details on the spatial ecology of polar cod in the northern Bering–Chukchi Sea LME. The Chukchi polar cod could be partly nourished by the north-flowing seasonal pulse of zooplankton (including large copepods and krill) advected with currents north through Bering Strait (Springer *et al.*, 1989). There is also the possibility of a second stock or stock component spawning somewhere in the northwestern Chukchi Sea, where the current pattern (south-flowing Siberian Coastal Current, north-flowing Anadyr Current, and flowing around Wrangel Island) may provide a spatial context allowing a population to persist.

There is likely a large population of polar cod in the eastern Beaufort Sea. A large aggregation of wintering and presumably spawning polar cod was recorded in Franklin Bay on the south side of Amundsen Gulf in winter 2003/2004 (Benoit *et al.*, 2008). The integrated biomass of polar cod at the site (the research icebreaker CCGS Amundsen was frozen into stable landfast ice) increased in March and April to a maximum of 56 kg m<sup>-2</sup>, with an average of 11 kg m<sup>-2</sup> for the February–April period. Polar cod (collected with trammelnet) ranged in length from 120 to 260 mm, with a mean of 164 mm (Benoit *et al.*, 2008, 2010). Extrapolating the density of fish to the area of Franklin Bay (deeper than 140 m) gave an estimate of several million tons, suggesting a very large population. During winter 2007/2008, the vessel Amundsen was mobile (breaking ice) and surveyed a large part of Amundsen Gulf. Aggregations of polar cod formed when freeze-up started, and were observed in the deep part (220–550 m), in the Atlantic layer below ice cover, from December to April (Geoffroy *et al.*, 2011). The highest densities of fish were found along the slope on the north side of Amundsen Gulf (south of Banks Island) with a maximum of 0.7 kg m<sup>-2</sup> in February. The results suggested that the very high densities observed in Franklin Bay reflected a progressive local build-up of exceptionally dense shoals (Geoffroy *et al.*, 2011). A pre-winter survey (in October–November 2003, prior to the winter observations in Franklin Bay) showed two distinct layers: an upper layer (0–60 m) of 0-group polar cod, and a deeper layer (about 200–400 m) of larger adult polar cod (Benoit *et al.*, 2014; [Figure 8.9](#)). The highest densities were observed close to the seabed, along the slopes, and in deeper parts of Amundsen Gulf, with a maximum of 37 g m<sup>-2</sup> (mean of 3 g m<sup>-2</sup> for the mesopelagic layer). Note that this is considerably lower (by 2–4 orders of magnitude) than the aggregations of polar cod found in winter in Amundsen Gulf (up to 0.7 kg m<sup>-2</sup>) and in Franklin Bay (average of 11 kg m<sup>-2</sup>; Benoit *et al.*, 2008; Geoffroy *et al.*, 2011).

The presence of an epipelagic layer of 0-group polar cod in autumn is clear evidence of spawning for polar cod, presumably under ice in winter in an area such as Franklin Bay, where the huge aggregations were observed. Mean density (determined acoustically) was 0.5 individuals m<sup>-2</sup> or about 0.02 individuals m<sup>-3</sup> (Benoit *et al.*, 2014). This is quite similar to the value of 0.03 individuals m<sup>-3</sup> found in the Chukchi Sea (Quast, 1974) and comparable to densities found in the Laptev Sea (range about 0.01–0.2 individuals m<sup>-3</sup>; Bouchard and Fortier, 2008). A summary of the biomass of 0-group polar cod in the upper (0–100 m) layer in the southeastern Beaufort Sea and Amundsen Gulf region showed very low values in late winter (< 0.01 g m<sup>-2</sup>, March–May), followed by increasing values in summer to a maximum biomass in autumn (1–2 g m<sup>-2</sup>; August–October; Geoffroy *et al.*, 2016). The 0-group fish in the epipelagic layer descended to join older polar cod deeper in the water column from September onward. Older polar cod descended deeper in the water as light increased in spring, presumably to avoid predation by seals and other predators such as beluga whales (*Delphinapterus leucas*; Benoit *et al.*, 2010; Geoffroy *et al.*, 2011, 2016).

It can be assumed that polar cod that aggregates to overwinter in Amundsen Gulf and Franklin Bay, where they presumably spawn, must disperse to feed in summer over a wider area in the southern and southeastern Beaufort Sea. A key question is whether, and to what extent, the

polar cod disperse pelagically out into Canada Basin. This is related to another key question, which is to what extent polar cod is a demersal species that is reluctant to leave the shelf and slope to forage in a truly pelagic mode out over deep water. Data from the Beaufort Sea show polar cod in concentrations along the slopes at depths of 300–500 m in summer. Individuals caught with bottom trawl had been feeding mainly on large copepods (*Calanus hyperboreus* and *C. glacialis*) and amphipods (*Themisto libellula* and *T. abyssorum*). Smaller polar cod took mainly copepods, while larger fish, which were distributed deeper, ate mainly amphipods (Majewski *et al.*, 2013, 2016). Acoustic records showed highest densities of polar cod along the slopes of Mackenzie Shelf and Amundsen Gulf (Benoit *et al.*, 2014). This suggests a demersal or benthopelagic lifestyle where individuals feed on zooplankton in the water column while maintaining some contact with the seabed, perhaps to seek relative safety from predators such as beluga whales, seals, and diving seabirds.

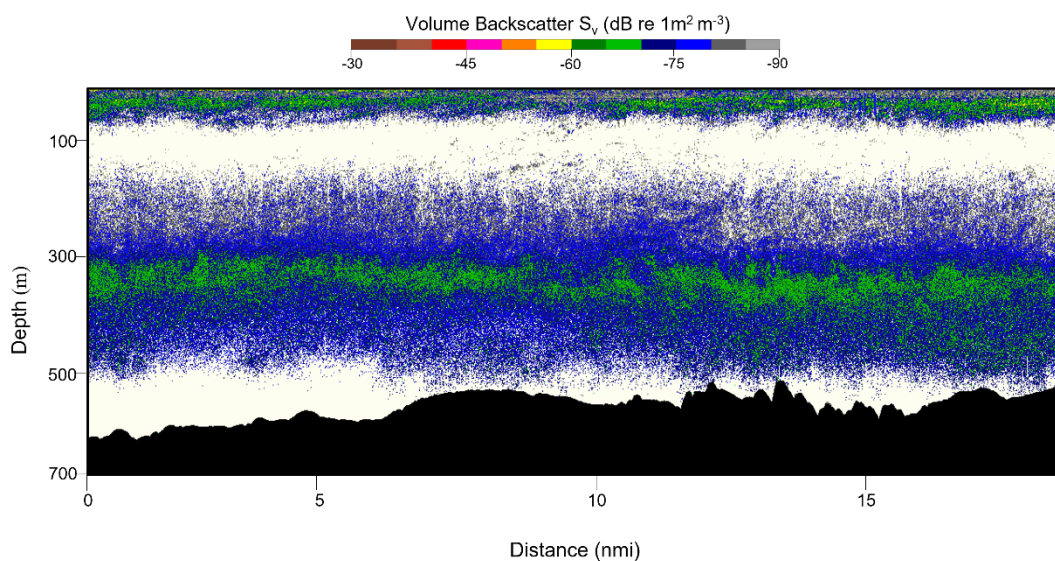


Figure 8.9. Echogram showing juvenile (young-of-year) polar cod (*Boreogadus saida*) at the surface and a layer of older polar cod deeper in the water column below 200 m depth. The strongest signals from concentrations of polar cod are coded with green color. The echogram was recorded in the North Water Polynya between Canada and Greenland in August 2016. Source: Jennifer Herbig and Maxime Geoffroy, Memorial University, Canada.

When leaving the wintering and spawning area in Amundsen Gulf (Franklin Bay), polar cod are probably following the slope westward in the Beaufort Sea, and possibly also northward along the slope west of Banks Island and into M'Clure Strait. Polar cod was the main species of fish caught by bottom trawl on the western Beaufort slope, with the highest catches in warmer water from 100 to 500 m depth (Logerwell *et al.*, 2011, 2015; Rand and Logerwell, 2011). It is not known whether these fish are from the eastern Beaufort stock, or whether they belong to a Chukchi stock that forages along the Chukchi and western Beaufort slopes, partly on zooplankton from the outflowing currents of water that had been advected north across the Chukchi Sea during summer (Logerwell *et al.*, 2018).

### 8.5.2 Arctic cod (*Arctogadus glacialis*)

Arctic cod (*Arctogadus glacialis*; note that the species is called polar cod in North America; and can also be called ice cod) is a larger species than polar cod, growing to a maximum size of about 60 cm total length (Mecklenburg *et al.*, 2018). Jordan *et al.* (2003) presented data for individuals with a standard length of up to nearly 50 cm (their Figure 5). Arctic cod matures at a length of more than 20 cm (Jordan *et al.*, 2003), compared to 15–20 cm for polar cod (Ajiad *et al.*, 2011).



The species described as East Siberian cod (*Arctogadus borisovi*) has been shown, genetically and morphometrically, to be the same species as Arctic cod (Møller *et al.*, 2002; Jordan *et al.*, 2003; Mecklenburg *et al.*, 2011, 2018; Mecklenburg and Steinke, 2015).

Arctic cod has a wide and circumpolar distribution in the high Arctic, and is found mainly in cold waters over outer shelves and slopes (Mecklenburg *et al.*, 2018). The distribution includes the Arctic shelves surrounding the CAO, extending south to Baffin Bay and waters around Greenland, including fjords (Boulva, 1972; Andriyashev *et al.*, 1980; Jordan *et al.*, 2003; Aschan *et al.*, 2009; Møller *et al.*, 2010; Mecklenburg *et al.*, 2011, 2014, 2018; Christiansen *et al.*, 2012). The species is assumed to be absent from the CAO basins (Aschan *et al.*, 2009; Mecklenburg *et al.*, 2018). It is important to further explore this assumption in relation to the role that Arctic cod might play in the CAO ecosystem. It occurs from shallow waters, including estuaries, to depths of 800–900 m, often near the bottom (Jordan *et al.*, 2003). Individuals collected in the European Arctic were mainly from between 200 and 500 m depth, and most of them from 300–400 m (Aschan *et al.*, 2009; Christiansen *et al.*, 2012).

Andriyashev *et al.* (1980) described observations and collections of Arctic cod (and polar cod) from Soviet ice-drift stations, most extensively from NP-16, which drifted in Canada Basin around 80°N, 170–180°E. In November–December, large numbers (hundreds) of small cod were caught with baited hooks down to 25 m below the ice. Visually, schools of thousands of fish were seen through holes in the ice. In the first part of winter, the fish were small (< 200 mm) and assumed to be mainly polar cod (*Boreogadus saida*). Small individuals, increasing in size from 70 mm in November to 100–110 mm in February, were assumed to be age-1 fish, probably polar cod, but possibly also Arctic cod (Andriyashev *et al.*, 1980). Later in winter, in February and March, larger fish predominated, with maximum sizes up to 30–43 cm. The large fish collected (> 20 cm) were confirmed to be Arctic cod. The maximum length of collected polar cod was usually 19 cm or less (although one individual was 25 cm; Andriyashev *et al.*, 1980). The fish were caught near the underside of the ice in the dark period of winter (November–February), but with the return of the sun, the fish were caught deeper, mainly at 10–25 m in late March (Andriyashev *et al.*, 1980). This observation from the ice-drift stations suggests that Arctic cod live pelagically in the water column under sea ice, descending deeper with increasing light in late winter and spring.

Arctic cod was found to be abundant over Chukchi Rise (at about 77°N) in winter, as observed under the ice from a US drift station (Walters, 1961). Arctic cod was found only in winter, which led Walters (1961) to conclude that the fish were not drifting with the ice, but instead undertook a winter migration, possibly to a spawning area in this region (AMAP/CAFF/SDWG, 2013). An alternative explanation could be that Arctic cod descended in the water column during spring, and was no longer observable from the ice platform.

The spawning period of Arctic cod is not well known, but it is assumed to be in winter. Females (27 cm or more) collected by Andriyashev *et al.* (1980) in February–March had gonads in a state suggesting that they had spawned within the last 2–3 months, i.e. spawning in mid-winter. Observations on the gonad status of Arctic cod from the European Arctic also suggest spawning during winter (Süfke *et al.*, 1998; Aschan *et al.*, 2009). However, spawning may also extend into spring or summer, as suggested by ripe ovaries of specimens of the borisovi type in the Russian Arctic, and elsewhere (Andriyashev, 1964; Jordan *et al.*, 2003; Aschan *et al.*, 2009). Larvae of Arctic cod were separated from polar cod by genetics, otolith structure, and size, in a recent study in the Amundsen Gulf region. They made up 8–9% of the total number of gadid larvae (Bouchard *et al.*, 2016). Arctic cod larvae hatched mainly in March and April (somewhat earlier than polar cod), confirming winter spawning a few months earlier. At the post-larval stage (0-group) in autumn, Arctic cod made up about 10% of the gadid larval numbers compared to polar cod during one year in the Laptev Sea (Bouchard and Fortier, 2011).

## 8.6 Potential expansion of boreal species into the Arctic Ocean

Hollowed *et al.* (2013) evaluated the potential for boreal species to extend their range into the Arctic Ocean. They considered deepwater (beaked) redfish (*Sebastes mentella*) to have a potential to expand into the Arctic Ocean on the Atlantic side, whereas Pacific ocean perch (*Sebastes alutus*) was considered to have a low potential for expansion on the Pacific side. This report includes deepwater redfish in [Table 8.1](#) as one of the species that is already found in the CAO basins, in the Atlantic gateway area, and has the potential to spread into the CAO LME.

Atlantic cod (*Gadus morhua*) has expanded to the northern shelf edge of the Barents Sea due to recent warming (Fossheim *et al.*, 2015), and has been found venturing into the pelagic realm over deep water in the Fram Strait region, although in low density (Ingvaldsen *et al.*, 2017). The observed cod were feeding on a mesopelagic layer of krill, amphipods, and myctophids (dominated by *Benthosema glaciale*; Knutsen *et al.*, 2017). The deep scattering layer becomes weaker (lesser abundance) from south to north in the Norwegian Sea (Siegelman-Charbit and Planque, 2016; Knutsen *et al.*, 2017), and is probably further weakened down-current into the Arctic Ocean. This may limit the potential expansion of Atlantic cod into the pelagic domain of the CAO basins, since it is an aberrant habitat for a shelf species. Despite this, three specimens of Atlantic cod were fished by line and hook from the deep scattering layer in the Amundsen Basin during the recent MOSAiC expedition (Snoeijs-Leijonmalm *et al.* 2022).

Atlantic herring (*Clupea harengus*) has been considered to have the potential for expansion into the Arctic (Hollowed *et al.*, 2013), but there is no evidence yet for movement north of western Spitsbergen (Haug *et al.*, 2017). Atlantic capelin (*Mallotus villosus*) is an additional candidate for expansion, especially if the spawning areas move from northern Norway to the Arctic islands (Hop and Gjøsæter, 2013; Haug *et al.*, 2017). Atlantic capelin and Pacific capelin (*Mallotus catervarius*) are shelf species found in the wider CAO, but they have not yet been documented in the CAO basins beyond the shelf break.

Northern rock sole (*Lepidopsetta polyxystra*), yellowfin sole (*Limanda aspera*), and Alaska plaice (*Pleuronectes quadrituberculatus*) were three more boreal species considered by Hollowed *et al.* (2013) to have the potential for movement into the Arctic Ocean (albeit low for northern rock sole) because they are currently found in the northern Bering Sea. Yellowfin sole and Alaska plaice are found on shelves and upper slopes to depths of 400–600 m, and have been recorded in the northeastern Chukchi Sea. They are predominantly shelf species, found typically in waters shallower than 100 and 150 m depth for Alaska plaice and yellowfin sole, respectively (Mecklenburg *et al.*, 2018). Whether the two species could expand their distributions beyond the shelf edge of the Chukchi and Beaufort seas is uncertain. Two more *Limanda* flounders have been recorded in the northeastern Chukchi Sea: longhead dab (*Limanda proboscidea*) and Sakhalin sole (*L. sakhalinensis*). Longhead dab is found on the Beaufort shelf extending east to Amundsen Gulf and Bathurst Inlet in the Canadian Arctic Archipelago (Mecklenburg *et al.*, 2018). It is a shallow shelf species (recorded to a maximum of 160 m depth) and is not likely to be found beyond the shelf edge in the CAO basins. Sakhalin sole has been recorded on the northern Chukchi shelf. This species is typically found shallower than 200 m, but it could possibly extend beyond the shelf edge in this area.

Hollowed *et al.* (2013) also considered additional species (including Greenland shark, Arctic skate, Greenland halibut, and Bering flounder) that are classified as Arctic-boreal. These have been included here on the list of species found on the Arctic shelves and slopes surrounding the Arctic Ocean basins ([Table 8.1](#)).

The Pacific and Atlantic gateways differ in one fundamental aspect related to their depths. The Pacific gateway consists of an approximately 1000-km stretch of very shallow water (around 50 m deep) that separates the slopes and basins of the Bering Sea from the slopes and basins of

the Arctic Ocean. This long stretch of water cools to freezing temperature, which is associated with ice formation in winter and could act as a barrier for seasonal migration if fish were to use the Arctic Ocean for summer feeding and return to winter in the Bering Sea. The net northward flow of water through Bering Strait and the Chukchi Sea adds to the difficulty of performing seasonal migrations in the Pacific gateway area. If Arctic-boreal and boreal species were to move into the CAO, they would have to establish new populations with spawning areas north of, or in the northern part of, the Pacific gateway area. This is not likely to happen until there is a very dramatic change in environmental conditions associated with further strong global warming.

In contrast, the Atlantic gateway is a deep connection between the Atlantic and Arctic oceans through Fram Strait, with a sill depth of about 2500 m. The basins of the CAO LME and those of the Nordic Seas are closely connected as parts of the Arctic Mediterranean Sea. The slope environment along the eastern side of the Norwegian Sea forms a habitat that continues into the Arctic Ocean along the slope to Nansen Basin. The WSC branch turns the northwestern corner of Svalbard over Yermak Plateau, and continues eastward along the slope north of the Barents and Kara seas as the Fram Strait branch of inflowing Atlantic water. While the slope habitat is continuous, the Atlantic water is cooled *en route*, and there may be discontinuities associated with the change in currents at Yermak Plateau, as well as in light conditions in the transition from open to ice-covered waters north of Svalbard. Dominant species in deep-water and cold-water slope communities in the Norwegian Sea, such as Arctic skate (*Amblyraja hyperborea*), glacial eelpout (*Lycodes frigidus*), and pale eelpout (*L. pallidus*; Bergstad *et al.*, 1999; Bjelland *et al.*, 2000; Bjelland and Holst, 2004), are also found in deep-water slope habitats in the Arctic Ocean.

Many boreal fish species found along the continental slopes have distributions that extend north along western Svalbard and, in some cases, also north of Svalbard. Examples are round ray (*Rajella fyllae*), roughhead grenadier (*Macrourus berglax*), and haddock (*Melanogrammus aeglefinus*), which are also found on shelves (Mecklenburg *et al.*, 2018). Stray individuals of these slope fish can be expected farther into the Arctic Ocean. With continued warming, their distribution can be expected to expand eastward along the slope of the Eurasian Basin and possibly beyond. Two commercially important boreal species, cusk or tusk (*Brosme brosme*) and ling (*Molva molva*), are found north to western Svalbard, but not further into the Arctic Ocean (Byrkjedal and Høines, 2007; Wienerroither *et al.*, 2011). Several Arctic and Arctic-boreal species that are considered Atlantic fish were found in the slope region (227–588 m depth) of the Chukchi Borderland in a RUSALCA expedition in 2009 (Mecklenburg *et al.*, 2014). This illustrates the continuous nature and connectivity of the slope habitat in the Arctic Ocean.

### 8.6.1 Walleye pollock (*Gadus chalcogrammus*)

One species of interest, which is found in the Pacific gateway, is walleye pollock (*Gadus chalcogrammus* or *Theragra chalcogramma*). It is now projected with a disjunct amphiboreal distribution, with the main population in the Pacific Ocean (Gulf of Alaska, Bering Sea, Sea of Okhotsk, and Sea of Japan), and a small Atlantic population known as Norwegian or Atlantic pollock in the Barents Sea (Mecklenburg *et al.*, 2018). The Atlantic population was earlier described as *Theragra finmarchica*, but it has now been established that this is not a valid species, and that these fish are the same as walleye pollock in the Pacific (Ursvik *et al.*, 2007; Byrkjedal *et al.*, 2008; Mecklenburg *et al.*, 2018). Juvenile walleye pollock have been recorded in the Chukchi Sea, presumably carried north with the currents through Bering Strait. Specimens collected in the Chukchi Sea are typically less than 17 cm in length, although larger individuals can be caught there (Mecklenburg *et al.*, 2016, 2018). Russian investigations in 2019 obtained individuals of walleye pollock up to 70 cm in length.

Walleye pollock avoid cold temperatures in the northern Bering Sea. The distribution of juveniles and adults extend farther north in warm years with less ice, than in cold years with heavier winter ice (Wyllie-Echeverria and Wooster, 1998; Wyllie-Echeverria and Ohtani, 1999). It is possible that some of the juveniles and adults may migrate into the southern Chukchi Sea in their seasonal feeding migrations in warm years, since large adults (55–81 cm) have been recorded in bottom-trawl catches (Wyllie-Echeverria, 1995). Such large specimens may have the capacity to swim back to the Bering Sea before autumn cooling prevents them from doing so. Juvenile walleye pollock of ages up to 4 years and sizes up to 32 cm have been recorded in bottom-trawl surveys at depths of 100–500 m along the Beaufort slope (Rand and Logerwell, 2011). An even larger individual (38 cm) was collected along the Chukchi slope at about 230 m depth (Mecklenburg *et al.*, 2014). Logerwell *et al.* (2018) also caught juvenile pollock in the Chukchi Sea, with a length range of 65–168 mm, and an average length of 102 mm ( $n = 32$ ). Juveniles and preadults of this size are not expected to swim south to winter in the Bering Sea, and their presence in fair numbers suggests that they can survive and live for some years in the warm Atlantic layer underlying the upper layer that cools to freezing in winter.

Specimens of walleye pollock collected in the Barents Sea have all been large (48–71 cm), most of them caught in commercial longline fisheries off Finnmark in northern Norway (Christiansen *et al.*, 2005; Byrkjedal *et al.*, 2008; Zhukova and Privalikhin, 2014; Mecklenburg *et al.*, 2018). The lack of smaller individuals is noteworthy, and suggests that walleye pollock in the Barents Sea may not be a locally reproducing population, but are rather expatriated individuals from the Pacific side. It should be noted that small juveniles ( $< 13$  cm) can be difficult to distinguish from polar cod (Mecklenburg *et al.*, 2016) and may have been "hidden" among the more numerous polar cod collected during scientific surveys. However, larger juveniles and preadults, 20–45 cm in length, should have been detected in the extensive surveys by Norway and Russia, especially since attention was given to the rare and red-listed *Theragra finmarchica*, described by Koefoed (1956), based on the collection of a few larger individuals in scientific surveys some years earlier (Fevolden *et al.*, 2008). Thus, it is likely that the Atlantic "population" of walleye pollock is not a true population, but rather stray individuals coming from the Pacific side across the CAO. Their appearance in the Barents Sea seems to be episodic (Christiansen *et al.*, 2005), suggesting that waves of walleye pollock, possibly in small schools, come across the CAO to enter the Barents Sea.

The distance from the Chukchi Borderland to Fram Strait is about 3000 km. For comparison, this is the same distance that an average Atlantic herring of the Norwegian spring-spawning stock migrates annually between feeding, overwintering, and spawning areas (Nøttestad *et al.*, 2004). The Atlantic layer, extending from about 200 m to more than 500 m depth, offers a wide corridor of tolerable temperatures (0–3°C) that walleye pollock could use to migrate across the CAO. Food would be available to sustain the migration in the form of copepods, amphipods, and small polar and Arctic cod. If this interpretation is correct, walleye pollock should be considered a species with regular occurrence in the CAO LME.

## 9 Marine birds: species occurrence and habitat use

*Maria Gavrilov, Kathy Kuletz, and Hein Rune Skjoldal*

### 9.1 Introduction

The CAO is a large, enclosed sea bordered by the northern shorelines of the Eurasian and North American continents. It consists of two deep basins (Eurasian and Amerasian basins, 3–4 km deep) with steep slopes to surrounding shelves, which are particularly broad and shallow on the Eurasian side (Bluhm *et al.*, 2015). For the purpose of this report, the CAO ecosystem is defined as the basins and slopes, but excluding the shelves (see [Figure 1.1](#)). The area of this ecosystem is about 3 million km<sup>2</sup>. In addition, for purposes of integrating important areas for seabirds that may use the CAO, this report also considers the associated shelves near the two main gateway into the CAO: the Chukchi Sea in the Pacific sector and Fram Strait and the Barents Sea in the Atlantic sector.

The CAO is an ice-covered sea characterized by drifting pack ice. It is an ecosystem in transition due to the substantial loss of sea ice that has taken place in recent decades (in what has been coined the "Great Melt"). This loss that is projected to continue, leading to an ice-free CAO in summer over perhaps the next few decades (Stroeve *et al.*, 2012; Overland and Wang, 2013; Brown and Caldeira, 2017; AMAP, 2017). However, even under a warmer climate, the CAO will continue to be an Arctic sea with seasonal sea ice cover, with ice forming in winter and melting in summer.

In order to assess and project the consequences of warming and sea ice loss on the CAO ecosystem, a baseline is needed which describes the current and recent situation. Here, the authors compile and review information on the occurrence of marine birds in the CAO and the degree to which they use and depend on habitats there during the annual cycle.

### 9.2 Observations of birds in the CAO

Many species of birds are adapted to life in ice-covered waters ([Figure 9.1](#)), and most of them are found in the southern ranges with seasonal ice cover (Karnovsky and Gavrilov, 2017). In the CAO, birds have been sighted all the way to the North Pole. The first well-documented records of birds were made during the drift of the ship Fram frozen into sea ice in 1893–1896 (Collett and Nansen, 1900). In the mid-20th century, data were collected over a large portion of the CAO in the course of long-term work on the Russian ice-drifting stations (North Pole stations), compiled by Rutilevskiy and Uspenskiy (1957) and Yudin (1964), and occasional from ships forced to drift (Buinitskiy, 1946; Portenko, 1946). More recently, icebreaker research vessels operating in the CAO have provided platforms for dedicated bird surveys (Hjort *et al.*, 1997; Joiris *et al.*, 2016; Gavrilov, 2009a; M. Gavrilov, unpublished data; K. Kuletz, unpublished data; C. Gjerdrum, unpublished data) and incidental observations (Todd *et al.*, 1992; Parmelee and Parmelee, 1994; Vuilleumier, 1996). Recently, with the introduction of new methods for animal tracking, data became available for selected seabird species instrumented with satellite transmitters or global location sensors (GLS; e.g. Gilg *et al.*, 2010, 2016a, 2016b; Maftai *et al.*, 2014, 2015; Davis *et al.*, 2016; Spencer *et al.*, 2014, 2016; Yurkowski *et al.*, 2019, and references herein; SEATRACK project<sup>3</sup>). [Section 9.3](#) reviews sightings and remote sensing information reported in

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<sup>3</sup> <https://seatrack.seapop.no/map/>



the literature, and [Section 9.4](#) presents information of new sightings from research vessels in Canada Basin, the adjacent Beaufort and Chukchi slope/shelves, and Eurasian Basin.

About 35 species of birds have been recorded in the CAO. Obviously, no species breed in the CAO itself, but the CAO is fringed with high-Arctic archipelagos, located along the edge of the surrounding shelves, that provide good breeding habitats for many Arctic seabird species. While breeding, birds are central-place foragers, and must regularly commute between their nesting colonies and foraging areas. Thus, only seabirds with long foraging ranges can potentially travel to the CAO to feed during their nesting period. This could be particularly the case for slope waters, e.g. in Nansen Basin north of Svalbard, Franz Josef Land, and northeast of Severnaya Zemlya. However, most of the birds recorded in the CAO are likely not commuting from their breeding colonies, but are instead free-range foragers. These birds include missed or failed breeders, non-breeders, or birds on seasonal migrations, and they may come to the CAO from colonies far from the CAO. [Section 9.5](#) summarizes information on high-latitude bird colonies, and examines the potential for birds nesting in these regions to forage in the CAO. [Sections 9.3](#) and [9.4](#) review available information on birds observed in the CAO, either during the breeding season or post-breeding season, after they leave the colonies and before they move south to wintering areas.

Two seabird species have their characteristic habitat in the Arctic Ocean: ivory gull (*Pagophila eburnea*) and Ross's gull (*Rhodostethia rosea*). Both are adapted to feed in ice-covered waters, and both may occur there with significant parts of their total populations during summer and (early) autumn (Divoky, 1976; Blomqvist and Elander, 1981; Meltofte *et al.*, 1981; Hjort *et al.*, 1997; Mallory *et al.*, 2008a; Gilg *et al.*, 2010, 2016a, 2016b). Other species occur there to a more limited extent, or sporadically as occasional visitors or vagrants. [Section 9.6](#) gives individual species accounts for those seabirds, besides ivory and Ross's gulls, which are most abundant in high-latitude breeding colonies and are most often encountered in the CAO. Transient migrants crossing the CAO on passage, like some waders do (Alerstam *et al.*, 2001, 2007; Hedenström *et al.*, 2009), are not considered here.



Figure 9.1. Black-legged kittiwake, one of the common species seen in the CAO. Photo: Liz Labunski, USFWS.

### 9.3 Bird fauna and general patterns of species distribution in the CAO

About 35 species of birds have been recorded in the CAO ([Table 9.1](#)). They belong to a wide range of families, but most species belong to the auks (family Alcidae, nine species), gulls (Laridae, five species), and skuas or jaegers (Stercorariidae, four species). Half of the recorded species are observed only as rare or occasional vagrants, and only eight species are found regularly within the CAO ([Figure 9.2](#)). In addition to ivory gull and Ross's gull, these are northern fulmar (*Fulmarus glacialis*), black-legged kittiwake (*Rissa tridactyla*), glaucous gull (*Larus hyperboreus*), dovekie or little auk (*Alle alle*), thick-billed murre (*Uria lomvia*), and black guillemot (*Cepphus grylle*). [Section 9.6](#) provides detailed accounts for these eight species, as well as for Sabine's gull (*Xema sabini*), and the Pacific ecological equivalent to the planktivorous dovekie, the least auklet (*Aethia pusilla*), because of its recent increases in the Pacific Arctic. Among these species are six of the eight seabirds identified as focal ecosystem components (FECs) for the Circumpolar Biodiversity Monitoring Program (CBMP) of the Arctic Council: glaucous gull, ivory gull, black-legged kittiwake, thick-billed murre, dovekie, and least auklet. Countries within an FEC species' range are encouraged to monitor populations and trends, colonies, at-sea interactions, and threats to these species (CAFF, 2017).

Among the long-distance flying seabirds feeding in the surface layers of the ocean, black-legged kittiwake has been observed north of 86°N (Baird, 1994; Parmelee and Parmelee, 1994), as has northern fulmar (Vuilleumier, 1996; Hatch and Nettleship, 1998), ivory gull, and Ross's gull (Rutilevskiy, 1970; Todd *et al.*, 1992; Parmelee and Parmelee, 1994; Vuilleumier, 1996; Joiris *et al.*, 2016). All four species have been sighted near the North Pole (Parmelee and Parmelee, 1994; Vuilleumier, 1996; M. Gavrilov, 2001–2016, unpublished data).

Glaucous gull is a coastal feeding species that can also occur far offshore, mostly within ice-filled waters in the marginal ice zone. It can be observed in CAO pack ice elsewhere, but in very small numbers. Sabine's gull (*Xema sabini*), in contrast to the other Arctic gulls considered here, winters in the southern hemisphere. Sabine's gull breeds in Arctic Canada and uses the Pacific flyway, across marginal portions of Canada Basin, on their seasonal migrations (Davis *et al.*, 2016). Skuas and Arctic tern (*Sterna paradisaea*) are also transequatorial migrants, and their presence in the Arctic is relatively short compared to northern hemisphere residents. Three species of skuas or jaegers [long-tailed jaeger (*Stercorarius longicaudus*), parasitic jaeger (*S. parasiticus*), and pomarine jaeger (*S. pomarinus*)] are visitors to the marginal ice zone of the CAO, but are seldom recorded as far north as 85°N (Rutilevskiy and Uspenskiy, 1957; M. Gavrilov, unpublished observations). Great skua (*Stercorarius skua*) has expanded north and east in the Atlantic sector, is now found breeding from Svalbard to Franz Josef Land and on northeastern Novaya Zemlya, and has been sighted recently north of Franz Josef Land (M. Gavrilov, S. Haugum, V. Buzun, 2016, unpublished observations). It also occurs regularly in the Northeast Water Polynya off northeast Greenland (Boertmann *et al.*, 2020b). Arctic tern is the rarest visitor to the CAO out of all observed Larids. On the Pacific side, short-tailed shearwater (*Ardenna tenuirostris*), which is an Austral winter visitor from the southern hemisphere, has been regularly observed in the slope waters of Canada Basin (Nishizawa *et al.*, 2017).

Among the auks, which are diving birds that feed in the water column, black guillemot is the most wide-spread in the CAO, while dovekie keep closer to the shelf slope and are less frequently observed in the CAO (Lönnberg, 1931; Buinitskiy, 1946; Portenko, 1946; Uspenskiy, 1956; Rutilevskiy and Uspenskiy, 1957; Yudin, 1964; Rutilevskiy, 1970; Todd *et al.*, 1992; Parmelee and Parmelee, 1994; Vuilleumier, 1996; M. Gavrilov, 2001, 2008, 2016, unpublished observations). These species are described in more details in [sections 9.6.7](#) and [9.6.10](#).

Benthos-feeding diving sea ducks also occur in the CAO, including long-tailed duck (*Clangula hyemalis*), common eider (*Somateria mollissima*), and king eider (*S. spectabilis*; Lönnberg, 1931;



Buinitzkiy, 1946; Portenko, 1946; Uspenskiy, 1956; Rutilevskiy and Uspenskiy, 1957; Yudin, 1964; Rutilevskiy, 1970). The long-tailed duck has been reported most often, and conducts, in general, longer-distance migrations. All sea ducks are vagrants to the CAO, since it lies beyond their preferred foraging habitat of shallow waters up to 50 m deep.

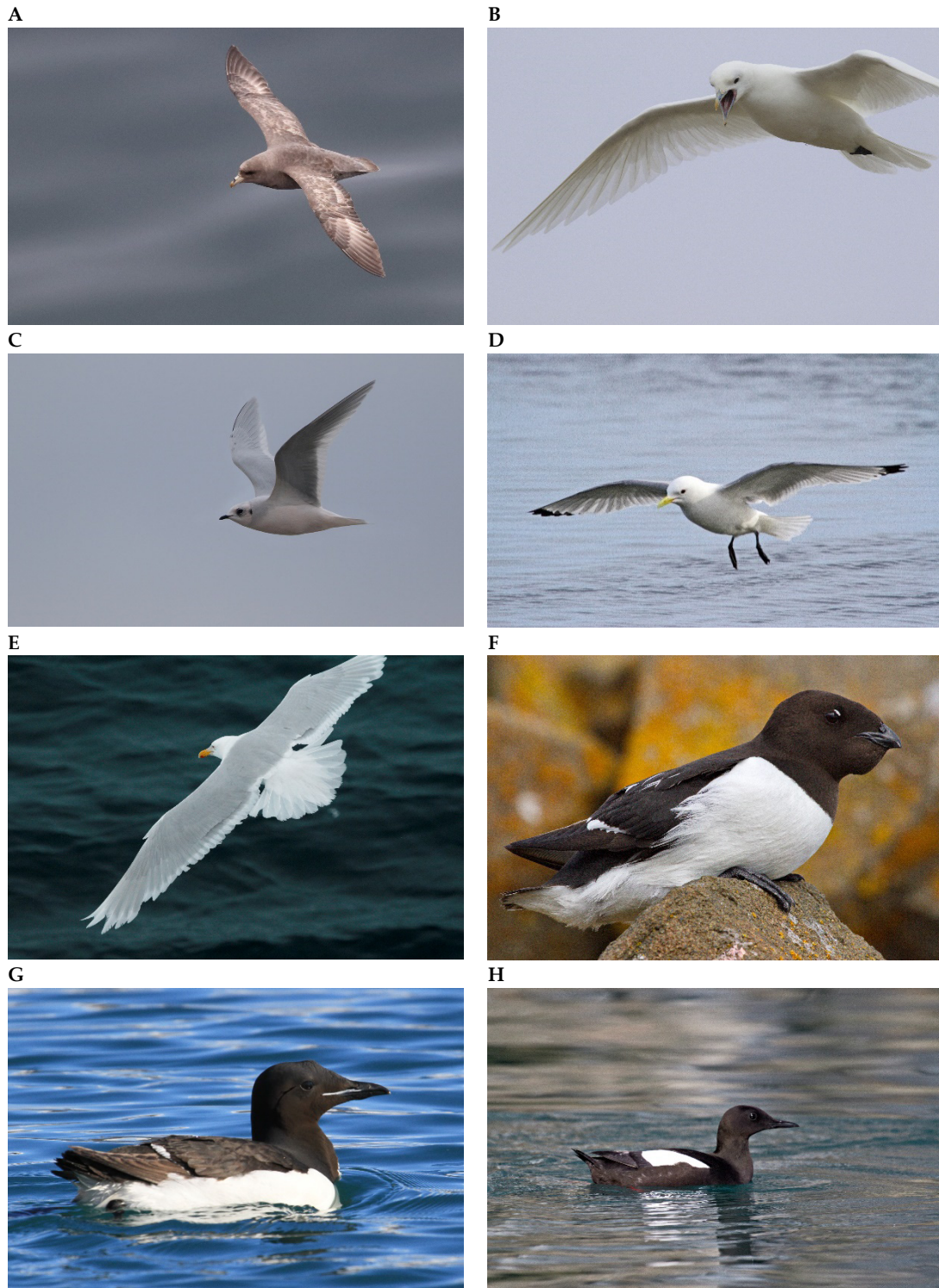


Figure 9.2. Photos of the eight most common species of birds in the CAO. A: northern fulmar; B: ivory gull; C: Ross's gull; D: black-legged kittiwake; E: glaucous gull; F: dovekie; G: thick-billed murre; and H: black guillemot. Photos: Maria Gavrilov (ivory gull, black-legged kittiwake, dovekie, thick-billed murre, and black guillemot), Kathy Kuletz (northern fulmar, and glaucous gull), and Zachary Pohlen (Ross's gull).

Other birds observed in the Arctic Basin are shorebirds, like purple sandpiper (*Calidris maritima*), grey phalarope (*Phalaropus fulicarius*), and snow bunting (*Plectrophenax nivalis*), when individuals occasionally deviate from their normal migration routes. Other species listed in [Table 9.1](#) are only occasional vagrants to the CAO area (Lönnberg, 1931; Buinitskiy, 1946; Portenko, 1946; Uspenskiy, 1956; Rutilevskiy and Uspenskiy, 1957; Yudin, 1964; Rutilevskiy, 1970; Todd *et al.*, 1992; Vuilleumier, 1996; M. Gavrilov, unpublished data collected from the drifting stations).

Seabirds in the Arctic Ocean are most commonly found in the peripheral parts of the pack ice, i.e. the marginal ice zone (Hunt *et al.*, 1996) and are increasingly scarce as one moves north into the central waters of the Arctic Basin and farther from the Atlantic and Pacific gateways. In general, birds in the CAO occur scattered and in small numbers during summer and autumn, when they can be found throughout the ocean in cracks and leads in the ice, all the way to the North Pole. Due to the very low pelagic productivity, birds depend on ice fauna as prey (e.g. ice amphipods) and occur almost entirely in ice-filled waters (Gavrilov, 2009b and unpublished data).

## 9.4 Seabird observations in the Pacific Arctic

Recent sightings from research vessels in the Pacific Arctic have provided more detailed information on seabird distribution in Canada Basin, the shelf slope, and the adjacent Chukchi shelf ([Figure 9.3](#)). During at-sea surveys conducted in 2006–2017, 27 species of marine birds were recorded within the slope or basin waters of the Chukchi and western Canadian Beaufort seas ([Table 9.2](#)). While some species nest on the mainland of Alaska or Canada (i.e. kittiwakes and other gulls, terns, murres, puffins), most appear to extend their foraging or migration routes northward during summer and autumn. The most abundant bird in the Pacific sector of the CAO and adjacent slopes is short-tailed shearwater (*Ardenna tenuirostris*), a long-distance migrant. This species is a summer visitor from breeding sites off Australia and Tasmania, spending its austral winter in the northern North Pacific (Springer *et al.*, 1999; Howell, 2012). Some of the other most commonly encountered birds in the Pacific CAO and adjacent slopes are surface feeders and scavengers, including northern fulmar, glaucous gull, Sabine's gull, black-legged kittiwake, and Arctic tern, all of which breed in Alaska and the Canadian Archipelago. The other commonly encountered gulls, ivory gull and Ross's gull, do not breed in the Pacific Arctic, but occur there regularly, particularly during spring or autumn migration. Results from the survey for eight species are given in [Section 9.6](#) under the species accounts ([Figure 9.9](#)).

Diving auks recorded in the Pacific CAO or slope include thick-billed murre, black guillemot, least auklet (*Aethia pusilla*), crested auklet (*A. cristatella*), horned puffin (*Fratercula corniculata*), Kittlitz's murrelet (*Brachyramphus brevirostris*), and ancient murrelet (*Synthliboramphus antiquus*; [Table 9.2](#)). These auks breed in seabird colonies in the Bering Sea or southern Chukchi Sea, though the ancient murrelet may originate from breeding sites in the Gulf of Alaska (T. Gaston, personal communication). Neither of the two *Aethia* auklets nest in the Chukchi Sea and, therefore, must move north through Bering Strait to forage in Chukchi Sea in the post-breeding period (Jones, 1993; Jones *et al.*, 2001; Piatt and Kitaysky, 2002a, 2002b; Piatt and Springer, 2003; Bond *et al.*, 2013; Kuletz *et al.*, 2015, 2019). Such movement may occur *en masse* at key locations, based on an August 2013 record of an estimated 10 560 000 crested auklets streaming past Cape Kekurnyi, on the Chukotski Peninsula, northward into Chukchi Sea (Maftei and Russ, 2014). At least some of the crested auklets that forage in Chukchi Sea and the adjacent slope come from breeding sites in the northern Bering Sea (A. Will, unpublished data), and least auklets may be from the Aleutian Islands (Robinson, 2015), based on birds fitted with geolocators.

**Table 9.1. Species of birds recorded in the CAO (including the slope), with information on the degree of occurrence and the role the CAO plays for the species.**

Species name	Latin name	Occurrence	Geographic area	Role of CAO
Northern fulmar	<i>Fulmarus glacialis</i>	Regular visitor	All	Low
Short-tailed shearwater	<i>Ardenna tenuirostris</i>	Irregular foraging migration	Pacific	Low
Ivory gull	<i>Pagophila eburnea</i>	Common	All	Nonbreeding and postbreeding habitat, migration
Ross's gull	<i>Rhodostethia rosea</i>	Common	All	Nonbreeding and postbreeding habitat, migration
Sabine's gull	<i>Xema sabini</i>	Rare	All	Low (on migration)
Black-legged kittiwake	<i>Rissa tridactyla</i>	Common	All	Low
Glaucous gull	<i>Larus hyperboreus</i>	Rare	All	Low
Arctic tern	<i>Sterna paradisaea</i>	Vagrant	All	Negligible
Great skua	<i>Stercorarius skua</i>	Occasional vagrant	Atlantic	Negligible
Long-tailed jaeger	<i>Stercorarius longicaudus</i>	Vagrant	All	Negligible
Parasitic jaeger	<i>Stercorarius parasiticus</i>	Vagrant	All	Negligible
Pomarine jaeger	<i>Stercorarius pomarinus</i>	Vagrant	All	Negligible
Dovekie	<i>Alle alle</i>	Common	Atlantic	Low
Thick-billed murre	<i>Uria lomvia</i>	Common	All	Low
Black guillemot	<i>Cephus grylle</i>	Common	All	Low
Least auklet	<i>Aethia pusilla</i>	Rare vagrant	Pacific	Negligible
Ancient murrelet	<i>Synthliboramphus antiquus</i>	Vagrant	Pacific	Negligible
Crested auklet	<i>Aethia cristatella</i>	Vagrant	Pacific	Low
Kittlitz's murrelet	<i>Brachyramphus brevirostris</i>	Vagrant	Pacific	Negligible
Atlantic puffin	<i>Fratercula arctica</i>	Vagrant	Atlantic	Negligible
Horned puffin	<i>Fratercula corniculata</i>	Rare Vagrant	Pacific	Negligible
Red-necked phalarope	<i>Phalaropus lobatus</i>	Rare vagrant	All	Negligible
Red phalarope	<i>Phalaropus fulicarius</i>	Vagrant	Pacific	Negligible



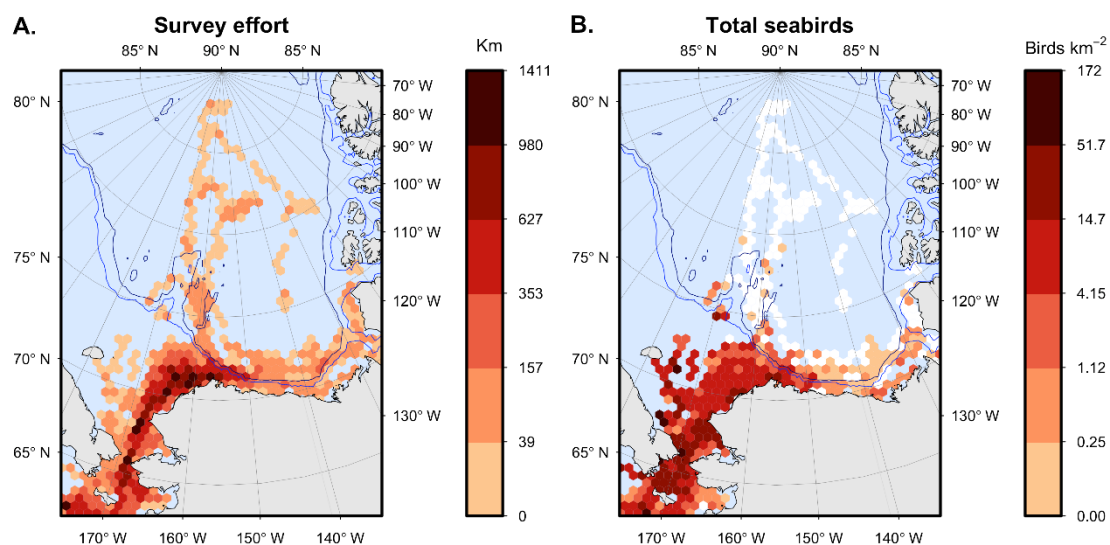
<b>Table 9.1 (cont.)</b>				
<b>Species name</b>	<b>Latin name</b>	<b>Occurrence</b>	<b>Geographic area</b>	<b>Role of CAO</b>
Purple sandpiper	<i>Calidris maritima</i>	Rare transit vagrant	All	Negligible
Common ringed plover	<i>Charadrius hiaticula</i>	Rare transit vagrant	Eurasia	Negligible
Common eider	<i>Somateria mollissima</i>	Rare vagrant	All	Negligible
King eider	<i>Somateria spectabilis</i>	Rare vagrant	Pacific	Negligible
Long-tailed duck	<i>Clangula hyemalis</i>	Rare vagrant	All	Negligible
Surf scoter	<i>Melanitta perspicillata</i>	Rare vagrant	Pacific	Negligible
Red-throated loon	<i>Gavia stellata</i>	Rare vagrant	Pacific?	Negligible
Pacific loon	<i>Gavia pacifica</i>	Rare vagrant	Pacific	Negligible
White wagtail	<i>Motacilla alba</i>	Occasional transit vagrant	Eurasia	Negligible
Wheatear	<i>Oenanthe oenanthe</i>	Occasional transit vagrant	Pacific	Negligible
Snow bunting	<i>Plectrophenax nivalis</i>	Transit vagrant	All	Negligible
Lapland Bunting	<i>Calcarius lapponicus</i>	Occasional transit vagrant	Pacific	Negligible

**Table 9.2. Mean densities (individuals km<sup>-2</sup>) for birds observed on Arctic Slope or Basin waters in the Pacific Arctic, 2006-2017, using 60 km hexagon grid. Shelf is north of 70°N, Slope is depth of 300–1000 m, while Basin is the Amerasian basin of the CAO. S. d. – standard deviation.**

<b>Common name</b>	<b>Latin name</b>	<b>Shelf</b>		<b>Slope</b>		<b>Basin</b>	
		<b>Mean</b>	<b>s. d.</b>	<b>Mean</b>	<b>s. d.</b>	<b>Mean</b>	<b>s. d.</b>
Red-throated loon	<i>Gavia stellata</i>	0.0006	0.0029	0.0020	0.0151	0	0
Pacific loon	<i>Gavia pacifica</i>	0.0294	0.0514	0.0169	0.0662	0	0
Northern fulmar	<i>Fulmarus glacialis</i>	0.1073	0.1638	0.0083	0.0278	0.0004	0.0034
Short-tailed shearwater	<i>Ardenna tenuirostris</i>	2.3692	4.4856	0.3022	1.2684	0.0156	0.1594
Long-tailed duck	<i>Clangula hyemalis</i>	0.2947	1.6074	0.0053	0.0264	0	0
Common eider	<i>Somateria mollissima</i>	0.0556	0.2838	0.0018	0.0097	0.0003	0.0038
King eider	<i>Somateria spectabilis</i>	0.0127	0.0493	0.0055	0.0514	0	0

**Table 9.2 (cont.)**

Common name	Latin name	Shelf		Slope		Basin	
		Mean	s. d.	Mean	s. d.	Mean	s. d.
Surf scoter	<i>Melanitta perspicillata</i>	0	0	0.0003	0.0030	0	0
Red phalarope	<i>Phalaropus fulicarius</i>	0.1349	0.2305	0.0199	0.1105	0	0
Red-necked phalarope	<i>Phalaropus lobatus</i>	0.0428	0.1163	0.0038	0.0167	0	0
Pomarine jaeger	<i>Stercorarius pomarinus</i>	0.0160	0.0244	0.0003	0.0014	0.0002	0.0023
Parasitic jaeger	<i>Stercorarius parasiticus</i>	0.0096	0.0233	0.0010	0.0049	0.0003	0.0029
Long-tailed jaeger	<i>Stercorarius longicaudus</i>	0.0020	0.0066	0	0	0.0005	0.0058
Glaucous gull	<i>Larus hyperboreus</i>	0.0863	0.2177	0.0654	0.2366	0.0164	0.0801
Glaucous-winged gull	<i>Larus glaucescens</i>	0.0002	0.0016	0.0003	0.0021	0.0002	0.0025
Ivory gull	<i>Pagophila eburnea</i>	0	0	0.0026	0.0123	0.0120	0.1045
Black-legged kittiwake	<i>Rissa tridactyla</i>	0.6056	2.4940	0.1401	0.5547	0.0138	0.0575
Ross's gull	<i>Rhodostethia rosea</i>	0.0098	0.0444	0.0335	0.1370	0.0285	0.1494
Sabine's gull	<i>Xema sabini</i>	0.0169	0.0680	0.0081	0.0697	0.0004	0.0040
Arctic tern	<i>Sterna paradisaea</i>	0.0345	0.1461	0.0152	0.0990	0	0
Thick-billed murre	<i>Uria lomvia</i>	0.1968	0.3479	0.0047	0.0204	0	0
Black guillemot	<i>Cepphus grylle</i>	0.0247	0.1017	0.0102	0.0395	0.0026	0.0229
Kittlitz's murrelet	<i>Brachyramphus brevirostris</i>	0.0120	0.0333	0.0002	0.0013	0	0
Ancient murrelet	<i>Synthliboramphus antiquus</i>	0.0262	0.0944	0.0057	0.0399	0	0
Crested auklet	<i>Aethia cristatella</i>	1.6132	2.3735	0.0060	0.0350	0.0139	0.1522
Least auklet	<i>Aethia pusilla</i>	0.9042	5.5333	0.0012	0.0100	0	0
Horned puffin	<i>Fratercula corniculata</i>	0.0099	0.0516	0	0	0.0033	0.0375
<b>Total birds</b>		<b>6.7064</b>	<b>8.1005</b>	<b>0.6957</b>	<b>1.9992</b>	<b>0.1139</b>	<b>0.3570</b>



**Figure 9.3.** Seabird sighting surveys in the Pacific Arctic. (a) Survey effort (km survey lines) and (b) observed densities of birds (individuals km<sup>-2</sup>) of all species combined, based on mean counts along survey lines for 60 km hexagon cell grids. Data for the summer season (June–October), 2006–2017, Kathy Kuletz and Elizabeth Labunski, US Fish and Wildlife Service. Maps produced by Daniel Cushing, Pole Star Ecological Research, LLC.

Kittlitz's murrelet, which occurs on the Chukchi slope in late summer and autumn, breed in mountain habitats in Alaska and far eastern Russia (including the mainland of the Chukotka coast). They typically forage nearshore, but move offshore after fledging chicks (Day *et al.*, 2017). For a number of years, Kittlitz's murrelet was listed as Critically Endangered by the International Union for the Conservation of Nature (IUCN), but was downlisted in 2014 to Near Threatened, because the rate of population decline was suspected to be less rapid and dramatic than previously thought (BirdLife International, 2016a). Another small auk, the ancient murrelet, has become a relatively common late summer and autumn visitor to the Chukchi shelf and slope, and even the western Beaufort Sea (Day *et al.*, 2013), although its nearest breeding sites are around the Sea of Okhotsk, the Aleutian Islands, and southeast Alaska to British Columbia (Gaston, 1994).

With ongoing global warming, more marine bird species are expanding their ranges north into the Arctic Ocean both from Atlantic and Pacific gateways (Day *et al.*, 2013; Descamps *et al.*, 2017). In the Pacific Arctic over the past decade, in addition to increasing observations of ancient murrelets, there have been rare sightings of more southerly species such as rhinoceros auklet (*Cerorhinca monocerata*) and short-tailed albatross (*Phoebastria albatrus*; Day *et al.*, 2013). The northern gannet (*Morus bassanus*), an Atlantic species, has been recorded in the Pacific Arctic, suggesting east–west movement through the Canadian Arctic (Day *et al.*, 2013, and references therein). Similar trends have been observed in the Barents and Greenland seas, with the most striking being a recent observation of black-browed albatross (*Thalassarche melanophrys*) in Franz Josef Land (Weiss, 2018). Lesser black-backed gull (*Larus fuscus*) has been observed as far north as 81°36'N in East Greenland, with breeding recorded as far north as 74°30'N (Boertmann *et al.*, 2020b).

Notably, there appears to be migrations along the CAO slope by many typically coastal marine bird species, including two species of loons, five species of sea ducks, and two phalarope species (Table 9.2). Presumably, these observations reflect migratory pathways and not important foraging locations. However, the onshelf waters of the Beaufort and Chukchi seas support large numbers of these groups of birds, particularly in nearshore coastal waters and lagoons (Johnson and Herter, 1989; Fischer and Larned, 2004). Red phalaropes are among the more abundant

offshore birds encountered in the Chukchi Sea, especially near Bering Strait (Kuletz *et al.*, 2015, 2019).

More information on the common or regularly visiting species are provided in [Section 9.6](#).

## 9.5 High Arctic seabird breeding colonies

There are breeding colonies of seabirds on the shelves surrounding the CAO, particularly in the archipelagoes on the Eurasian side: Svalbard, Franz Josef Land, Novaya Zemlya, Severnaya Zemlya, New Siberian Islands, and Wrangel and Herald Islands ([Figure 9.4](#)). The main species that breed in the high latitude colonies are dovekie, thick-billed murre, black guillemot, black-legged kittiwake, and glaucous gull ([Figure 9.5](#)). In the European archipelagos of Svalbard and Franz Josef Land, northern fulmar is also abundant breeder. Other species occur, but in very small numbers. Ivory gulls breed in North Greenland and on high-Arctic archipelagos within the Atlantic sector, but prefer to nest separately from other species and never nest in large mixed colonies. During the breeding season, seabirds are central-place foragers and seek food within a certain zone around the colonies, at distances that vary between species and with food resource availability. There is limited data available on foraging distances from most of the high-Arctic colonies, but Critchley *et al.* (2019) provided estimates which suggest some species might be capable of visiting the CAO during their breeding period. The instrumentally recorded foraging range was greatest for northern fulmar (> 500 km), intermediate for black-legged kittiwake (> 300 km) and great skua (> 200 km), and shortest for black guillemot (15 km; references in Critchley *et al.*, 2019). Although dovekies are one of the smallest seabirds, they can fly up to 200 km over the continental slope to favoured foraging areas (Amélineau *et al.*, 2016). GPS-tracked ivory gulls from breeding colonies in North Greenland foraged mostly in ice-covered waters north of Greenland, with average length of trips about 200 km and a maximum distance from the colonies of 500 km (Frederiksen *et al.*, 2020).

The following text is a circum-Arctic description of breeding colonies around the periphery of the CAO:

### Northeast Greenland

There are small colonies in northeast Greenland adjacent to the Northeast Water (NEW) polynya. The most numerous breeder is the northern fulmar, with an estimated 2550 pairs (Falk *et al.*, 1997). Other breeding seabirds include black-legged kittiwake (few), Sabine's gull, Arctic tern, common eider, black guillemot, and occasionally Ross's gull (Falk *et al.*, 1997). Ivory gull breeds in fairly large numbers (around 2000 pairs) inland in this region, concentrated on and around Kronprins Christian Land, adjacent to the NEW polynya (Gilg *et al.*, 2009; Boertmann *et al.*, 2020b, 2020c). Much larger numbers of seabirds breed farther south in East Greenland, notably in and around Scoresby Sound, where colonies were estimated to hold 3.5 million dovekies (Kampp *et al.*, 1987). Large colonies of northern fulmars, thick-billed murres, and black-legged kittiwakes are also found here (Boertmann and Mosbech, 2012; Boertmann *et al.*, 2020a).

### Svalbard

The Barents Sea LME holds some of the largest concentrations of seabirds in the world, with about 20–25 million seabirds, consuming approximately 1.2 million t of biomass annually from the area (Anker-Nilsen *et al.*, 2000; Barrett *et al.*, 2002). Many of these seabirds breed on Svalbard, in colonies on steep sea-facing cliffs or screes. The largest colonies are found near the oceanographic polar front, on Bjørnøya (Bear Island) and around Storfjorden in the southern



part of the archipelago, and along the west coast of Spitsbergen (Mehlum and Fjeld, 1987; Anker-Nilsen *et al.*, 2000). The most abundant species are thick-billed murre (1.75 million pairs), dovekie (> 1.3 million pairs), black-legged kittiwake (0.9 million pairs), and northern fulmar (0.1–1 million pairs; Anker-Nilssen *et al.*, 2000).

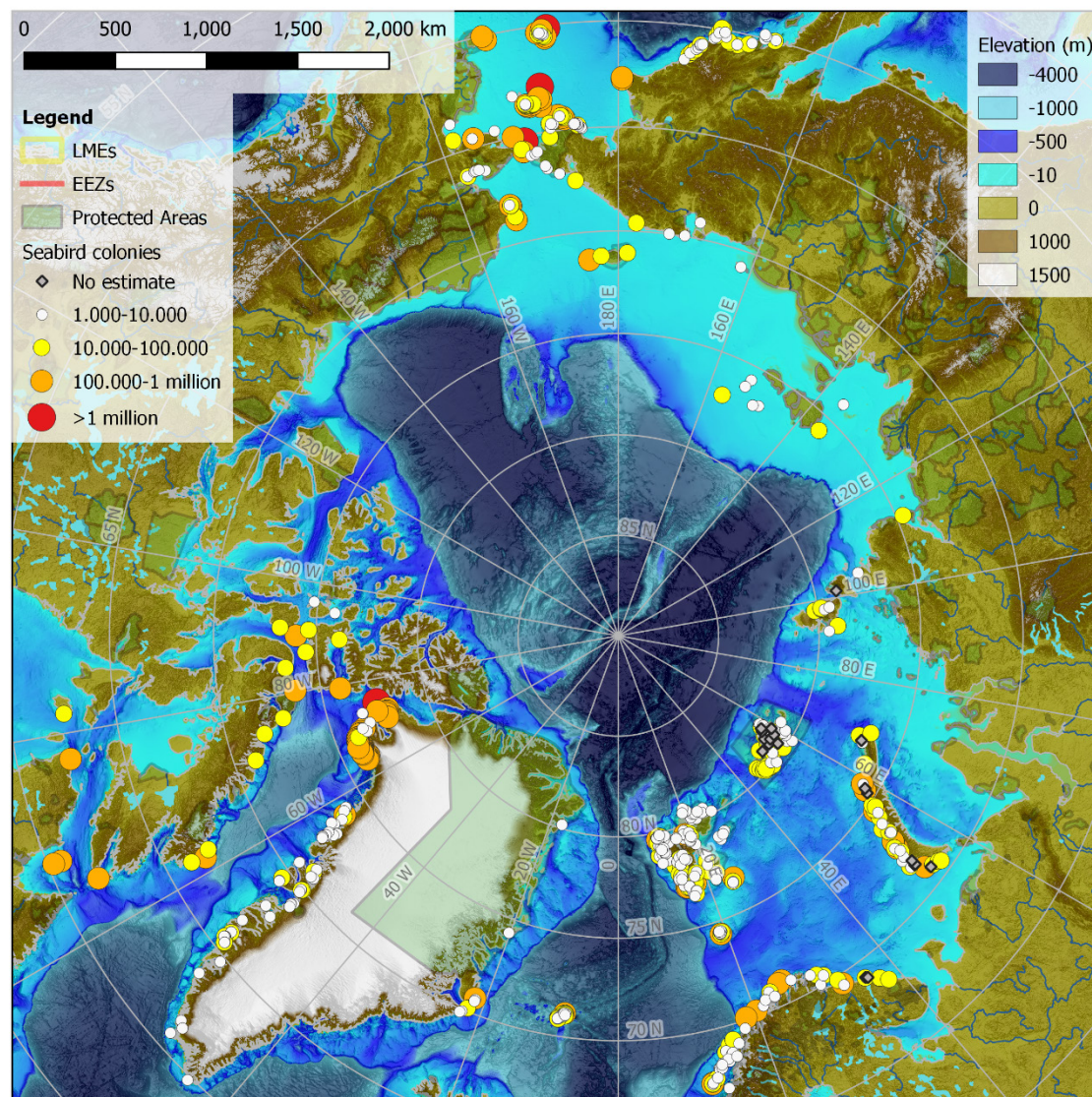


Figure 9.4. Breeding colonies of seabirds around and adjacent to the CAO. Colonies are shown in four size categories (number of individual birds): 1000–10 000, 10 000–100 000, 100 000–1 million, > 1 million. A fifth category is for colonies where the number of breeding birds is not estimated. The size of the colonies is for all species of seabirds combined – see the text for information on species. Note that the map does not include colonies in Iceland, Labrador, Gulf of Alaska, southern Bering Sea, Sea of Okhotsk, and the White Sea.

### Franz Josef Land

There are over a hundred colonies of seabirds located mostly in the southern and central parts of the Franz Josef Land archipelago (Gavrilo *et al.*, 1993; Anker-Nilsen *et al.*, 2000; Tertitskiy *et al.*, 2000; Gavrilo and Popov, 2011). The main species breeding here are dovekie (*polaris* subspecies, over 500 000 pairs), thick-billed murre (200 000–250 000 pairs), black-legged kittiwake (some 100 000 pairs), and northern fulmar (7000–8000 pairs; Strøm *et al.*, 2016). Franz Josef Land is an important breeding area for ivory gull, with 1500–2000 pairs found here (Gavrilo, 2021).



### Novaya Zemlya

This archipelago holds large numbers of breeding seabirds, with many colonies along the west coasts facing the eastern Barents Sea (Tertitskiy *et al.*, 2000). The main species breeding here is thick-billed murre (250 000–500 000 pairs; Strøm *et al.*, 2016), followed by black-legged kittiwake (about 100 000 individuals; Barrett and Tertitskiy, 2000), and dovekie (*alle* subspecies, 30 000–50 000 pairs; Strøm *et al.*, 2016). Few seabirds breed along the east coasts facing the Kara Sea, and their colonies are located at the northeastern tip of the Northern Island (Gavrilo and Bakken, 2000).

### Kara Sea islands

There are several smaller offshore islands in the northern Kara Sea which are important breeding areas for ivory gull, with estimated numbers of 2000–2500 pairs (Gavrilo, 2011a; M. Gavrilo, unpublished observations). The islands do not provide suitable habitats for cliff-breeding seabirds, and kittiwakes breed only on some islands in small numbers (Gavrilo, unpublished data).

### Severnaya Zemlya

This high-Arctic archipelago holds many smaller colonies scattered over the islands (de Korte *et al.*, 1995; Gavrilo and Bakken, 2000). Ivory gull breeds here in relatively large numbers (earlier estimated up to 5000–6000 pairs; Gavrilo, 2011a). Other species that breed here are dovekie (*polaris* subspecies; 10 000–80 000 pairs), black-legged kittiwake (about 10 000 pairs), black guillemot (about 5000 pairs), and glaucous gull (500–1000 pairs; de Korte *et al.*, 1995; Gavrilo and Bakken, 2000; Gavrilo and Volkov, 2008; numbers are probably underestimates). Thick-billed murre and northern fulmar do not breed on Severnaya Zemlya.

### New Siberian Islands

There are two colonies on smaller islands (Stolbovoy and Belovskiy) in the western part of the archipelago and several colonies on De Longa Islands in the northeastern part (Gavrilo, 2011b; Gavrilo and Popov, 2011). The main species that breed here are thick-billed murre (described as subspecies *eleonorae*, but subspecies status is uncertain; previously estimated at around 30 000 pairs; Rutilevskiy, 1963), black-legged kittiwake, and black guillemot, with the latter abundant at De Longa Islands. In addition, there is a large colony of thick-billed murres and kittiwakes at Preobrazhenya Island in Khatanga Bay in the southwestern Laptev Sea.

### Wrangel and Herald islands

There are two main colonies at Wrangel Island, one on each end at Cape Blossom and Cape Uering, as well as a major colony on nearby Herald Island in the northwestern Chukchi Sea (Stishov *et al.*, 1991; Kondratyev *et al.*, 2000; Gavrilo, 2011b). The main species here are thick-billed murre (described as subspecies *heckeri*, but subspecies status is uncertain; 200 000–300 000 individuals; Kondratyev *et al.*, 2000) and black-legged kittiwake (Pacific subspecies *pollicaris*; 70 000–175 000 individuals; Stishov *et al.*, 1991; Kondratyev *et al.*, 2000). Black guillemot breeds in relatively large numbers on Wrangel and, especially, Herald Islands (about 50 000 and 100 000 individuals, respectively; [Table 9.3](#)). Besides glaucous gull, other seabirds that breed here are boreal Pacific species, including small numbers of horned puffin (*Fratercula corniculata*), tufted puffin (*F. cirrhata*), and pelagic cormorant (*Phalacrocorax pelagicus*).



Figure 9.5. High-Arctic breeding colonies of seabirds adjacent to the CAO. Upper panel – Rubini Rock on Hooker Island, Franz Josef Land, Russia. Mixed colony of black-legged kittiwakes and thick-billed murre. Lower panel – Sredniy Island, Sedov Archipelago, western Severnaya Zemlya. Colony of black-legged kittiwakes with some black guillemots on top of the cliff. Photos: Maria Gavrilov.

**Table 9.3 – Part 1 of 2. Population estimates for seabird colonies in the Bering Strait region and the Chukchi Sea. The population estimates are based on best available information from Seabird Information Network, 2014. North Pacific Seabird Data Portal. Please note that parts 1 and 2 of this table together provide the species composition for each of the listed colonies.**

	<b>Pelagic cormorant</b>	<b>Black-legged kittiwake</b>	<b>Glaucous gull</b>	<b>Herring gull</b>	<b>Dovekie</b>	<b>Common murre</b>	<b>Thick-billed murre</b>	<b>Unidentified murre</b>
Fairway Rock	<100	3000	1000			5000	15 000	5000
Little Diomedé	100–1000	100 000	100–1000		<100	35 000	25 000	29 000
Big Diomedé	100–1000	23 000	100–1000			9700	4000	12 000
Puffin Island		6000	<100			11 000	4000	10 000
Ostrov Kolyuchin	100–1000	23 000	100–1000	<100		11 000	95 000	
Artigotrat	<100	10 000	100–1000					123 000
Agate		10 000	100–1000					44 000
Cape Thompson	<100	6000	<100					12 000
Imnakpak Cliff	<100	3000	<100					208 000
Cape Lewis	<100	3000	<100			8000	18 000	
Cape Lisburne	<100	15 000	<100			70 000	130 000	261 000
Mys Yakan		35 000						
Mys Zapadnyy	6000	198 000	2000				138 000	
Mys Uering	2000	372 000	4000			<100	541 000	
Ostrov Geral'd	100–1000	27 000	1000			2000	159 000	
<b>Total</b>	<b>10 000</b>	<b>835 000</b>	<b>10 000</b>	<b>&lt;100</b>	<b>&lt;100</b>	<b>151 000</b>	<b>1 129 000</b>	<b>704 000</b>

**Table 9.4 – Part 2 of 2. Population estimates for seabird colonies in the Bering Strait region and the Chukchi Sea. The population estimates are based on best available information from Seabird Information Network, 2014. North Pacific Seabird Data Portal. Please note that parts 1 and 2 of this table together provide the species composition for each of the listed colonies.**

	<b>Black guillemot</b>	<b>Pigeon guillemot</b>	<b>Crested auklet</b>	<b>Least auklet</b>	<b>Parakeet auklet</b>	<b>Unid. auklet</b>	<b>Horned puffin</b>	<b>Tufted puffin</b>
Fairway Rock		100–1000	10 000	15 000	100–1000		100–1000	2000
Little Diomede		100–1000	494 000	1 517 000	20 000		27 000	1000
Big Diomede		4000	550 000	3 500 000	70 000	2 000 000	18 900	2000
Puffin Island							20 000	<100
Ostrov Kolyuchin	100–1000						100–1000	<100
Artigotrat	<100	<100					100–1000	<100
Agate							100–1000	
Cape Thompson							100–1000	
Imnakpak Cliff	<100	<100					100–1000	<100
Cape Lewis	<100						100–1000	<100
Cape Lisburne	100–1000						1 000	<100
Mys Yakan	<100							
Mys Zapadnyy	15 000						<100	
Mys Uering	30 000						100–1000	<100
Ostrov Geral'd	100 000						1000	<100
<b>Total</b>	<b>147 000</b>	<b>4 000</b>	<b>1 054 000</b>	<b>5 032 000</b>	<b>91 000</b>	<b>2 000 000</b>	<b>73 000</b>	<b>5 000</b>

### Coast of Chukotka

There are several smaller colonies along the mainland coast. The largest is found on Kolyuchin Island (Konyukhov *et al.*, 1998; Kondratyev *et al.*, 2000) and holds about 100 000 individuals of thick-billed murre and 23 000 black-legged kittiwakes ([Table 9.3](#)).

### Bering Strait region

There are many smaller colonies along the east coast of Chukotka and large colonies on islands in the Bering Strait region, notably Little and Big (Ratmanova) Diomedes and King islands (Hunt *et al.*, 1981; Konyukhov *et al.*, 1998; Kondratyev *et al.*, 2000). These colonies hold relatively large numbers of black-legged kittiwakes (> 100 000), thick-billed murres, and common murres (about 50 000 individuals each; [Table 9.3](#)). Very large numbers of auklets breed on the Bering Strait islands, with ca. 5 million least auklets, 1 million crested auklets, and 100 000 parakeet auklets (*Aethia psittacula*; Jones, 1993; Jones *et al.*, 2001; Bond *et al.*, 2013; [Table 9.3](#)). Farther south, on St Lawrence Island, there are also large breeding colonies of *Aethia* auklets (Hunt *et al.*, 1981). The large numbers of plankton-feeding auklets are supported by the very high productivity and abundance of large copepods transported with the north-flowing currents through the Bering Strait region (Springer and Roseneau, 1985; Hunt and Harrison, 1990; Hunt *et al.*, 1993; Piatt and Springer, 2003).

### Lisburne Peninsula

There are two relatively large colonies at Cape Lisburne and Cape Thompson (including Imnakpak Cliff), which together may hold about 1 million breeding seabirds (Sowls *et al.*, 1978; Seabird Information Network, 2022; [Table 9.3](#)). The most abundant species are thick-billed murre and common murre, followed by black-legged kittiwake and small numbers of black guillemots and horned puffins.

### Cape Parry

There are no cliffs to support nesting seabirds, and thus no large colonies along the Beaufort Sea coast. However, the low-lying coasts, with barrier islands, spits, beaches, and other coastal features, offer breeding habitats for larids, notably glaucous gull and Arctic tern, as well as sea ducks like common eider, and phalaropes (Dickson and Gilchrist, 2002). An exception are the cliffs at Cape Perry in the Amundsen Gulf area, which has the only breeding colony of thick-billed murre in the Beaufort Sea, with several hundred pairs nesting there (Latour *et al.*, 2006) that are assumed to be of the Pacific *arra* subspecies (Gaston and Hipfner, 2000). There are also cliffs at Nelson Head, at the southernmost point on Banks Island, but these are unoccupied by seabirds, possibly due to lack of an appropriate food source (Dickson and Gilchrist, 2002).

### Canadian Arctic Archipelago

There are no breeding colonies of seabirds in the western and northern parts of the Canadian Arctic archipelago. However, there are large colonies in the central part, in the area of Lancaster Sound, on Prince Leopold Island, Bylot Island, and along southern Devon Island. The colonies are often mixed-species assemblages, dominated by thick-billed murres, black-legged kittiwakes, and northern fulmars (Gaston and Nettleship, 1981; Gaston, 2002; Mallory and Fontaine, 2004; Gaston *et al.*, 2006; Mallory *et al.*, 2007, 2009).

### North Water area

This area between Canada and Greenland holds large colonies on both sides, notably on Coburg Island at the opening to Jones Sound and along the Qaanaaq (Thule) coast south from Inglefield



Fiord to Cape Melville (Boertmann *et al.*, 1996; Boertmann and Mosbech, 1998; Mallory and Fontaine, 2004; Bakken *et al.*, 2006; Merkel *et al.*, 2014). The main species which breed here are dovekie, thick-billed murre, black-legged kittiwake, and northern fulmar. The population of dovekies was estimated to be on the order of 30 million breeding pairs (Egevang *et al.*, 2003), making up a substantial fraction of the total global population (Montevecchi and Stenhouse, 2020). The breeding populations in the North Water area are about 0.5 million breeding pairs of thick-billed murre, 100 000 pairs of black-legged kittiwake, and around 50 000 pairs of northern fulmar (Kampp, 1990; Mallory, 2006; Boertmann and Mosbech, 2011; Gaston *et al.*, 2012). There appears to be little connectivity between the seabirds breeding in the North Water region, as well as in the Lancaster Sound region in the Canadian Archipelago, and the waters of the CAO to the north.

## 9.6 Species accounts

### 9.6.1 Ivory gull (*Pagophila eburnea*)

Ivory gull is a medium-sized bird (body mass of 500–600 g) that characteristically has completely white adult plumage (Figure 9.6). It reaches sexual maturity after 2–3 years and lays typically one or two eggs (rarely three eggs), depending on feeding conditions. Ivory gull breeds in colonies, varying in size from a few pairs to 1000–2000 pairs, in remote and inaccessible locations. These are often some distance inland on steep mountains and nunataks (rocky projections above glaciers), but can also be on flat and barren ground (most birds in the Russian breeding range; Figure 9.7; Gilchrist *et al.*, 2008; Gavrilov, 2011c). A colony of ivory gulls was even found on a mostly stationary ice floe covered with gravel and on an iceberg, both in North Greenland (Boertmann *et al.*, 2010; Nachtsheim *et al.*, 2016).

Two important habitat requirements for breeding ivory gulls are relative safety from terrestrial predators, particularly Arctic fox (*Vulpes lagopus*), and the presence of ice-covered waters or glacier fronts within foraging range (100–200 km) of the nesting area throughout the breeding season (COSEWIC, 2006a; Gilchrist *et al.*, 2008; Gavrilov, 2011a). Avoiding predators may be one factor why there appears to be large variation in the use of specific sites within the breeding areas that are accessible for Arctic foxes (Gavrilov, 2011a, 2012). Ivory gull breeds in northeastern Canada (Ellersmere, Devon, Seymour, Perley, and northern Baffin islands; Gilchrist and Mallory, 2005; COSEWIC, 2006a; Robertson *et al.*, 2007), northern and eastern Greenland (Gilg *et al.*, 2009), Svalbard (Bakken and Tertitskiy, 2000), and in Russia from Victoria Island and the Franz Josef Land eastward to Severnaya Zemlya Archipelago, including offshore islands in the northeastern Kara Sea (Gavrilov, 2009a; Figure 9.8).

Ivory gull is assessed as “Near Threatened on the IUCN Red List (BirdLife International, 2018a). This ranking is based on a rapid decline in parts of its range, notably in Canada (Gilchrist and Mallory, 2005; Robertson *et al.*, 2007), and threats from climate change, environmental pollution, and human intrusion and disturbance (BirdLife International, 2018a). The total global population was estimated at 58 000–78 000 individuals, with 38 000–52 000 mature individuals (BirdLife International, 2018a), but this estimate is under revision after a pan-Arctic survey conducted throughout the entire breeding range of the species in 2019. Russia supports a major breeding population, which was estimated to be 11 000–13 000 pairs, based on 2006 survey data and historical references for unvisited colonies. By regions, this estimate included 2000–3000 breeding pairs on Franz Josef Land, 5000–6000 pairs on Severnaya Zemlya and adjacent small islands, and 3000–4000 pairs on other islands in the northeastern Kara Sea (Gavrilov, 2011a). The breeding population in Canada is estimated to be about 1000 pairs, while 900–2000 pairs are estimated to breed in Greenland, and 800–1500 pairs in Svalbard (Gilg *et al.*, 2009; BirdLife International, 2018a). These data are somewhat uncertain, given the new national and global

estimates that are under evaluation. Results from surveys in East Greenland suggest that the numbers of ivory gulls did not change over the past decade (Boertmann *et al.*, 2019).

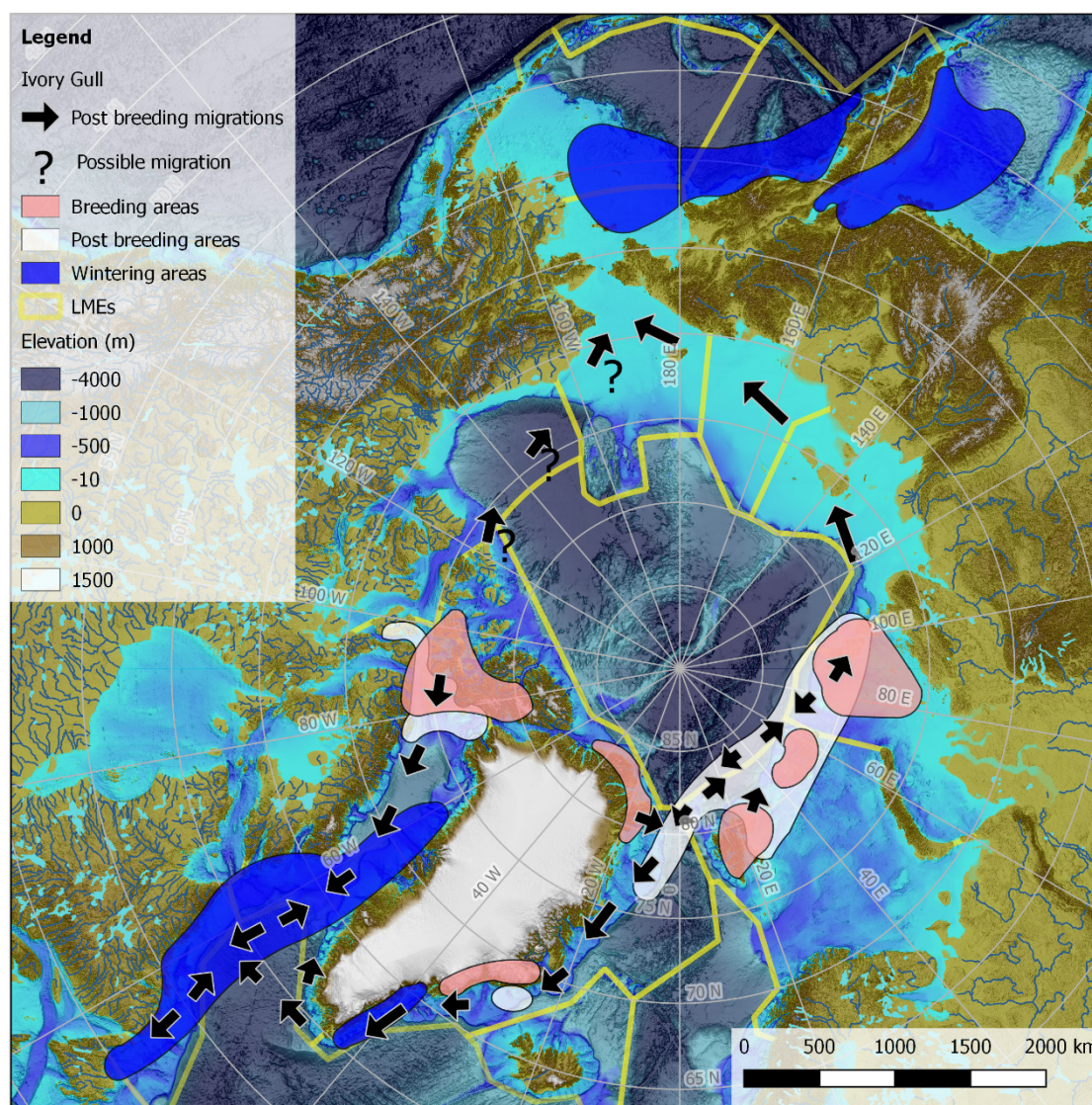


Figure 9.6. Ivory gull at Domashny Island, Severnya Zemlya. Photo: Maria Gavrilov.



Figure 9.7. Breeding colony of ivory gulls at Domashny Island, Severnya Zemlya, Russia. Photo: Maria Gavrilov.





**Figure 9.8. Ivory gull.** Distribution during the annual cycle showing breeding areas, post-breeding foraging areas, migration patterns, and wintering areas in the marginal ice zone in the Atlantic and Pacific sectors.

Ivory gull winters on pack ice and in the marginal ice zone both in the Atlantic and Pacific sectors. Atlantic wintering grounds in the Davis Strait region and the northwestern Labrador Sea into northern Gulf of St Lawrence are well described (Orr and Parsons, 1982; COSEWIC, 2006a; Mallory *et al.*, 2008a) and were recently documented with satellite tracking (Gilg *et al.*, 2010; Spencer *et al.*, 2014). Birds from Greenland, Svalbard, and Russia also winter in the northern Bering Sea and Sea of Okhotsk (Trukhin and Kosygin, 1987; Gilg *et al.*, 2010; Artyukhin, 2018, 2019). Ivory gulls return to the breeding areas from late winter to spring, with a distribution dependent on where they find open water in polynyas and leads (Mallory *et al.*, 2008a). Breeding is compressed into a two-month period, with egg-laying typically in late June to late July and hatching after a 24–26-day incubation period, from late July to late August (Bateson and Plowright, 1959; Volkov and de Korte, 2000; Mallory *et al.*, 2008a). Fledging occurs in 30–35 days, and the colonies are typically vacated by late August to mid-September (Volkov and de Korte, 2000; Mallory *et al.*, 2008a; Gilg *et al.*, 2010). Pacific sector at-sea surveys during 2006–2017 recorded ivory gulls in the northern Bering Sea and Bering Strait in spring, along the marginal ice zone (Figure 9.9, panel a). However, most of the Pacific observations have been in autumn along the CAO slope, particularly around the continental shelf extension known as the Chukchi Borderlands [Figure 9.9, panel a; US Fish and Wildlife Service (USFWS), unpublished

data]. In the Canadian Arctic, at-sea surveys have recorded ivory gulls in northern Baffin Bay and Lancaster Sound (C. Gjerdrum, unpublished data). In the Barents Sea, ivory gulls roam widely in spring in ice-covered waters, often far from the breeding colonies that they occupy later in the year. They are seen in the Pechora Sea and are found concentrated in polynyas around the northern tip of Novaya Zemlya (Krasnov *et al.*, 2002; Matishov *et al.*, 2002; Gavrilov, 2016).

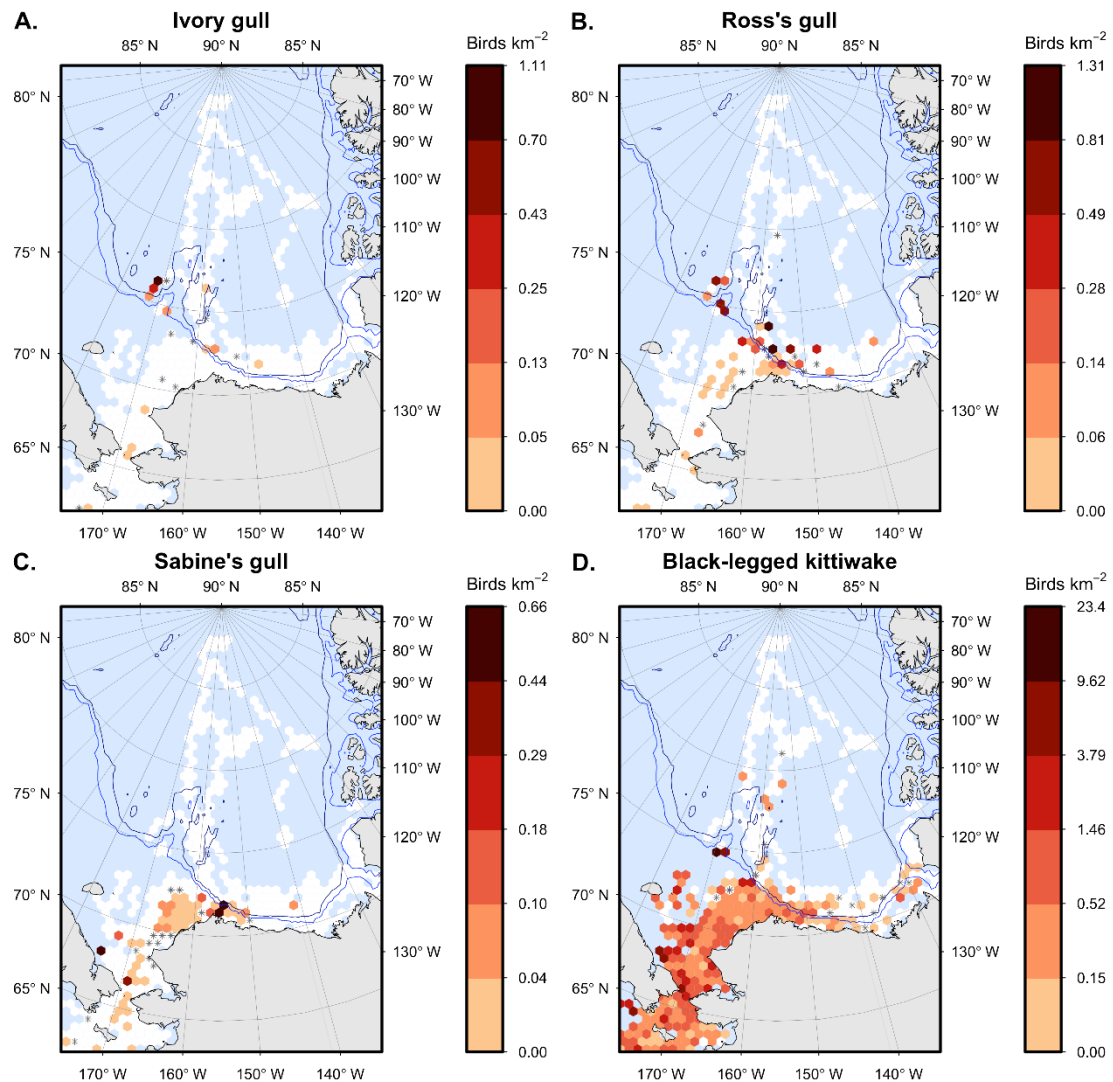


Figure 9.9 – part 1 of 2 (part 2 can be found on page 181). Sighting results for eight species of seabirds in the Pacific Arctic (see [Figure 9.3](#)). Results are given as numbers of birds per km<sup>2</sup> by colour code according to the scale to the right of each panel. Note that the scale differs for the different species. (A) ivory gull, (B) Ross's gull, (C) Sabine's gull, (D) black-legged kittiwake, (E) glaucous gull, (F) northern fulmar, (G) thick-billed murre, (H) black guillemot. Asterisks denote observations of birds off the systematic line transects which were used to estimate density of birds by grid cells. Data for the summer season (June–October), 2006–2017, K. Kuletz and E. Labunski, US Fish and Wildlife Service. Maps produced by Daniel Cushing, Pole Star Ecological Research, LLC.

After breeding and before flying to wintering grounds, ivory gulls move to the productive marginal ice zone in order to replenish body reserves (Mallory *et al.*, 2008a; Gilg *et al.*, 2016a). Satellite-tracked birds from North Greenland, Svalbard, and Franz Josef Land were found to concentrate in waters north of Svalbard and eastward to waters off east Severnaya Zemlya in August–October 2007 (Gilg *et al.*, 2010). This staging area includes the continental slope and



adjacent portions of Nansen Basin (Figure 9.8). A geographic pattern was observed with birds from Greenland tending to stay in the western part, while birds from Franz Josef Land stayed farther east, with some of them moving into the Laptev Sea. It should be noted that 2007 was a year with exceptionally little sea ice in the Laptev Sea, so the marginal ice zone there was largely absent (Gilg *et al.*, 2010). During a RV Polarstern cruise in 2014, many ivory gulls (as well as Ross's gulls) were counted over the Siberian end of Lomonosov Ridge in mostly open water (Joiris *et al.*, 2016; 2014 was also a low ice year in this region).

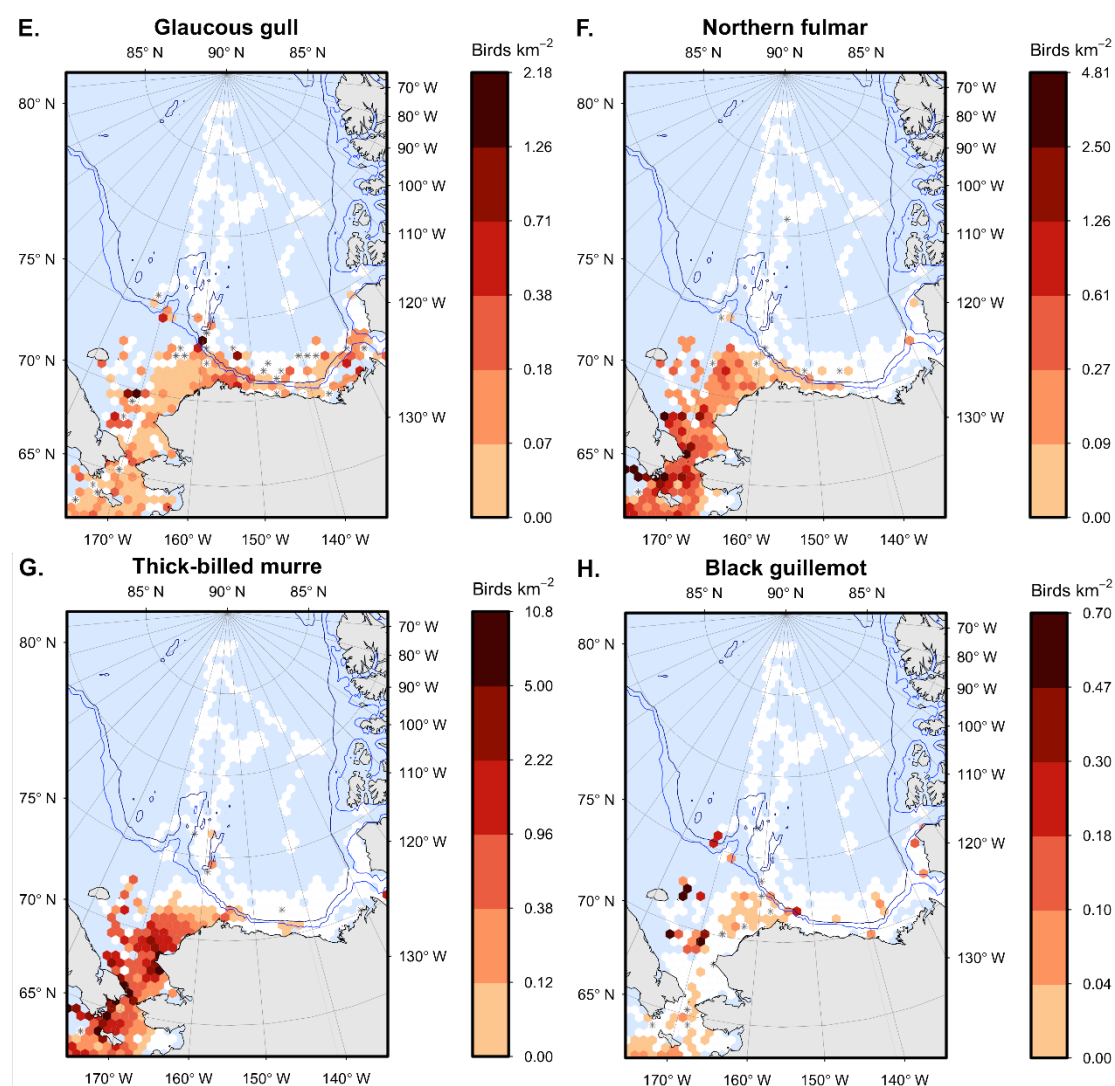


Figure 9.9 – part 2 of 2 (part 1, including the figure caption, can be found on page 180).

The southern Nansen Basin, with the adjacent slope and shelves, is considered a productive region, serving as an important post-breeding foraging area for a large part of the Ivory gull population (Gilg *et al.*, 2010). Gulls from Greenland, Svalbard, and Franz Josef Land move east to this region and then return west and southwest along the marginal ice zone east of Greenland in November and December to wintering areas in Davis Strait, off Labrador, and along southern Greenland (Gilg *et al.*, 2010). Some birds, however, move east towards wintering areas in the northern Bering Sea and Sea of Okhotsk. Ivory gulls breeding in the Canadian Arctic (Seymore Island and other places) use the waters in and around Barrow Strait and Lancaster Sound as a post-breeding foraging area before moving south to the same wintering areas in Davis Strait



and off Labrador used by the birds from Greenland, Svalbard, and Russia (Spencer *et al.*, 2014, 2016).

Ivory gull is an opportunistic feeder that forages predominantly on small fish, e.g. juvenile polar cod (*Boreogadus saida*) and sympagic amphipods (e.g. *Apherusa glacialis*), and is also a scavenger. These gulls often feed on marine mammals killed by polar bears and on placentae from seal pupping, e.g. from harp and hooded seals in the wintering areas in Davis Strait and Labrador Sea (MacDonald, 1976; Mallory *et al.*, 2003, 2008a). As a result, stable isotope data suggest a relatively high trophic level (around 4, which represents a secondary level of carnivory; Campbell *et al.*, 2005; Karnovsky *et al.*, 2009). In the CAO, juvenile polar cod and ice-associated amphipods are probably an important part of the diet of ivory gulls in the post-breeding period before they move south to wintering areas.

### 9.6.2 Ross's gull (*Rhodostethia rosea*)

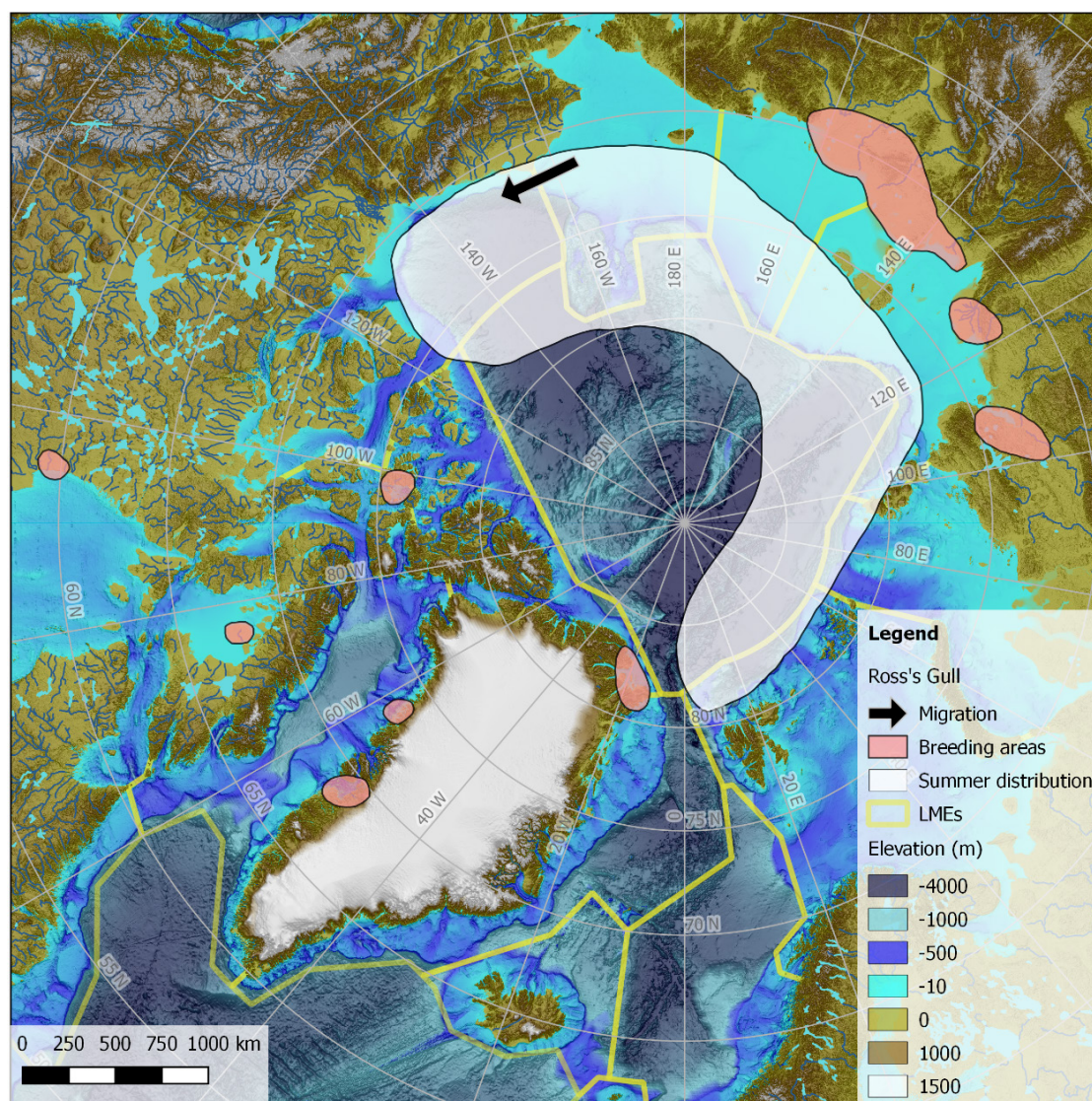


Figure 9.10. Ross's gull in breeding plumage. Photo: Andrey Kamenev.

Ross's gull (Figure 9.10) is a relatively small, tern-like gull (body mass of 150–200 g; Burger *et al.*, 2020). It has a characteristic rose coloured head and body in breeding plumage (hence the species scientific name *rosea*). The global population is assessed to be 25 000–100 000 individuals and is listed as a species of Least Concern in the IUCN Red List (BirdLife International, 2018b). The main breeding ground, perhaps for 95% or more of the global population, is in northeastern Siberia in the area between Taymyr Peninsula and Chaun Bay (Figure 9.11). The core breeding area is the northern part of the Yana–Indigirka Lowlands and the Kolyma plain (Degtyarev *et al.*, 1987; Degtyarev, 1991; Densley, 1991, 1999). Small numbers of Ross's gull also breed in Svalbard, Greenland (Disco Bay and Northeast Water area), and Arctic Canada (Cheyne Island and Penny Strait north of Barrow Strait, Prince Charles Island in Foxe Basin, and the Churchill area in Manitoba; Blomqvist and Elander, 1981; Béchet *et al.*, 2000; Mallory *et al.*, 2006; COSEWIC, 2007; Egevang and Boertmann, 2008; Maftei *et al.*, 2012). The breeding habitats are boggy or marshy grounds located in the coastal tundra zone, typically near water (Densley,

1991; BirdLife International, 2018b). However, on the high-latitude islands of Svalbard, Greenland, and Canada, they breed on barren tundra.

Ross's gull matures early, in their second year of life. Like other gulls with undetermined clutch size, they lay between one and three eggs, depending on feeding conditions, and the breeding period is compressed (even more so than for ivory gull), with an incubation period of 21–22 days and fledging after 20+ days (Yudin and Firsova, 2002). Ross's gull breeds in small and loose colonies (< 20 pairs), often together with Arctic tern (Degtyarev *et al.*, 1987; Densley, 1991).



**Figure 9.11. Ross's gull. Breeding areas and tentative summer and post-breeding distribution in the marginal ice zone of the CAO. The black arrow denotes a pronounced migration of large numbers of Ross's gulls past Point Barrow into the Beaufort Sea in autumn. The birds are assumed to return west later in autumn and fly south to wintering areas in the Bering Sea and Sea of Okhotsk.**

Non-breeding birds move north in spring and are found in ice-covered waters over the Arctic shelves and well into the CAO. The Fram expedition of Fridtjof Nansen (1893–1896) observed adults at 84–85°N in summer 1895 and juvenile birds at 81°N 127°E in summer 1894 (Collett and Nansen, 1900). Observations from Russian ice-drift stations documented the occurrence of Ross's gulls north to 85°N between late June and late August (Uspenskiy, 1984). Later, they were reported to occur all the way to the North Pole (Vuilleumier, 1996; M. Gavrilov,



unpublished data). Ross's gulls were regularly observed from the Swedish icebreaker *Oden* from late July to late August 1996, when the ship sailed through ice across Eurasian Basin, from Franz Josef Land to Lomonosov Ridge at about 87°N (Hjort *et al.*, 1997). After 2 September, when the ship moved into the northern Makarov Basin and then crossed over the North Pole and back to Svalbard (20 September), no Ross's gulls were observed. Low temperatures and early freeze-up were considered a reason why birds might have left these northern waters in 1996 (Hjort *et al.*, 1997). Joiris *et al.* (2016) reported counts of Ross's gulls from RV *Polarstern* in August–September 2014. No individuals were observed during August as the ship sailed north through closed pack ice through Fram Strait and further along Lomonosov Ridge from north of Greenland (along approximately 40°W – 140°E), across the North Pole, to about 85°N on the Siberian side. There, in mostly open water in the region of Lomonosov Ridge (at about 81–84°N), Ross's gulls were seen regularly, along with ivory gulls and black-legged kittiwakes (Joiris *et al.*, 2016).

The lack of observations of Ross's gull (and small numbers for ivory gull) in the Fram Strait region by RV "Polarstern in 2014 may reflect a drastic decrease in these species in this area compared to the period around 1990 (Joiris, 2017). Observations from the Swedish icebreaker *Ymer* in August–September 1980 recorded Ross's gulls regularly in ice-covered waters across Fram Strait, and fairly large numbers were observed in Nansen Basin around 82°N north of Nordaustlandet (Meltofte *et al.*, 1981). On an earlier leg of the cruise (in July), many Ross's gulls were observed in pack ice in the northern Barents Sea and adjacent parts of the Nansen Basin north to 82.5°N. Meltofte *et al.* (1981) noted that Ross's gull had been seen in this area previously by early explorers (Collett and Nansen, 1900; Løvenskiold, 1964).

After breeding, Ross's gulls have been observed to move north and northwest from the breeding areas in Siberia ([Figure 9.11](#)). They are followed about a week later by the juveniles, which occur regularly on the New Siberian Islands in early August (Degtyarev *et al.*, 1987; Zubakin *et al.*, 1990; Lindstrøm *et al.*, 1998a). This has been recently documented by satellite tracking of two birds tagged at the breeding area in the Kolyma Delta (Gilg *et al.*, 2016b). They moved northwest after aborted nesting in July. One individual (a female) moved to the water around the New Siberian Islands. The other bird (a male) moved farther to the northwestern Laptev Sea, where it remained from early July to late September, between 80–85°N and 100–140°E. In late September, the bird flew to the northeastern Chukchi Sea and the north coast of Chukotka (Gilg *et al.*, 2016b).

A notable feature with Ross's gull is that they concentrate and migrate in large numbers of individuals past Point Barrow in Alaska in autumn, moving east into the Beaufort Sea from late September to late October (Divoky *et al.*, 1988; Maftai *et al.*, 2014). Ross's gulls are said to concentrate in the northwestern Chukchi Sea in August and September before they move farther east (COSEWIC, 2007). Studies in the 1980s gave estimates of 15 000–25 000 birds flying into the Beaufort Sea (Divoky *et al.*, 1988), whereas a more recent and comprehensive study in 2011 counted over 27 000 Ross's gulls, with a peak record of 7000 in a three-hour observation period (Maftai *et al.*, 2014). In the latter study, there was a net movement of birds northeast into the Beaufort Sea, with no indication of a return movement even after freeze-up had begun by the end of October. Maftai *et al.* (2014) suggested that up to two-thirds of the global population of Ross's gull could be concentrated in the region around Point Barrow for a relatively short period just prior to freeze-up in autumn. Ship-based surveys of the eastern Chukchi Sea and western Beaufort Sea in 2007–2012 (nearly 50 000 km of survey lines) showed small numbers of Ross's gull in the Hanna Shoal area of the northeastern Chukchi Sea in summer (June–August) and large numbers during autumn (September–November). In autumn, the gulls were spread across the northeastern Chukchi and western Beaufort Sea, notably on the outer shelf and over slope waters (Kuletz *et al.*, 2015). These data, combined with additional surveys through 2017, show a clear concentration of Ross's gulls along the CAO slope near the mouth of Barrow Canyon

and near the Chukchi Borderlands ([Figure 9.9](#), panel b). In contrast, few Ross's gulls were observed during surveys in the Canadian Arctic gateways, including Davis Strait (C. Gjerdrum, unpublished data).

Little is known about wintering areas for Ross's gull, but they are believed to winter mainly in the Bering Sea and Sea of Okhotsk (Yudin and Firsova, 2002 and references therein; COSEWIC, 2007). The gulls are assumed to move back from the Beaufort Sea into the Chukchi Sea in late October and November, possibly over drifting pack ice offshore, and then to move south through Bering Strait to wintering grounds (COSEWIC, 2007). Recently, Atlantic wintering grounds have also been revealed (Maftei *et al.*, 2015)

### 9.6.3 Sabine's gull (*Xema sabini*)

Sabine's gull ([Figure 9.12](#)) is another small Arctic gull (body mass of 150–200 g) with long, narrow, and pointed wings, effective for long-range migration (Day *et al.*, 2020). It has a striking upper wing pattern, with black, white, and grey triangles, and a dark grey head in breeding plumage. It has a buoyant, tern-like flight (Day *et al.*, 2020). In contrast to ivory and Ross's gulls, Sabine's gull leaves the Arctic and migrates to wintering areas in upwelling systems in the southern hemisphere (Humboldt and Benguela currents; Blomqvist and Elander, 1981; Stenhouse *et al.*, 2012; Davis *et al.*, 2016).



Figure 9.12. Sabine's gull nesting on Severnaya Zemlya at the shore of the Arctic Ocean. Photo: Maria Gavrilov.

Sabine's gull has a circumpolar breeding distribution in the Arctic. It nests from Taymyr east to Chukotka in Russia (with single nests also known from the Kara Sea; Dmitriev *et al.*, 2015; M. Gavrilov, 2019, unpublished data), in western and northern Alaska, through northern Canada, in northern and eastern Greenland, and on Svalbard (Blomqvist and Elander, 1981; Ilyichev and Zubakin, 1988; Boertmann, 1994; Yudin and Firsova, 2002; Day *et al.*, 2020). The global population is estimated to be ca. 330 000–700 000 individuals, with most of them breeding in North America (Wetlands International, 2015). The species is listed as Least Concern in the IUCN Red List (BirdLife International, 2018c).

Sabine's gull returns north from wintering areas in May–early June, depending on ice melt and the availability of open water (Day *et al.*, 2020). It nests on moist ground, often in swampy, low-lying tundra with freshwater pools and lakes, usually within 20–50 km of the Arctic coasts. It also nests in coastal marshes and on small islands. Clutch size is 1–3 eggs that are incubated for 20–25 days before hatching, and the chicks fledge as early as 20 days. The entire breeding period is thus compressed to less than two months (Mallory *et al.*, 2012a; Day *et al.*, 2020). After breeding, the families move to the sea where they feed prior to autumn migration, with most of them leaving in late August and September (Day *et al.*, 2020).

Sabine's gull can occur in the CAO in the post-breeding period in late summer, but apparently only as a small fraction of the total global population. Only one individual was observed during the Fram expedition in 1894–1896, at 83°N north of Svalbard (Collett and Nansen, 1900). One individual was seen during the RV "Polarstern" cruise across the CAO in August–September 2014 (Joiris *et al.*, 2016). In contrast, relatively large numbers of Sabine's gull were seen in the northwestern Chukchi Sea and Point Barrow region in summer, and somewhat less in autumn, in the extensive sighting data from 2007–2012 (Kuletz *et al.*, 2015). At-sea surveys farther north, including data for 2006–2017 (Figure 9.9, panel c) recorded only one sighting in the offshore waters of CAO, but high densities near the mouth of Barrow Canyon (near Point Barrow) and the adjacent slope. Most sightings were on the Chukchi shelf, including near the Chukotka Peninsula and south to the northern Bering Sea. It is likely that most birds from northern Alaska and northwestern Canada move through this area following breeding and before they move south through Bering Strait toward their wintering area off Peru (Davis *et al.*, 2016). Satellite-tracking of 24 individuals tagged at a breeding site in Penny Strait (Nasaruvaalik Island, 75.8°N, 96.3°E) in the Canadian High Arctic revealed that they flew over the Beaufort Sea in a band between roughly 70–78°N towards the northwestern Chukchi Sea (Davis *et al.*, 2016).

#### 9.6.4 Black-legged kittiwake (*Rissa tridactyla*)

Black-legged kittiwake is a small pelagic gull (body mass of approximately 400 g), with a wide circumpolar distribution on both the Atlantic and Pacific sides of the Arctic. Two subspecies are recognized, with the nominate *tridactyla* located around the North Atlantic and Arctic basins and the subspecies *pollicaris* in the North Pacific (Hatch *et al.*, 2020). Black-legged kittiwake breeds on cliffs in boreal to Arctic areas, with the main concentrations in subarctic areas. The Pacific subspecies breeds from southcentral Alaska north to Cape Lisburne on the eastern Chukchi Sea coast. In the western Chukchi Sea, it nests from Wrangel and Herald islands west to Chetrekhtolbovoy Island near the Kolyma River delta in Russia (Kondratyev *et al.*, 2000; Hatch *et al.*, 2020). The Atlantic subspecies breeds in High Arctic Canada in Jones Sound, Lancaster Sound, and Barrow Strait, north through Wellington Channel (Mallory and Fontaine, 2004; Mallory *et al.*, 2009). In Greenland, it breeds from the Thule area and south along the west coast. In east Greenland it breeds more scattered, with the largest colonies in Scoresby Sound and the northernmost in the Northeast Water Polynya area (Mallemukfjeld; Boertmann *et al.*, 1996; Labansen *et al.*, 2010). Overall, it breeds widely distributed in Europe from Portugal to Svalbard, and east on Franz Josef Land, Severnaya Zemlya, and Taymyr Peninsula in Russia (Barrett and Tertitskiy, 2000; Yudin and Firsova, 2002; Varty and Tanner, 2009).

The number of breeders on the northern colonies has been estimated to be about 270 000 pairs on Svalbard, some 100 000 pairs on Franz Josef Land, and about 10 000 pairs on islands in the Kara Sea, including western Severnaya Zemlya (Barrett and Tertitskiy, 2000; Gavrilov and Volkov, 2008; Strøm *et al.*, 2016). In the Chukchi Sea, an estimated 33 000 birds nest along the Alaskan coast, about half of those at Cape Lisburne. In total, an estimated 835 000 kittiwakes nest in colonies on both Russian and Alaskan coasts from the northern Bering to the southern Chukchi seas (Table 9.3).





**Figure 9.13. Black-legged kittiwakes. Photo: Maria Gavrilov.**

Black-legged kittiwake has a large global population of around 15 million individuals (Wetlands International, 2015). The species was recently assessed as Vulnerable in the IUCN Red List, due to population declines in Europe and the North Pacific (by 40% or more over three generations, since around 1980; BirdLife International, 2018d).

Black-legged kittiwakes venture into the CAO in summer and autumn ([Figure 9.13](#)), presumably primarily birds from adjacent northern colonies. Vessel-based surveys of the Chukchi and Beaufort seas in 2007–2015 found kittiwakes widely dispersed at fairly high densities from Bering Strait to the northern Chukchi and western Beaufort shelves (Kuletz *et al.*, 2015, 2019). Including surveys farther north and through 2017, kittiwakes occurred regularly along the slope area, including the Chukchi Borderlands and occasionally into the deep waters of the CAO as far as ~ 79°N ([Figure 9.9](#), panel d). Kittiwakes were also commonly encountered during surveys in the Canadian gateways of Davis Strait through Lancaster Sound.

Kittiwakes were seen regularly, although in small numbers, from June to September when Fram drifted across the Eurasian basin in the 1890s, north to about 85°N (Collett and Nansen, 1900). The kittiwakes hovered over open waters in leads, where they fed on small crustaceans. One individual that was shot also had a juvenile polar cod (7 cm) in its stomach (Collett and Nansen, 1900). Black-legged kittiwakes were recorded from RV Polarstern in 2014 in relatively large numbers north from Fram Strait to about 85°N, and again in a zone between about 81 and 84°N over Lomonosov Ridge on the opposite side at about 125–160°E (Joiris *et al.*, 2016). No kittiwakes were seen between these two zones, when crossing over the North Pole along Lomonosov Ridge, which was similar to the pattern shown by ivory gull (Joiris *et al.*, 2016, their Figure 4e, g).

During cruises to the North Pole, kittiwakes are recorded regularly, although in small numbers, all the way to the North Pole (Parmelee and Parmelee, 1994; Vuilleumier, 1996; M. Gavrilov, S. Haugum, V. Buzun, unpublished data). Recent GLS tracking of birds breeding in the eastern Barents Sea revealed migration of some kittiwakes (breeding in south Novaya Zemlya) across the CAO to North Pacific wintering grounds (Ezhov *et al.*, 2021).

### 9.6.5 Glaucous gull (*Larus hyperboreus*)

Glaucous gull is a large Arctic gull species (body mass of 1.5–2.5 kg), with a circumpolar breeding distribution (Figure 9.14). It breeds on Arctic coasts in the Low and High Arctic zones, including around the CAO and the High Arctic archipelagoes (Weiser and Gilchrist, 2012; Petersen *et al.*, 2015). Glaucous gull has four subspecies: nominate *hyperboreus* from Jan Mayen and Svalbard east to Taymyr, *pallidissimus* from Taymyr to the Bering Sea, *barrovianus* in Alaska and western Arctic Canada, and *leucereetes* east from the eastern Mackenzie region to Greenland and Iceland (Burger and Gochfeld, 1996). It nests in a variety of coastal habitats, usually near water and inaccessible to terrestrial predators (Weiser and Gilchrist, 2012). Glaucous gull is a generalist feeder, and takes a wide range of prey including invertebrates, fish, bird eggs, chicks, and adults (e.g. dovekies, black-legged kittiwakes, thick-billed murres), lemmings, berries, carrion, and human refuse, as well as scavenging on marine mammal remains (e.g. Barry and Barry, 1990; Stempniewicz, 1995; Gilchrist, 1999; Weiser and Gilchrist, 2012).



Figure 9.14. Glaucous gull. Photo: Maria Gavrilov.

Glaucous gull has a large total global population (0.4–1.5 million individuals) and is listed as a species of Least Concern in the IUCN Red List (Wetlands International, 2015; BirdLife International, 2018e). The European subspecies (*hyperboreus*) has been estimated to number 135 000–360 000 individuals, while the *barrovianus* and *leucereetes* subspecies are estimated to number in the range of 0.1–1 million individuals (Delany and Scott, 2006). Recently, Petersen *et al.* (2015) estimated the total Arctic population at 138 600–218 600 breeding pairs (277 200–437 200 breeding individuals) distributed among a minimum of 2768 colonies. This circumpolar review found evidence of population declines in some portions of the range where trend data were available, but not in the Russian Arctic and Greenland, where populations appeared stable or increasing.

Glaucous gulls are primarily coastal feeding birds with a limited foraging range. They may venture into the pack ice of the CAO in summer and autumn, but in small numbers. They have been seen occasionally in the ice, but usually only as scattered single individuals (Collett and



Nansen, 1900; Portenko, 1946; Uspenskiy, 1956; Vuilleumier, 1996). The 2007–2012 vessel-based surveys off Alaska found glaucous gulls widely dispersed in the eastern Chukchi and western Beaufort seas at low-moderate densities, with higher densities in offshore waters during autumn (September–November; Kuletz *et al.*, 2015). With additional surveys through 2015, Kuletz *et al.* (2019) found glaucous gull to be the only species with a consistent presence in the Pacific Arctic north of the Chukchi shelf and east across the Beaufort shelf. Including surveys farther north and through 2017, glaucous gulls were found on the slope and into CAO waters of the Canada Basin, but not north of  $\sim 75^{\circ}\text{N}$  (Figure 9.9, panel e). Glaucous gulls were also common in the Canadian gateways of Davis Strait and Lancaster Sound.

#### 9.6.6 Northern fulmar (*Fulmarus glacialis*)

Northern fulmar resembles a gull in appearance, but it is a tube-nosed bird in the family of petrels and shearwaters (Procellariidae; Figure 9.15). It is a medium-sized bird (body mass of 0.5–1 kg) and occurs with colour morphs ranging from mostly white to uniformly dark grey. The colour morphs are not taxonomically distinct, and light- and dark-morph birds may breed as coupled pairs. The northern fulmar has three recognized subspecies: the nominate *glacialis* in the Arctic part of the North Atlantic, *auduboni* in the subarctic and boreal North Atlantic (northeastern Canada, west Greenland, Iceland, Jan Mayen, and UK), and *rodgersii* in the North Pacific (Carboneras, 1992; Mallory *et al.*, 2012b). The *glacialis* subspecies breeds on Baffin and Devon islands in Canada (Gaston *et al.*, 2006; Mallory, 2006), in northeast Greenland (Boertmann, 1994; Falk and Møller, 1995), and on Svalbard, Novaya Zemlya, and Franz Josef Land (Bakken and Gavrilov, 2000; Mallory *et al.*, 2012b). Subspecies *rodgersii* breeds, with 99% of all individuals, in four large colonies, the northernmost being at the Pribilof Islands and St Matthew and Hall islands in the Bering Sea (Mallory *et al.*, 2012b). A genetic study found that the Pacific subspecies was sufficiently different that it could be regarded as a separate species (Kerr *et al.*, 2007).



Figure 9.15. Northern fulmar of the light color morph. Photo: Kathy Kuletz, USFWS.

Northern fulmar is a cliff-breeder, often found in mixed colonies with black-legged kittiwakes and murre. It is a long-lived species with slow reproduction. Most individuals start to breed when they are 8–10 years old (Dunnet, 1992).

The total global population of northern fulmars is estimated to be about 20 million individuals, and the species is listed as species of Least Concern in the IUCN Red List (BirdLife International, 2018f). The European breeding population is estimated to be about 7 million individuals.

The breeding population at Svalbard is estimated to be 0.1–1 million pairs (Mehlum and Bakken, 1994; Bakken and Gavrilov, 2000). In the Northeast Water (NEW) polynya in northeast Greenland, small colonies (the largest at Mallemukfjeld) were estimated to hold about 1500 pairs (Falk and Møller, 1995; Falk *et al.*, 1997). About 7000–8000 pairs were estimated to breed in several colonies at Franz Josef Land (Strøm *et al.*, 2016). Fulmars are long-distant foragers and may range hundreds of kilometres from their nesting colony (maximum 500–600 km; Thaxter *et al.*, 2012). Fulmars with unknown breeding status are regularly observed in summer far from breeding colonies, in open or loose pack ice waters throughout the Siberian shelf seas, as well as in the CAO. Immature birds and mature birds after breeding may move north to feed in summer and autumn, many to the Fram Strait region and waters north of Svalbard. Mehlum (1989) reported a widespread distribution and relatively high abundance of fulmars in waters west of Spitsbergen and in the northeastern Greenland Sea west to 0–5°W between 77 and 81°N (typically 3–10 individuals per 10-min observation period). Lower densities were recorded in the Northeast Water area (typically 1–3 individuals per 10 min).

During North Pole cruises, fulmars are recorded regularly as single birds in the CAO all the way to the North Pole. They occur in the vicinity of the Pole even more often than kittiwakes (Parmelee and Parmelee, 1994; Vuilleumier, 1996; M. Gavrilov, unpublished data)

Fulmars were found in mixed-species groups along with black-legged kittiwakes, thick-billed murre, and dovekies in the northern Greenland Sea, often with a negative association with sea ice (Mehlum, 1997). Satellite-tracking of three failed breeders from a colony (Mallemukfjeld) in the Northeast Water area showed that they moved into the Fram Strait area, where they generally followed the ice edges while foraging in the marginal ice zone (Falk and Møller, 1995). Individual birds alternated between long flights and stays within restricted areas where they presumably were feeding. The longest distance covered was over 2000 km in 14 days, and the maximum daily distance was 369 km (Falk and Møller, 1995). Satellite-tagging of five breeding fulmars at the northernmost colony in Canada (at Cape Vera on northern Devon Island, at the head of Jones Sound) showed that they moved between the colony and the North Water Polynya to the east (at about 77°N, 75°W) for about two months (Mallory *et al.*, 2008b). When they left the area in mid- to late September, they flew south to Davis Strait (> 750 km) in less than a week, from where they dispersed to winter in the North Atlantic.

With a flight speed of around 30 km h<sup>-1</sup> and a tendency to travel long distances, northern fulmars could cover the distance to the North Pole and back (between 80 and 90°N) in 1–2 weeks. During the RV “Polarstern” cruise in 2014, northern fulmars were seen regularly, although in small numbers, in the ice north of Greenland and up to the North Pole (Joiris *et al.*, 2016). They were also seen regularly on the Siberian side at 81–84°N, in the region of Lomonosov Ridge. On the Pacific side, northern fulmars fly north in summer through Bering Strait to Chukchi Sea, where they can be common and abundant. Divoky (1987) estimated that 45 000 fulmars were in the Chukchi Sea in late summer, mainly in the southern part north to Cape Lisburne. They occasionally wander as far north as Cape Barrow and Herald Island in the northern Chukchi Sea, but rarely beyond (Mallory *et al.*, 2012b).

Vessel-based surveys during 2006–2015 found that northern fulmar abundance declined abruptly north of Bering Strait. However, they remained present in small numbers throughout

the eastern Chukchi and western Beaufort, with highest densities around Bering Strait, and lowest densities near the Chukchi slope and east in the Beaufort Sea as far as  $\sim 156^{\circ}\text{W}$  (Kuletz *et al.*, 2019). In additional surveys through 2017, including northernmost transits, there were few sightings on the Beaufort slope east of  $130^{\circ}\text{W}$ , and one sighting at  $\sim 82^{\circ}\text{N}$  north of the Chukchi Borderlands (Figure 9.9, panel f). In the Canadian Arctic, vessel-based surveys found northern fulmars widely distributed from Davis Strait north to Lancaster Sound, with the highest densities on the southern end of Davis Strait and along the Labrador coast.

### 9.6.7 Dovekie (*Alle alle*)

Dovekie or little auk (*Alle alle*) is a small plankton-feeding auk (body mass of approximately 150–200 g) that breeds primarily in the Atlantic sector of the Arctic (Figure 9.16). Dovekie breeds in high Arctic colonies, from eastern Baffin Island in the west, over western and eastern Greenland, Jan Mayen, and Svalbard, Franz Josef Land, and Novaya Zemlya, to Severnaya Zemlya in the east (de Korte *et al.*, 1995; Nettleship, 1996; Isaksen and Gavrilov, 2000; Stempniewicz, 2001; Montevecchi and Stenhouse, 2020). It also breeds in very small numbers in the northern Bering Sea and the Bering Strait region (Day *et al.*, 1988). The birds from Franz Josef Land and Severnaya Zemlya are considered a separate subspecies *polaris* (Stenhouse, 1930; Golovkin, 1990a; Nettleship, 1996; Stempniewicz *et al.*, 1996; Stempniewicz, 2001; Koblik *et al.*, 2006), which is morphologically distinct (birds from Franz Josef Land are statistically 10–20% bigger than birds from Svalbard; Stempniewicz *et al.*, 1996), but attempts to find genetical differentiation have failed so far (Wojczulanis-Jakubas *et al.*, 2014, 2015).



Figure 9.16. Dovekie (or little auk) on Hooker Island, Franz Josef Land (subspecies *polaris*). Photo: Maria Gavrilov.

Dovekie breeds in large colonies on Svalbard, the largest in southern and western parts around Hornsund, Bellsund, and Magdalenefjorden (Isaksen and Bakken, 1995a; Isaksen and Gavrilov, 2000). It also breeds in northern Svalbard in the Hinlopen Strait area and along the north coast of Nordaustlandet. Dovekies breed in scree slopes on mountain sides and in rock crevices, mainly along coasts, but also inland up to 30 km from the coast (Isaksen and Bakken, 1995b).



On Franz Josef Land, dovekie breeds in many colonies scattered over much of the archipelago, except for on the easternmost islands (Gavrilo *et al.*, 1993; Stempniewicz *et al.*, 1996; Isaksen and Gavrilo, 2000; Stempniewicz, 2001; Grémillet *et al.*, 2015). It also breeds farther east, on Severnaya Zemlya, mostly on the eastern side of the archipelago.

Dovekie is one of the most numerous of all seabird species, occurring with an estimated population of possibly around 50 million individuals or more (BirdLife International, 2018g). The breeding population on Svalbard is assumed to be more than 1 million breeding pairs, while the population on Franz Josef Land has been very roughly estimated at over 0.5 million pairs (Strøm *et al.*, 2016). The population of dovekies in the Severnaya Zemlya archipelago has been roughly estimated to be less than 100 000 breeding pairs (de Korte *et al.*, 1995). The largest concentrations of dovekies breed in the Qaanaaq (Thule) district in northwestern Greenland, adjacent to the North Water polynya, where possibly over 80% of the global population is found (Boertmann and Mosbech, 1998; Egevang *et al.*, 2003; Boertmann and Rasmussen, 2011). Dovekies also breed in large colonies in the Scoresby Sund area in East Greenland (Kampp *et al.*, 1987; Boertmann, 1994; Harding *et al.*, 2009).

During the breeding period, dovekies can range from the colonies an estimated 150–200 km or even more (Brown, 1976; Welcker *et al.*, 2009; Amélineau *et al.*, 2016). Dovekies at Spitsbergen were found to have a bimodal foraging pattern, whereby they alternated between one long and several shorter foraging trips (Steen *et al.*, 2007). The short trips lasted about two hours and were considered foraging to provide food for the chicks, while the long trips lasted 12–17 hours and were believed to be primarily for foraging by the parents themselves (Steen *et al.*, 2007; Welcker *et al.*, 2009). Dovekies have high metabolic rate and must eat an amount of food nearly equivalent to their own body weight per day (Gabrielsen *et al.*, 1991; Karnovsky and Hunt, 2002; Harding *et al.*, 2009).

Dovekies feed primarily on large Arctic copepods and amphipods. Studies at colonies in Hornsund and Magdalenefjorden at Svalbard found that *Calanus glacialis* stage CV was the primary prey (Karnovsky *et al.*, 2003, 2010; Wojczulanis *et al.*, 2006; Kwasniewski *et al.*, 2010). Adult dovekies feeding their chicks also brought back pelagic amphipods (*Themisto abyssorum* and *T. libellula*), the ice-associated amphipod *Apherusa glacialis*, decapod larvae, and krill (*Thysanoessa inermis* and *T. longicaudata*; Karnovsky *et al.*, 2003, 2010; Wojczulanis *et al.*, 2006; Steen *et al.*, 2007; Kwasniewski *et al.*, 2010). Dovekies collected in the marginal ice zone east of Svalbard in late summer (August 1982) had eaten predominantly ice-associated gammarid amphipods (*Apherusa glacialis* and *Gammarus wilkitzkii*), along with the pelagic amphipod *Themisto libellula* and copepods (Mehlum and Gabrielsen, 1993). Dovekies feeding in multiyear ice north of Svalbard collected in summer took a large proportion of ice-associated amphipods, primarily *Apherusa glacialis* (Lønne and Gabrielsen, 1992). It is a common pattern that dovekies shift from eating mainly copepods during the breeding period to more amphipods and other prey that are higher in the trophic ladder later in the summer season (Bradstreet, 1982; Karnovsky and Hunt, 2002; Karnovsky *et al.*, 2008; Fort *et al.*, 2010).

The waters north of Svalbard and Franz Josef Land in Nansen Basin may be used as part of the foraging area for dovekies from adjacent northern colonies. In the slope waters, they can feed on large copepods and other plankton transported with Atlantic water into the Arctic Ocean (Wassmann *et al.*, 2015; Hunt *et al.*, 2016). In the marginal ice zone of the seasonally retreating ice edge, they can feed on ice-associated amphipods as well as the pelagic *Themisto* species. A similar situation appears to be the case for dovekies from Severnaya Zemlya, which can feed in the slope region and marginal ice zone in the northwestern Laptev Sea. Dovekies were seen in large numbers during the Fram expedition in summer 1896 in Nansen Basin, at around 83°N north of Svalbard, where they occurred in leads and channels in the ice (Collett and Nansen, 1900). Dovekies were also seen at about 84.5°N northeast of Franz Josef Land in summer 1895,

although in small numbers, possibly because Fram was drifting in closely packed ice (Collett and Nansen, 1900). The same summer, Nansen (during his sledge journey) observed large numbers of dovekies around 82°N, closer to Franz Josef Land, where birds were seen searching for food in leads and openings in the ice.

### 9.6.8 Least auklet (*Aethia pusilla*)

Least auklet is the smallest alcid (body mass of 80–90 g) and the most abundant breeding seabird in the Pacific Arctic (Figure 9.17; Bond *et al.*, 2013). Like the dovekie, it specializes in copepods and other zooplankton (Hunt and Harrison, 1990; Sheffield Guy *et al.*, 2009; Bond *et al.*, 2013). Pairs nest in talus and rock crevices, laying a single egg which they incubate for ~30 days. They bring food to their chicks by regurgitating zooplankton from a sublingual pouch, and will themselves consume 80–90% of their body mass per day (Bond *et al.*, 2013). The estimated global population of least auklets is about 20 million birds, although reliable counts have not been possible, due to its nesting habitat and dense concentrations in relatively few colonies (Bond *et al.*, 2013). Because of its abundance and its ecological equivalence to the dovekie, the least auklet was selected as a FEC for the CBMP (CAFF, 2017). It is categorized by the IUCN as a species of Least Concern (BirdLife International, 2020).



Figure 9.17. Least auklet at bird cliff on St Paul Island (Pribilof Islands), Alaska. Photo: Daniel Cushing.

Least auklets nest in colonies scattered along rocky coastlines of the Bering Sea and Aleutian Islands (Hunt, 1997; Stephensen and Irons, 2003), with the largest colonies in Bering Strait (Big and Little Diomed islands), and just south of Bering Strait, particularly on St Lawrence Island. An estimated 5 million least auklets breed on islands and along the mainland of the northern

Bering Sea ([Table 9.3](#)). Although they are not known to breed north of Bering Strait, they are abundant offshore throughout the southeastern Chukchi Sea (Gall *et al.*, 2017; Kuletz *et al.*, 2019), including on the slope near the mouth of Barrow Canyon in summer, with their highest densities near Bering Strait in autumn (Kuletz *et al.*, 2015, 2019). Least auklets have become more common in the Chukchi Sea since the 1980s (Gall *et al.*, 2017). Based on birds fitted with geolocators, some of those summer visitors may be from colonies on St Lawrence Island (A. Will, personal communication) or possibly the Aleutian Islands, where birds finish raising their chicks earlier than birds in the north. Offshore surveys in 2007–2017 found least auklets to be among the most common seabird on the Chukchi shelf, but there have been few observations on the slope of the CAO, and none in the deeper CAO basin.

### 9.6.9 Thick-billed murre (*Uria lomvia*)

Thick-billed murre is a black and white auk species with an almost circumpolar distribution in the Arctic ([Figure 9.18](#)). It is one of the most numerous seabird species, with a total global population of more than 20 million individuals and is categorized by the IUCN as a species of Least Concern (BirdLife International, 2018h). Thick-billed murre occurs with four subspecies (Nettleship, 1996; Gaston and Hipfner, 2000). The nominate *lomvia* breeds in the Atlantic sector from eastern Arctic Canada to Franz Josef Land and Novaya Zemlya in Russia, while subspecies *arra* breeds in the North Pacific, north from northern Japan and British Columbia through the Bering Sea to the Chukchi Sea. The Pacific subspecies is generally larger and darker than the Atlantic subspecies (Gaston and Hipfner, 2000). Two more subspecies are found in Siberia, with *eleonorae* breeding from the eastern Taymyr Peninsula east to the New Siberian Islands, and *heckeri* breeding on Wrangel and Herald islands and the north coast of the Chukotka Peninsula (Portenko, 1972; Golovkin, 1990b; Nettleship, 1996; Gaston and Hipfner, 2000). These two races are poorly differentiated and should perhaps be treated as part of the Pacific *arra* subspecies (Gaston and Hipfner, 2000).

The nominate *lomvia* subspecies breeds in eastern Arctic Canada, north and west to Prince Leopold Island in Barrow Strait and Coburg Island near the North Water Polynya, and south to the Gulf of St Lawrence and Newfoundland. On the opposite side of Baffin Bay, it breeds in western Greenland, south from the Qaanaaq (Thule) district (Kampp, 1990; Boertmann, 1994; Boertmann and Mosbech, 2011). The breeding population in the North Water area is just over 0.5 million pairs (150 000 on Coburg Island, 160 000 on Bylot Island, and 225 000 in Qaanaaq), with another 100 000 pairs breeding on Prince Leopold Island inside Lancaster Sound (Kampp, 1990; Boertmann and Mosbech, 2011; Gaston *et al.*, 2012, 2013; Merkel *et al.*, 2014). It breeds in the Scoresby Sound area in East Greenland (about 6000 breeding pairs) and at Jan Mayen (10 000 to 100 000 pairs; van Franeker *et al.*, 1998). At Svalbard, the largest concentration of birds is found in southeastern Spitsbergen (Stellingfjellet, Kovalskifjellet, and others) where nearly half the total population at Svalbard breeds (from a total of 850 000 breeding pairs; Bakken and Pokrovskaya, 2000). The northernmost colonies are located in Hinlopen Strait and along the north coast of Nordaustlandet (Isaksen and Bakken, 1995a; Bakken and Pokrovskaya, 2000; Bakken and Mehlum, 2005). The breeding population at Novaya Zemlya used to be the greatest in the region, but is now assumed to number between 250 000 and 500 000 breeding pairs (Strøm *et al.*, 2016). Smaller numbers breed on Franz Josef Land in about 20 colonies, with an estimated total population of up to 200 000–250 000 pairs (Strøm *et al.*, 2016).

Thick-billed murre (described as subspecies *eleonorae*) breeds in one colony in southeastern Taimyr (Preobrazhenia Island in the Khatanga Bay) as well as in the New Siberian Archipelago. The population in Laptev Sea has previously been estimated at approximately 32 000 breeding pairs (Uspenskiy, 1957, 1959; Rutilevskiy, 1963), and no new censuses have been done since that time. Thick-billed murre (subspecies *heckeri*) also breeds on Wrangel Island, Herald Island, and the northern Chukotka Peninsula (Portenko, 1972; Nettleship, 1996; Gaston and Hipfner, 2000).



The Pacific subspecies *arra* nests in large colonies in the southern Bering Sea along the Aleutian Islands and on the Pribilof Islands, in the northern Bering Sea at St Matthew and St Lawrence islands, and on islands in the Bering Strait region (Stephensen and Irons, 2003). The total population has been estimated at 5 and 1.5 million individuals in the eastern and western Bering Sea, respectively (Loughlin *et al.*, 1999; Shuntov, 1999; Springer *et al.*, 1999). The *arra* subspecies also breeds in the Chukchi Sea, with fairly large colonies at Cape Thompson and Cape Lisburne on the Alaskan side (100 000–400 000; Gaston and Hipfner, 2000; Dragoo *et al.*, 2004) and along the northeast coast of Chukotka west to Cape Serdze–Kamen (Konyukhov *et al.*, 1998; south and east of the tentative subspecies *heckeri*). There is a small colony (some hundred pairs) at Cape Parry in Amundsen Gulf in the eastern Beaufort Sea, which is assumed to be *arra* (Johnson and Ward, 1985; Gaston and Hipfner, 2000; Latour *et al.*, 2006). For the Pacific gateway region of northern Bering and southern Chukchi seas on both Russian and Alaskan sides, an estimated 1.08 million thick-billed murres are distributed among 15 major colonies ([Table 9.3](#)).



**Figure 9.18. Thick-billed murre at Franz Josef Land. Photo: Maria Gavrilov.**

Thick-billed murre catch a variety of prey by underwater pursuit, and regularly dive to 100 m and occasionally down to 200 m depth (Gaston and Hipfner, 2000). It feeds to a large extent on polar cod and amphipods in the northern part of its distribution (Nettleship, 1996; Gaston and Hipfner, 2000; Bakken and Pokrovskaya, 2000). Its diet included a large proportion of euphausiids in the Bering and Chukchi seas (Hunt *et al.*, 2000; Jones *et al.*, 2014).

Thick-billed murres can forage up to 50–100 km from their breeding colonies, but typically travel smaller distances (Gaston and Hipfner, 2000; Falk *et al.*, 2002). In theory, birds from the northernmost colonies may forage out over slope waters in the CAO. Birds from colonies at western Spitsbergen and the north coast of Svalbard feed out in the eastern Fram Strait and waters north of Svalbard. After just two weeks in the nest, the single chick jumps to the water and joins the male parent, where it is raised at sea for another two months, and during which time it is flightless (Gaston and Hipfner, 2000). The chicks and adults undergo a swimming migration, where the adult birds moult their wing feathers and are also flightless (Gaston and

Hipfner, 2000). Birds from the main colonies in southern Svalbard (which hold most of the Svalbard breeding population) move south and east into the western Barents Sea where they feed in autumn (Bakken and Mehlum, 1988; Steen *et al.*, 2013). Therefore, it seems that few birds move north to feed in the slope waters of Nansen Basin in autumn. Sightings from RV Polarstern in 2014 found thick-billed murre to be one of the more common species in the northern Norwegian and Greenland seas west of Svalbard, but only a few individuals were recorded in the NEW polynya off northeast Greenland, and one individual was recorded over Lomonosov Ridge on the Siberian side (81–84°N; Joiris *et al.*, 2016). The Fram expedition observed few thick-billed guillemots in the ice north of Svalbard in summer 1896, in contrast to large numbers of dovekies and black guillemots (Collett and Nansen, 1900).

Birds from the colonies at Franz Josef Land could feed in the slope waters, but observations suggest that few individuals do so, and that most birds forage in the northern Barents Sea. The colonies are situated in the southern and western portions of the Franz Josef Land archipelago, and very few birds have been observed during North Pole cruises north of Franz Josef Land (Parmelee and Parmelee, 1994; Vuilleumier, 1996; M. Gavrilov, unpublished data). Nansen, likewise, observed very few (only three) thick-billed murres on the sledge journey coming from the north toward Franz Josef Land in summer 1895 (Collett and Nansen, 1900). It is believed that thick-billed murres from Franz Josef Land winter in the eastern Barents Sea (Bakken and Pokrovskaya, 2000), which was recently confirmed with data from geolocator tracking (SEATRACK data). High densities of thick-billed murres during the migration and moulting period in August and September (1995 and 1996) were observed south of Franz Josef Land, as well as south of Novaya Zemlya and in the southeastern Barents Sea (Decker *et al.*, 1998). Tagging with geolocators of thick-billed murres in Svalbard, Franz Josef Land, and northernmost Novaya Zemlya showed very limited, if any, movements northward beyond the shelf waters of the archipelagos (SEATRACK data).

Thick-billed murres from the colonies in the Laptev Sea (subspecies *eleonorae*) forage out on the outer shelf, and probably also in the slope area where juvenile polar cod are known to occur as a potential food source (Bouchard and Fortier, 2008, 2011). Murres from Wrangel Island (subspecies *heckeri*) can potentially forage out in slope waters. However, the distance is long, and most of them presumably forage around Wrangel Island, notably in the productive waters flowing north through Harold Canyon to the east of Wrangel Island (Weingartner *et al.*, 2005a; Berline *et al.*, 2008).

Thick-billed murres from the colonies at Cape Thompson and Cape Lisburne (subspecies *arra*) forage in the eastern Chukchi Sea, and there are high densities near the colonies in summer (Kuletz *et al.*, 2015, 2019). Tagged murres from the two colonies were found to feed in separate areas in the southern and northern sectors offshore of the Lisburne Peninsula, respectively (Hatch *et al.*, 2000). However, murres are found throughout the eastern Chukchi Sea in summer and autumn, including sites 500–600 km from colonies, such as Hanna Shoal and near the CAO slope at the mouth of Barrow Canyon (Kuletz *et al.*, 2015). Their regular occurrence beyond foraging distance from colonies in summer, as well as in autumn, indicates that the northern Chukchi Sea is a foraging location for non-breeding and post-breeding birds, perhaps due to the late summer abundance of euphausiids in the region (Berline *et al.*, 2008). During at-sea surveys in 2007–2017, small numbers of thick-billed murres were recorded near the Chukchi Borderlands of the CAO, as well as on the slope near the mouth of Barrow Canyon and in the Camden Bay/slope area of the Beaufort shelf (Figure 9.9, panel g). On the Atlantic side, at-sea surveys found thick-billed murres in low densities throughout Davis Strait to the Lancaster Sound area, with high densities near the Newfoundland coast and areas of northeastern Baffin Island.



#### 9.6.10 Black guillemot (*Cepphus grylle*)

Black guillemot is a medium-sized auk (body mass of approximately 400 g), with a circumpolar breeding distribution (Figure 9.19; Butler and Buckley, 2002). It occurs with five subspecies: *mandtii* is a high-Arctic breeder, while *arcticus* breeds south of it in the Atlantic sector (three more subspecies are nominate *grylle* in the Baltic Sea, *islandicus* on Iceland, and *faeroeensis* on the Faroe Isles; Nettleship, 1996; Butler and Buckley, 2002). The breeders (*mandtii*) from northeastern Canada and Greenland have sometimes been considered a separate subspecies (*ultimus*; Nettleship, 1996; Butler and Buckley, 2002). The total global population of black guillemots is estimated to be in the range of 0.4–1.5 million individuals and is categorized by the IUCN as a species of Least Concern (BirdLife International, 2016b; IUCN, 2021).



Figure 9.19. Black guillemot of the subspecies *mandtii*. Photo: Maria Gavrilov.

Subspecies *mandtii* breeds in the northern Bering, eastern Chukchi, and western Beaufort seas, central and eastern parts of the Canadian Arctic Archipelago (north to southern Ellesmere Island and Devon Island, but is lacking from the northern Queen Elisabeth Islands and Banks and Victoria islands in the western part), and in Foxe Basin, Hudson Basin, and Hudson Strait (Butler and Buckley, 2002). The breeding population of black guillemots (*mandtii* and *arcticus*) in the eastern Canadian Arctic was estimated to be about 200 000 pairs, with about 80 000 pairs breeding along Baffin Bay and Davis Strait (Gaston *et al.*, 2012). In Greenland, subspecies *mandtii* breeds south from the Qaanaaq (Thule) area to about 72°N along the west coast, and from Wollaston Foreland and Liverpool Land (north of Scoresby Sound) and south to about 69°N on the eastern side (Boertmann, 1994). The breeding population in West Greenland (including *arcticus*) was estimated to be 25 000–100 000 pairs (Boertmann *et al.*, 1996; Lyngs, 2003). Fewer birds breed in East Greenland, with < 100 individuals in the Northeast Water area in the Fram Strait region (Falk *et al.*, 1997). Subspecies *mandtii* breeds on Jan Mayen (100–1000 pairs; van Franeker *et al.*, 1998), and on Svalbard, Franz Josef Land, and Novaya Zemlya in the Barents Sea (about 30 000 pairs; Lorentsen and Pokrovskaya, 2000; subspecies *grylle* breeds on coasts along the southern Barents Sea and in the White Sea). Farther east, *mandtii* breeds on Severnaya Zemlya and on islands in the Kara Sea (but very few along the mainland coast). In the Laptev Sea region, it breeds in eastern Taymyr, on the New Siberian Islands, where it is found in high

concentrations in the western part of the archipelago (Uspenskiy, 1963), and on the remote De Longa Islands (a rough estimate was that more than 35 000 pairs were breeding here; Gavrilov *et al.*, 1998b).

Black guillemot is a common and abundant breeder on Wrangel and Herald Islands (estimated numbers of about 50 000 and 100 000 individuals, respectively; [Table 9.3](#)). It also breeds in smaller numbers along the Russian coast in the western Chukchi Sea, and locally in northwestern Alaska on barrier islands near Point Barrow and at Cape Thompson (Kondratyev *et al.*, 2000; Butler and Buckley, 2002). The number of breeders in Alaska was estimated to be < 2000 individuals (Divoky, 1987). Small numbers of black guillemots are found in the Beaufort Sea, where they nest on some barrier islands, on Herschel Island, and on sea cliffs at Cape Parry in the Amundsen Gulf region (Butler and Buckley, 2002; Latour *et al.*, 2006).

Black guillemot breeds scattered along Arctic barrier islands or where there are rocky coasts, often as single pairs or as small loose colonies in crevices, scree, or among boulders (Butler and Buckley, 2002). They lay one or two eggs and bring their chicks single prey items whole, usually a variety of fish species. It is a pursuit diver that forages near the seabed in coastal waters, typically at depths < 50 m (Cairns, 1992; Masden *et al.*, 2013). Small benthic fish species including blennies, gunnels, pricklebacks, eelpouts, and sculpins are often predominant food, along with benthic invertebrates, such as shrimp and crabs, and pelagic amphipods (Nettleship, 1996; Butler and Buckley, 2002). The *mandtii* subspecies is often found in open water leads within drift ice, where they feed largely on polar cod and pelagic and ice-associated amphipods (Bradstreet, 1980; Cairns, 1987; Lydersen *et al.*, 1989; Lønne and Gabrielsen, 1992). They were seen frequently during the Fram expedition in summers 1894–1896, when the ship drifted with the ice in Eurasian Basin at latitudes north to about 84.5°N (Collett and Nansen, 1990). Many were shot (as food items for the expedition) and examined individuals in June and July were found to be immature birds. Black guillemots were seen in more recent sighting surveys, with relatively high abundance north of Svalbard, although with the highest abundance (up to 30–100 individuals per 10-min observation period) in the central northern Barents Sea east of Kong Karls Land (around 79°N, 35–40°E; Mehlum, 1989). In late August they were found associated with generally light ice conditions (median one-fourth ice cover) in the area between Kong Karls Land and Franz Josef Land (Mehlum, 1990). Most birds collected were in moulting stage, suggesting that the pack ice of the northern Barents Sea is an important moulting area for black guillemots (Mehlum, 1989).

Black guillemots of the *mandtii* subspecies are abundant in the marginal ice zone in the Chukchi Sea, with an earlier estimate of 70 000 individuals in the mobile pack ice during late summer (Divoky, 1987). Kuletz *et al.* (2015) found them in moderate numbers in the northeastern Chukchi Sea, with concentrations (hot spots) in the slope region off Barrow Canyon and in Camden Bay in the central Beaufort shelf. Adding surveys through 2017 (Kuletz, unpublished data), black guillemots were recorded on the eastern Beaufort shelf and slope, in the deep waters of the CAO off MacKenzie Canyon, at the slope near Point Barrow, and at the base of the Chukchi Borderlands at ~ 76°N ([Figure 9.9](#), panel h). The large number of breeders on Herald, Wrangel, and De Long islands suggest that the outer shelf region between the Laptev and Chukchi seas hold a large fraction of the total *mandtii* population. Satellite-tagged black guillemots from Cooper Island, in the western Beaufort Sea, were found to forage in the marginal ice zone in summer and then follow the marginal ice zone from autumn through spring (Divoky *et al.*, 2016). Polar cod of Laptev and Chukchi stocks are likely a main prey for the black guillemots here, along with benthic and demersal fish and ice-associated and pelagic amphipods. During breeding, black guillemots at Cooper Island were affected by the retreat of summer sea ice, which forced adults to fly farther to obtain ice-associated cod or return with low quality prey for their chicks. As a result, fledging success declined in recent years and colony size decreased (Divoky *et al.*, 2015).

## 10 Marine mammals

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### 10.1 Species and habitat use

#### 10.1.1 Species

A total of 35 species of marine mammals are found in the wider Arctic area, which extends south to 60°N or even lower in some areas: 22 whales, 11 pinnipeds, polar bear, and sea otter. Of these, 11 species are true Arctic ice-associated species that are found or can potentially occur in the CAO ([Table 10.1](#)): seven species of pinnipeds (walrus and ringed, bearded, harp, hooded, spotted, and ribbon seals), three species of whales (bowhead, beluga, and narwhal), and polar bear. Ringed seal and polar bear are the species most frequently found in the core areas of the CAO. Bearded seal and walrus are mainly benthic feeders, and are only occasionally seen beyond the shelf edge. Bowhead, beluga, and narwhal may seasonally move into the marginal ice zones of the central pack ice during summer and autumn. This may also be the case for harp and hooded seals but probably to more limited extent. Spotted and ribbon seals are found in the Chukchi Sea in summer, but there are also records of them beyond the shelf edge in the adjacent Canada Basin. In addition to the ice-associated marine mammals, a few species of whales may seasonally move north into the peripheral areas of the CAO. This can be the case for killer whale, and for blue, fin, and humpback whales among the large baleen whales. Altogether 17 species of marine mammals may occur in the CAO on a regular basis or as sporadic visitors ([Table 10.1](#)).

Ringed and bearded seals have amorphous population structures, where individuals live mostly solitary lives with some degree of territorial behavior during the breeding season (Hammill, 2009; Kovacs, 2009). The other marine mammals in the CAO occur with more or less distinct subpopulations or stocks. Information on subpopulations or stocks is included in [Table 10.1](#), and more details are given in the species accounts in [Section 10.2](#).

#### 10.1.2 Habitat use

Polar bears use sea ice as a platform for hunting, breeding, migration between geographical areas, and, in some areas, for maternity denning during the seasonal cycle ([Figure 10.1](#)). Although they are good swimmers, polar bears require a solid sea ice surface for most aspects of their life history. Different subpopulations of polar bears have adapted to the seasonal variation in sea ice in several ways, including following the seasonally retreating sea ice northward or coming ashore and waiting for new sea ice to form in late autumn (Aars *et al.*, 2006; Stirling, 2009). Polar bears that use the CAO in summer and autumn may belong to one of the subpopulations surrounding the polar basin (Durner and Amstrup, 1995) or to the Arctic Basin subpopulation, about which little is known (Durner *et al.*, 2018).

Ringed seals breed mainly in fast ice habitats along the periphery of the continents and archipelagoes, but the species is also known to breed in pack ice in Baffin Bay and Barents Sea (Finley *et al.*, 1983; Wiig *et al.*, 1999; Kovacs *et al.*, 2008; Hammill, 2009). Whether ringed seals breed in the pack ice of the CAO is not known, but it is possible. Other ice-associated seals use sea ice as a breeding habitat, typically in the southern extent of winter sea ice cover. Access to these southerly areas can be difficult for polar bears, the primary predator of ice-associated seals, because rapid ice melt in summer requires bears to make a long northward retreat.

**Table 10.1. Species, subspecies, and/or (sub)populations (or stocks) of marine mammals that are found, or may be found, in the CAO. Geographical area describes the part of the CAO in which the species occur or may occur. Conservation status is as assessed by IUCN (2021 Red List) at the species level (LC: Least Concern, NT: Near Threatened, VUL: Vulnerable, EN: Endangered, DD: Data Deficient; \* indicates assessment at subspecies level), while population size is given for (sub)populations where available (na – not available). The last column is a qualitative assessment of the importance of the CAO to (sub)populations on a three-level scale (low, moderate, high). See Section 10.2 for more details on the species and (sub)populations.**

Species	Latin name	Subspecies and/or subpopulation/stock	Geographical area	Population size	Conservation status	Importance of CAO
Polar bear	<i>Ursus maritimus</i>	Barents Sea	Western Nansen Basin	2600	VUL	High
		Kara Sea	Central Nansen Basin	3200		Moderate
		Laptev Sea	Eastern Nansen Basin	2000		Moderate/High
		Chukchi Sea	Western Canada Basin	2000		High
		Southern Beaufort	Southern Canada Basin	900		High
		Northern Beaufort	Eastern Canada Basin	1000		Moderate/High
		Arctic Basin	E Amerasian, W Eurasian	na		High
		East Greenland	Western Nansen Basin	2000		Low
Ringed seal	<i>Pusa hispida</i>	<i>hispida</i>	Eurasian Basin	na	LC	Low/Moderate
			Amerasian Basin	1 000 000		Low
Bearded seal	<i>Erignathus barbatus</i>	<i>barbatus</i> (Atlantic)	Barents–Laptev	na	LC *	Low
		<i>nautica</i> (Pacific)	Laptev–Beaufort	> 400 000	LC *	Low
Harp seal	<i>Pagophilus groenlandicus</i>	Barents Sea (East Ice)	Western Nansen Basin	1 400 000	LC	Low
		Greenland Sea (West Ice)	Western Nansen Basin	630 000		Low
Hooded seal	<i>Cystophora cristata</i>	Greenland Sea (West Ice)	Western Nansen Basin	84 000	VUL	Low
Spotted seal	<i>Phoca largha</i>	Bering Sea	Canada Basin	> 460 000	LC	Low
Ribbon seal	<i>Histiophoca fasciata</i>	Bering Sea	Canada Basin	18 000	LC	Low
Walrus	<i>Odobenus rosmarus</i>	<i>rosmarus</i> /Svalbard–Franz Josef Land	Western Nansen Basin	5000	VUL; NT *	Low

Table 10.1 (cont.)						
Species	Latin name	Subspecies and/or subpopulation/stock	Geographical area	Population size	Conservation status	Importance of CAO
Walrus (cont.)		<i>rosmarus</i> /Kara Sea–Southern Barents Sea–Novaya Zemlya	Nansen Basin	4000	DD *	Low
		<i>divergens (laptevi)</i> /Laptev Sea	Eastern Nansen Basin	4–5000		Low
		<i>divergens</i> /Bering–Chukchi Seas	Canada Basin	200 000		Low
Bowhead	<i>Balaena mysticetus</i>	Bering–Chukchi–Beaufort	Canada Basin	17 000	LC	Moderate/Low
Beluga	<i>Delphinapterus leucas</i>	East Greenland–Svalbard–Barents Sea	Nansen Basin	300	EN	High
		Eastern Beaufort Sea stock	Canada Basin	40 000	LC	Moderate/High
		Eastern Chukchi Sea stock	Canada Basin	20 000		Moderate/High
		Svalbard	Nansen Basin	na		Low
		Kara and Laptev seas	Nansen Basin	20 000		Moderate
Narwhal	<i>Monodon monoceros</i>	E Greenland–Svalbard	Nansen Basin	2 000+	LC	Moderate/High
Blue whale	<i>Balaenoptera musculus</i>	<i>musculus</i> /E North Atlantic	Nansen Basin	1–2 000	EN	Low
Fin whale	<i>Balaenoptera physalus</i>	<i>physalus</i> /NE North Atlantic	Nansen Basin	4000	VUL	Low
Humpback whale	<i>Megaptera novaeangliae</i>	Barents Sea	Nansen Basin	1500	LC	Low
Common minke whale	<i>Balaenoptera acutorostrata</i>	<i>acutorostrata</i> /NE Atlantic	Nansen Basin	80 000	LC	Low
Grey whale	<i>Eschrichtius robustus</i>	E North Pacific	Canada Basin	27 000	LC	Low
Killer whale	<i>Orcinus orca</i>	E North Atlantic	Nansen Basin	3000	DD	Low
		North Pacific	Canada Basin	1000		Low



Ice-associated seals also use sea ice for haul-out and resting between feeding bouts. For the benthic-feeding bearded seals and walrus, sea ice does not serve this purpose over deep water beyond the shelf edge, because the animals are not able to reach the benthos. However, bearded seals may also feed on pelagic and ice-associated biota (e.g. amphipods and polar cod; Kovacs and Lowry, 2008; Kovacs, 2009) and could, therefore, occasionally be found over deep water.

The three ice-associated Arctic cetaceans (narwhal and bowhead and beluga whales) have different prey preferences and feeding mechanisms. Bowhead filter-feed on copepods and other small prey, beluga feed predominantly on polar cod, and narwhal are deep divers that feed on larger prey, such as Greenland halibut. All three species are adapted to cope with, and benefit from, sea ice. For example, sea ice may provide some protection from predation by killer whales. However, these three Arctic cetaceans need openings to breathe and, therefore, are thought to usually avoid very heavy, consolidated ice.

The other large baleen whales and killer whales are mainly open-water species found predominantly in boreal waters south of the Arctic. However, they can go into waters with light ice conditions, such as in the marginal ice zone in some areas, e.g. the northern Barents Sea. It is food that draws them into ice-covered waters, and sea ice is a hindrance to them rather than a positive habitat feature.

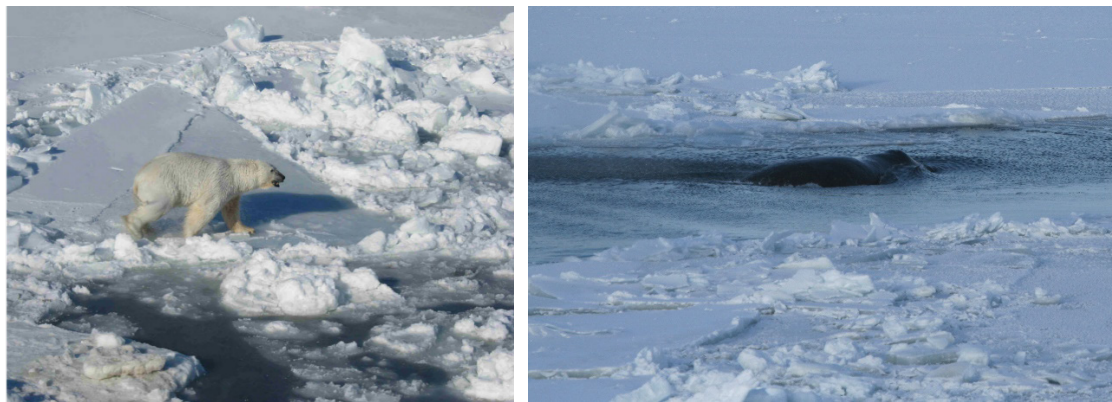


Figure 10.1. Habitat use of marine mammals in ice-covered waters. Polar bear on ice floes (left panel) and bowhead whale swimming in lead (right panel). Photos: USFWS.

## 10.2 Species accounts

### 10.2.1 Polar bear (*Ursus maritimus*)

Polar bears occur within 19 recognized subpopulations (Figure 10.2; Durner *et al.*, 2018). It was once considered to be a circumpolar nomadic species, wandering the vast ice-covered Arctic (Pedersen, 1945). However, due to seasonal fidelity to specific areas or habitats (e.g. Wilson *et al.*, 2016) and discontinuities created by land masses and sea ice conditions, the global polar bear population is known to consist of multiple subpopulations of varying discreteness. Seven of the 19 subpopulations occur, at least partially, on the shelves surrounding the Arctic Ocean basins: the East Greenland, Barents Sea, Kara Sea, Laptev Sea, Chukchi Sea, and Southern and Northern Beaufort Sea subpopulations (Durner *et al.*, 2018). Bears of these subpopulations may follow the retreating ice north into the peripheral areas of the pack ice of the CAO in summer. In addition, there is an Arctic Basin subpopulation that may use the CAO, possibly mainly on the western side toward northern Canada and Greenland, where sea ice typically persists year-round. Loss of sea ice due to climate warming (Laidre *et al.*, 2008; Stern and Laidre, 2016) is the primary threat to polar bears and is expected to result in distribution shifts and subpopulation declines

in coming decades (Atwood *et al.*, 2016a; Regehr *et al.*, 2016). For this reason, polar bear is listed as Vulnerable in the IUCN Red List (Wiig *et al.*, 2015).

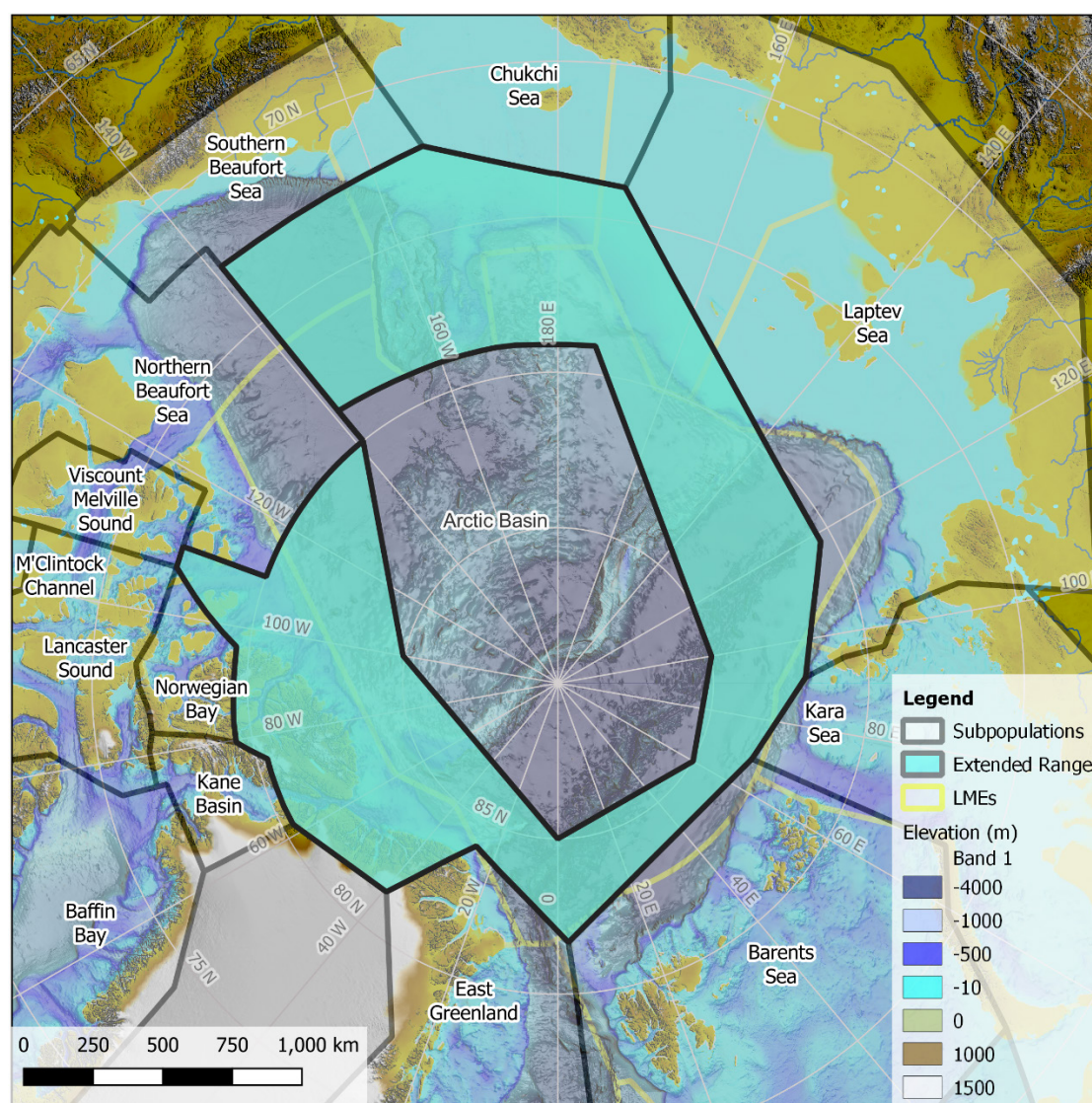


Figure 10.2. Polar bear subpopulations in and around the CAO. The black lines show the delineation of subpopulations recognized by the Polar Bear Specialists Group of IUCN, with the names of the subpopulations given (Barents Sea subpopulation, etc.). The green areas are extended ranges of the subpopulations in ice-covered waters of the CAO as revealed by satellite-tracked individuals.

### Arctic Basin subpopulation

The Arctic Basin subpopulation is not well understood. It effectively serves as a geographic catchall to account for polar bears that may be resident in areas of the circumpolar Arctic but are not clearly part of other subpopulations (Durner *et al.*, 2018). Observations of polar bears in the CAO have been made by Soviet and Russian aerial ice surveys and from the North Pole ice-drift stations from the 1950s to the early 1990s (Belikov and Gorbunov, 1991; Gorbunov and Belikov, 2008; Belikov, 2011), and more recently from icebreakers going to the central part of the Arctic Ocean, including near the North Pole (van Meurs and Splettstoesser, 2003; Gorbunov and Belikov, 2008; Belikov, 2011). Although quantitative data on polar bear abundance and habitat use in the Arctic Basin subpopulation are not available, the aforementioned studies suggest that densities are low, and it is possible that the CAO contains few year-round residents. Bears have been observed feeding on ringed seals in the CAO (Ovsyanikov, 2010), but it is generally

thought that ice-associated seals are uncommon in this region when compared to peripheral waters over the continental shelf (Harwood *et al.*, 2012), which would result in limited foraging opportunities for polar bears. Indeed, recent studies have found that members of the Southern Beaufort Sea and Chukchi Sea subpopulations that spent summers on pack ice over the polar basin were less active (Ware *et al.*, 2017) and food-deprived (Whiteman *et al.*, 2015, 2017). As loss of sea ice due to climate change continues (Post *et al.*, 2013), some areas within the Arctic Basin subpopulation are expected to be among the last to become seasonally ice free, making this an increasingly important region for polar bears and highlighting the need for scientific research.

Polar bears give birth in dens typically located in snow drifts on land (Harington, 1968; Jonkel *et al.*, 1972; Belikov *et al.*, 1977; Larsen, 1985; Uspenskiy, 1989; Stirling and Andriashek, 1992; Belikov, 1993; Amstrup and Gardner, 1994; Durner *et al.*, 2003; Andersen *et al.*, 2012). However, bears of the Southern Beaufort Sea subpopulation also den on consolidated offshore pack ice (Lentfer, 1975; Lentfer and Hensel, 1980; Fischbach *et al.*, 2007). Therefore, denning on pack ice is a possibility for bears in the CAO, although this has not yet been confirmed. Denning can also take place in the northernmost part of the Queen Elisabeth Islands and northern Greenland. Durner and Amstrup (1995) tracked a female polar bear (with two cubs which she probably lost) captured in Prudhoe Bay. It moved across the Arctic Ocean to northern Greenland, passing within 2° of the North Pole and moving at an average speed of a short marathon per day (34 km) from June to September. This bear was tracked for nearly two years, and it entered dens in northern Greenland in two winters, the first time on offshore pack ice and the second time probably in a maternity den located on the coast (Durner and Amstrup, 1995). Larsen *et al.* (1983) tagged a female polar bear with two small cubs in early May at 83.5°N off northeastern Greenland. This bear must have emerged from a maternity den either on the pack ice or on the coast of northern Greenland. Aerial surveys with helicopter around ice-drift station Fram I in this area, located at about 84°N, revealed polar bear tracks, almost all of them of females with small cubs, heading southeast to the area north of Fram Strait (Larsen *et al.*, 1983). This indicates that the area along northern Greenland is a denning area for polar bears. A recent study found denning in snowdrifts around icebergs frozen into the fast ice or grounded on the seabed in North and Northeast Greenland (Laidre and Stirling, 2020).

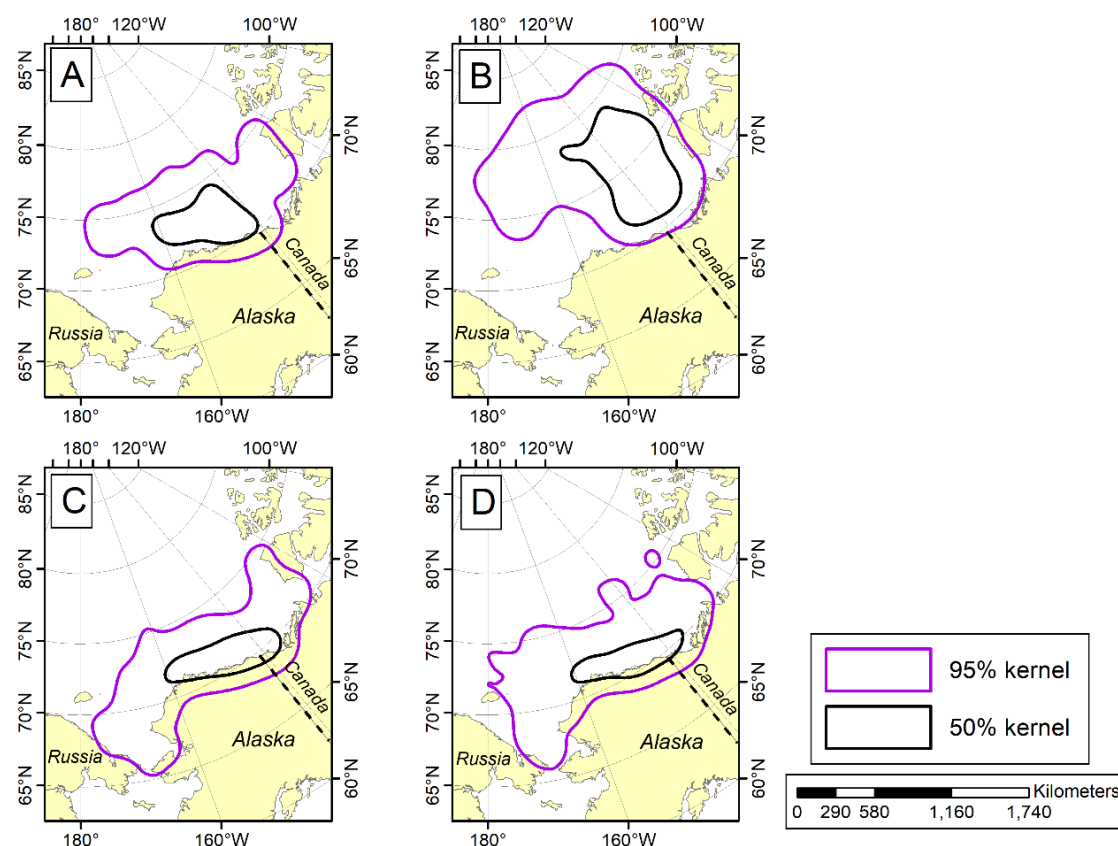
In the Canadian High Arctic, there are two small subpopulations of polar bears bordering the polar basin: the Norwegian Bay subpopulation, in the area between Axel Heiberg Island and southwestern Ellesmere Island, and the Kane Basin subpopulation, between Ellesmere Island and northwestern Greenland (Taylor *et al.*, 2001; COSEWIC, 2008). Satellite telemetry has shown that these bears generally have restricted ranges and do not move north to the Arctic Ocean (Taylor *et al.*, 2001; SWG, 2016). Polar bears are found in the northernmost part of the Queen Elisabeth Islands including Ellesmere Island and are assumed to be members of the Arctic Basin subpopulation (Aars *et al.*, 2006; COSEWIC, 2008), which previously was called the Queen Elisabeth Island subpopulation (Taylor and Lee, 1995).

### **Northern Beaufort Sea subpopulation**

Bears in the Northern Beaufort Sea subpopulation move north and east with the retreating ice in summer. Their distribution includes the westernmost part of the Queen Elisabeth Islands, including Prince Patrick Island north of M'Clure Strait (Lunn *et al.*, 1995; Amstrup *et al.*, 2000, 2004; Stirling, 2002; Stirling *et al.*, 2011). The northern boundary of this subpopulation is not well known. Satellite telemetry has shown that bears captured along western Prince Patrick Island and the western entrance to M'Clure Strait tended to remain in this area, with limited mixing with bears found along western Banks Island (Lunn *et al.*, 1995; Stirling, 2002). Some of the bears tagged at Prince Patrick Island were found to move east along the shore lead system off Queen Elisabeth Islands to Greenland (Stirling, 2002). Tracking of polar bears captured in the M'Clure Strait and Viscount Melville Sound region showed a clear separation in M'Clure Strait between



bears of the Northern Beaufort Sea and Viscount Melville subpopulations (Bethke *et al.*, 1996; Taylor *et al.*, 2001). The Northern Beaufort Sea polar bears move north from Amundsen Gulf when ice clears in summer to areas with remaining pack ice west of Banks Island and M'Clure Strait and into the adjacent part of the CAO (Stirling, 2002; Stirling *et al.*, 2011). The Northern Beaufort Sea subpopulation was considered stable through the early 2000s (Stirling *et al.*, 2011).



**Figure 10.3.** Summer (A, B) and winter (C, D) distributions of polar bears of the Southern Beaufort Sea subpopulation. Distributions are shown as 50% and 95% probability kernels based on satellite-tracked bears for an early period (1985-1995; A, C) and a recent period (2007-2016; B, D). The figure shows a northward extension of the range in summer to beyond 80°N in the CAO, related to reduced sea ice in the recent period. Figure provided by George M. Durner, US Geological Survey; see Durner *et al.* (2019).

### Southern Beaufort Sea subpopulation

The Southern Beaufort Sea subpopulation of polar bears is distributed west from Amundsen Gulf to around Icy Cape in northwestern Alaska (Stirling, 2002; Amstrup *et al.*, 2004, 2005; COSEWIC, 2008; Obbard *et al.*, 2010). Most of this subpopulation has traditionally moved north with the receding ice edge into the Beaufort Sea during summer (Figure 10.3; Amstrup, 2000; Amstrup *et al.*, 2000; Stirling, 2002; Durner *et al.*, 2004). The northern boundary has typically been set at about 72–73°N, which corresponds to the minimum summer ice edge in most years (Obbard *et al.*, 2010). However, polar bears of this subpopulation venture farther north in the pack ice both in summer and winter, with the 95% probability contour for satellite-tracked bears extending north to about 76°N (during 1985–1993; Amstrup, 2000). Including data from later years (up to 2003), some bears were found to move even farther north to around 80°N (Amstrup *et al.*, 2004, 2005; Durner *et al.*, 2009). The home ranges of bears of the Southern Beaufort subpopulation have been recorded to be large, up to 600 000 km<sup>2</sup> (Amstrup *et al.*, 2000). Some Southern Beaufort polar bears have maternity dens on drifting pack ice in the Beaufort Sea, located north to 76°N or beyond (Lentfer, 1975; Amstrup and Gardner, 1994; Amstrup, 2000).

However, in recent decades there has been an apparent shift to more land-based denning (Fischbach *et al.*, 2007).

Not all Southern Beaufort Sea bears withdraw to the north with the receding ice in summer. Through the early 2000s, approximately 4–8% of the subpopulation was estimated to remain on land (Monnett and Treacy, 2005; Miller *et al.*, 2006; Schliebe *et al.*, 2008; Gleason and Rode, 2009), and this may have increased to approximately 15% by 2014 (Wilson *et al.*, 2017). The increasing proportion of the subpopulation that spends the summer on land may be partially attributed to declines in subpopulation size associated with sea ice loss, rather than increases in the numbers of bears on land (Regehr *et al.*, 2010; Bromaghin *et al.*, 2015). Furthermore, Southern Beaufort Sea bears currently spend approximately one month longer on land than in the 1990s (Atwood *et al.*, 2016b). Polar bears can swim long distances across extensive open water (up to nearly 700 km) to get to ice or land (Durner *et al.*, 2011; Pagano *et al.*, 2012), which allows them flexibility when responding to declining sea ice. However, long-distance swimming is energetically costly and may be associated with increased risk of mortality (Monnett and Gleason, 2006; Pagano *et al.*, 2012). Reductions in the body size of both adult and juvenile bears have been observed in recent decades with declining sea ice, along with lowered reproductive output and survival of cubs and juveniles (Rode *et al.*, 2010, 2014). There have also been several observations of nutritionally stressed bears in the southern Beaufort Sea, including bears that apparently starved to death (Amstrup *et al.*, 2006; Stirling *et al.*, 2008; Cherry *et al.*, 2009). Population modelling has shown a positive relationship between sea ice availability and polar bear survival rates (Regehr *et al.*, 2010), leading to negative population growth in years with long ice-free seasons as well as likely subpopulation declines in the future (Hunter *et al.*, 2010). The size of the Southern Beaufort Sea subpopulation is estimated to have decreased from approximately 1500 bears in 2006 (Regehr *et al.*, 2006) to 900 bears in 2010 (Bromaghin *et al.*, 2015), although this apparent decline may have been partially due to changes in sampling methods.

### **Chukchi Sea subpopulation**

Polar bears of the Chukchi Sea subpopulation generally use large areas over the year, including movements north into the Arctic Ocean with the seasonally retreating sea ice (Wilson *et al.*, 2014, 2016). The subpopulation is distributed between Alaska and eastern East Siberian Sea. The eastern boundary with the Southern Beaufort Sea subpopulation is characterized by a substantial overlap in spatial distribution (Amstrup *et al.*, 2004, 2005). Most of the Chukchi Sea bears den on the Russian side, with Wrangel and Herald islands as important areas for denning and as terrestrial refugia during the ice-free season (Uspenski and Kistchinski, 1972; Belikov *et al.*, 1977, 1986; Garner *et al.*, 1990, 1994, 1995; Stishov, 1991; Belikov, 1993; Ovsyanikov, 1995; Belikov and Boltunov, 1998). Due to declining sea ice, a larger proportion of the Chukchi Sea subpopulation is currently spending nearly one month longer on Wrangel Island each summer, compared to the 1990s (Rode *et al.*, 2015). However, unlike the adjacent Southern Beaufort Sea subpopulation, bears in the Chukchi Sea appear to have maintained good nutritional condition and reproduction despite sea ice loss (Rode *et al.*, 2014; Regehr *et al.*, 2018). A recent study estimated the size of this subpopulation at approximately 3000 animals (Regehr *et al.*, 2018), making it one of the largest polar bear subpopulations (Durner *et al.*, 2018). The northern boundary for the Chukchi Sea subpopulation has been drawn at about 72–73°N (Durner *et al.*, 2018), although the seasonal distribution of bears extends far north of this (Amstrup *et al.*, 2005; Durner *et al.*, 2009; Wilson *et al.*, 2014).

### **Laptev Sea subpopulation**

Polar bears of the Laptev Sea subpopulation are found from the Severnaya Zemlya in the west to about the location of the Aion Ice Massif in the East Siberian Sea in the east (Belikov and



Boltunov, 1998; Obbard *et al.*, 2010). The Laptev Sea subpopulation is poorly studied compared to most others, and its abundance is unknown (Durner *et al.*, 2018). Mauritzen *et al.* (2002) tracked two bears that used the ice over at the eastern ends of Nansen and Amundsen basins. Durner *et al.* (2009) presented more locations for polar bears in the Laptev Sea, showing positions out into the CAO northeast of the New Siberian Islands. Bears in the Laptev Sea are genetically similar to those in the Barents Sea, East Greenland, and Kara Sea subpopulations, suggesting a substantial degree of exchange among these areas (Peacock *et al.*, 2015).

### **Kara Sea subpopulation**

Mauritzen *et al.* (2002) identified a northern Kara Sea population unit of the Kara Sea subpopulation. A few position fixes for these bears were located in the Arctic Ocean, beyond the shelf north of Franz Josef Land and the Kara Sea. With less sea ice, there is a possibility that polar bears of the Kara Sea subpopulation will retreat seasonally with the receding ice edge into the adjacent Nansen Basin of the Arctic Ocean, as has been found for the Barents Sea polar bears (described below). There has been little contemporary research on the Kara Sea subpopulation, and the abundance estimate of approximately 3200 animals, based on vessel-transect counts during 1997–2013 (Matishov *et al.*, 2014), is not widely used.

### **Barents Sea subpopulation**

Polar bears of the Barents Sea subpopulation have, in recent years, withdrawn with the sea ice into adjacent parts of Nansen Basin north of the Barents Sea (Obbard *et al.*, 2010). This subpopulation is distributed in the northern and central Barents Sea, between Svalbard in the west and Franz Josef Land and Novaya Zemlya in the east (Mauritzen *et al.*, 2002; Aars *et al.*, 2006; Obbard *et al.*, 2010). The subpopulation has been shown to have substructure, with nearshore and pelagic types of bears, apparently both in southern and northern parts of Svalbard (Mauritzen *et al.*, 2001, 2002, 2003; Aars *et al.*, 2009, 2017; Andersen and Aars, 2016). Recent tagging data have shown that polar bears of the pelagic type from northern Svalbard move north to the Arctic Ocean in summer and return south again as ice forms in winter (Aars *et al.*, 2009). An aerial survey in August 2004 included Svalbard, Franz Josef Land, and the ice edge zone located roughly between 81 and 83°N over the Barents slope and adjacent Nansen Basin (Aars *et al.*, 2009). The ice edge zone was surveyed with parallel transects 9 km apart and extending 100–150 km into the ice (equivalent to about 1–1.5 degree of latitude). About 700 polar bears were estimated to be present in the surveyed marginal ice zone in addition to about 250 at Svalbard and 550 at Franz Josef Land (Aars *et al.*, 2009). In addition, a ratio estimator method was used to estimate that about 1150 additional polar bear were present in the pack ice north of the surveyed area between roughly 83 and 85°N (Aars *et al.*, 2009). The ratio estimator was based on position fixes of satellite-tracked female polar bears from the outer marginal ice zone (equivalent to the surveyed area) and farther into the ice (equivalent to the non-surveyed area).

The results of Aars *et al.* (2009) suggest that about two-thirds of the Barents Sea polar bear subpopulation was present in Nansen Basin of the CAO between about 82 and 85°N in August 2004. This may be typical for the more recent climate situation, where the northern Barents Sea clears more or less completely of ice in late summer in warm years (Stern and Laidre, 2016). The Barents Sea subpopulation has been identified as one of the most vulnerable subpopulations (Durner *et al.*, 2009). A recent aerial survey, conducted in the Norwegian portion of the Barents Sea in 2015 ([Figure 10.4](#)), confirmed the existence of two separate ecotypes of bears in the Barents Sea subpopulation, one that inhabits the area on and around Svalbard and another that primarily uses the pack ice (Aars *et al.*, 2017). Although a comparison of the 2004 and 2015 abundance estimates was complicated by the lack of sampling in Russia in 2015, there is no evidence that the large declines in sea ice habitat in the Barents Sea have led to a reduction in the size of the polar bear subpopulation (Aars *et al.*, 2017).

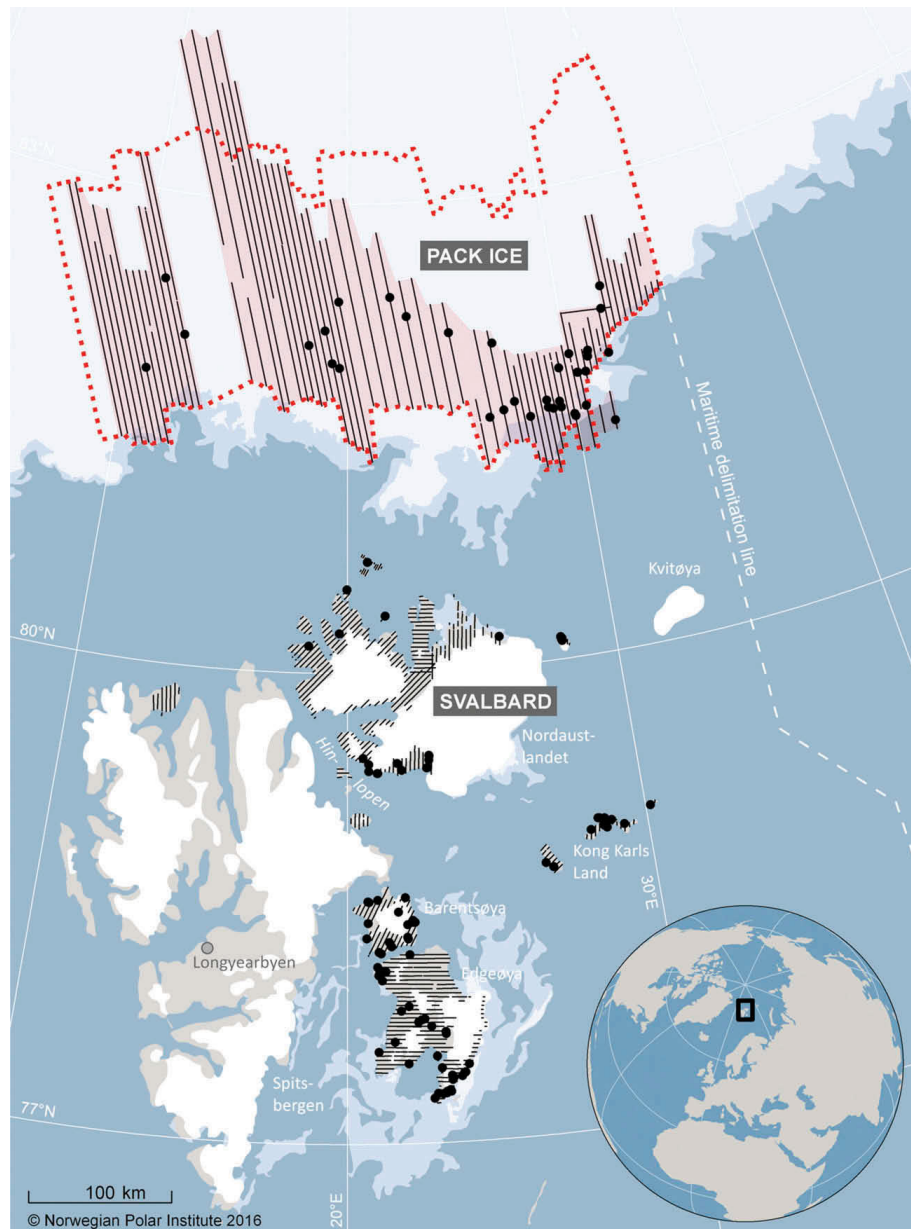


Figure 10.4. Observations of polar bears (black dots) in aerial surveys with helicopters at the Svalbard archipelago and in the marginal ice zone (MIZ) of the polar pack in the CAO (Nansen Basin) north of Svalbard in August 2015. The red dotted area of the MIZ is the planned survey area, and the parallel lines are the flown sighting transects. From Aars *et al.* (2017).

### East Greenland subpopulation

The East Greenland subpopulation occupies one of the largest geographic areas of all polar bear subpopulations, extending from approximately 60 to 80°N, and encompassing part of Fram Strait (Durner *et al.*, 2018). The size of the East Greenland subpopulation is unknown, although a multiyear subpopulation assessment was started in 2015. Satellite tracking studies indicate that polar bears in this region range widely along the east coastline of Greenland and into the pack ice in Fram Strait and the Greenland Sea (Laidre *et al.*, 2013, 2015). Previous studies have suggested that there may be several resident groups of bears in East Greenland (Dietz *et al.*, 2000) with limited exchange with other polar bear subpopulations (Born *et al.*, 2012). Loss of sea ice has led to changes in habitat use for the East Greenland subpopulation. Female bears use areas with significantly lower ice concentrations and spend more time near open water in the 2000s than in the 1990s (Laidre *et al.*, 2015).

### 10.2.2 Ringed seal (*Pusa hispida*)

Ringed seals ([Figure 10.5](#)) have a wide circumpolar Arctic distribution with five recognized subspecies: the Arctic ringed seal (*Pusa hispida hispida*), the Sea of Okhotsk ringed seal (*ochotensis*), the Baltic Sea ringed seal (*botnica*), and two freshwater subspecies in Finland and northwestern Russia (*saimensis* and *ladogensis*, respectively; Reeves, 1998; Rice, 1998; Wozencraft, 2005; Kovacs *et al.*, 2008; Hammill, 2009). Arctic ringed seals are considered to be widely distributed, probably all over the CAO (Reeves, 1998; Boveng, 2016a). They are regularly seen from icebreakers going through the Arctic Ocean pack ice, even at the North Pole (Todd *et al.*, 1992; Ramsay and Farley, 1996; van Meurs and Splettstoesser, 2003). Ringed seals have also been observed regularly from Soviet/Russian ice-drift stations and aerial ice surveys (Gorbunov and Belikov, 2008).



Figure 10.5. A group of ringed seals hauled-out, basking on sea ice. Photo: Jessica Lindsay.

Ringed seals are assumed to be the main prey for polar bears in the CAO. Ice amphipods and Arctic and polar cod can, in turn, be assumed to be the main prey items available for ringed seals. These fauna components are widely distributed in the ice-covered waters of the CAO (Andriyashev *et al.*, 1980; Melnikov, 1997). The generally low productivity in the pack ice areas of the Arctic Ocean limits ringed seals (and polar bears) to scarce occurrence at low density. Little is known about potential areas of higher production and/or higher aggregation of prey that could lead to aggregations of ringed seals. There is also little knowledge of the spatial ecology of ringed seals in the CAO.

Ringed seals have been found to move up to 2000 km or more on a seasonal basis between different areas and habitats (Freitas *et al.*, 2008a, 2008b; Kelly *et al.*, 2010a, 2010b; Crawford *et al.*, 2012b; Harwood *et al.*, 2012). The distance to the North Pole from the northern archipelagos (Svalbard, Franz Josef Land, Severnaya Zemlya) and northern Greenland is around 1000 km, while the distance from the southern Beaufort and northern Chukchi seas is on the order of 2000 km. This means that ringed seals are capable of moving into and out of the drift ice of the

CAO. Ringed seals tagged in northern Storfjorden (between Spitsbergen and Barentsøya) at Svalbard were found to make long offshore movements of up to 600 km into the pack ice northeast and north of Svalbard (Freitas *et al.*, 2008a). The seals could alternate between coastal and offshore movement behavior, and two (out of 22) seals made two offshore trips in a season. Seven ringed seals captured in the Amundsen Gulf area travelled long distances, mainly in an east–west direction, traversing the roughly 1000-km distance across the southern Beaufort Sea from Cape Parry to Point Barrow in about a month (traveling at a mean speed of  $0.9 \text{ m s}^{-1}$ ; Harwood *et al.*, 2012). These seals continued through the Chukchi Sea and into either the eastern East Siberian Sea or the northern Bering Sea. The longest distance recorded was for a pup that swam more than 6000 km, more than half of it through ice (Harwood *et al.*, 2012). Some ringed seals tagged along the coast in Alaska used the deep waters of the CAO during May–November (Citta *et al.*, 2018a).

Ringed seals reproduce in shore-fast ice, where they maintain breathing holes and give birth to single pups in lairs in snow drifts (Smith and Stirling, 1975; Smith and Hammill, 1981; Smith *et al.*, 1991; Reeves, 1998; Hammill, 2009). They can also breed on stable drifting pack ice, as has been shown to occur in Baffin Bay and the central Barents Sea (Finley *et al.*, 1983; Wiig *et al.*, 1999) and possibly also in the Greenland Sea (Dietz *et al.*, 1985). It is not known whether ringed seals breed on pack ice in the CAO, but it is possible.

### 10.2.3 Bearded seal (*Erignathus barbatus*)

Bearded seal ([Figure 10.6](#)) occurs with two recognized, although intergrading, subspecies: *barbatus* in the Atlantic sector and *nauticus* in the Pacific sector (Rice, 1998; Kovacs, 2009, 2016a). The boundaries between the two subspecies is thought to be in the central Canadian Arctic and the Laptev Sea. Bearded seal is a strongly ice-associated species, with a wide circumpolar distribution in seasonally ice-covered seas. It occurs mostly solitary and at relatively low densities, although it can form loose aggregations in some cases (Bengtson *et al.*, 2005; Cameron *et al.*, 2010). This dispersed distribution is related to the territorial behavior of males. They court females using elaborate downward-trilling vocalizations during mating season (Cleator *et al.*, 1989; van Parijs *et al.*, 2001). Bearded seals use sea ice preferentially as a haul-out platform, preferring small and medium-sized floes and generally avoiding large floes. In many areas they move with the seasonal advance and retreat of sea ice (Simpkins *et al.*, 2003; Cameron *et al.*, 2010). In the marginal ice zone in summer they can occur concentrated, because of the limited availability of ice. During this period they spend much of the time hauled out while moulting (Kovacs *et al.*, 2004; Kovacs, 2009).

Bearded seals feed predominantly on a variety of epibenthic invertebrates that live on the seabed, including crabs, shrimps, and molluscs, but they also catch benthic infauna, and schooling and demersal fish, including polar cod (Lowry *et al.*, 1980; Hjelset *et al.*, 1999; Cameron *et al.*, 2010; Kovacs, 2009, 2016a; Quakenbush *et al.*, 2011; Crawford *et al.*, 2015). They commonly dive to depths less than 100 m on Arctic shelves (although they can dive to over 300 m) and are, therefore, generally restricted to shelf areas (Gjertz *et al.*, 2000; Cameron *et al.*, 2010). The northern Bering Sea and Chukchi Sea provide the largest continuous shallow-shelf habitat for bearded seals in the Arctic (Cameron *et al.*, 2018). Here, many seals are believed to migrate south through the Bering Strait with the advance of sea ice in winter, and to return north to the Chukchi Sea with sea-ice retreat in summer (Cameron *et al.*, 2010, 2018). Adult bearded seals have been known to associate with the southern extent of pack ice in the northern Chukchi Sea and southern Beaufort Sea in summer and autumn (Burns and Frost, 1979; Cameron *et al.*, 2010, 2018). With the decrease in sea ice and northern location of the ice edge in recent years, it is not known to what extent bearded seals are retreating with sea ice out over deeper water. Satellite tagging has been done mainly with juvenile seals that tend to remain further south in summer (Cameron *et al.*, 2018).





**Figure 10.6.** Three species of ice seals: bearded seal, spotted seal, and ribbon seal. Photos: John Jansen, Gavin Brady, and David Withrow.



#### 10.2.4 Spotted seal (*Phoca largha*)

Spotted seals ([Figure 10.6](#)) breed in the winter sea ice of the Bering Sea, Sea of Okhotsk, Sea of Japan, and Yellow Sea. Many individuals from the Bering Sea breeding population spend the summer/autumn open-water period in the Chukchi and Beaufort seas (Citta *et al.*, 2018a). They are mostly found in continental shelf waters, but have been documented in Canada Basin (Citta *et al.*, 2018a), as far north as 74°N, in water of 3800 m depth (P. Boveng, personal communication). The diet of spotted seals in Canada Basin is undocumented, but, based on the species' food habits elsewhere, is likely to include Arctic and polar cod.

Spotted seal is closely related to harbour seal, and was previously considered a subspecies of the latter (Burns, 2009). It is distributed with three distinct populations in the Bering Sea, the Sea of Okhotsk, and the Sea of Japan and the northern Yellow Sea (Boveng *et al.*, 2009; Burns, 2009; Boveng, 2016b). The population in the Bering Sea extends from the Alaska Peninsula and eastern Kamchatka, north through the Chukchi Sea, to the eastern East Siberian Sea and the Beaufort Sea (Burns, 2009; Lowry and Burkanov, 2008; Boveng *et al.*, 2009). Spotted seals of this population breed on sea ice in the northern Bering Sea in late winter, usually in early April (Boveng *et al.*, 2009). After breeding and moulting on ice (May–June), the seals disperse, and many of them move north through Bering Strait. During summer and autumn, they haul-out on land, with Kasegaluk Lagoon in northwestern Alaska being an important site for spotted seals in the Chukchi Sea (Frost *et al.*, 1993; Lowry *et al.*, 1998, 2000; Quakenbush *et al.*, 2009). Spotted seals are generalist feeders that eat primarily a variety of fish species, cephalopods, and crustaceans (Quakenbush *et al.*, 2009). Satellite-tracked spotted seals tagged in Kasegaluk Lagoon spent much of their time in coastal waters, but all tagged individuals went on offshore trips of up to 1000 km or more in the Chukchi Sea, presumably to feed on polar cod, which is one of their prey (Lowry *et al.*, 1998). Their distribution ranges north to the shelf edge of the Arctic Ocean in the eastern East Siberian, Chukchi, and Beaufort seas (Boveng, 2016b). Some individuals may stray out in Canada Basin, but apparently only in small numbers.

The global population of spotted seal has been estimated to be over 640 000 individuals, with more than 460 000 in the Bering Sea and 180 000 in the Sea of Okhotsk. It is listed by the IUCN as a species of Least Concern (Boveng *et al.*, 2016b).

#### 10.2.5 Ribbon seal (*Histiophoca fasciata*)

Ribbon seals ([Figure 10.6](#)) breed in the winter sea ice of Bering Sea and Sea of Okhotsk. Approximately one-fourth to one-third of ribbon seals from the Bering Sea population spend part of the summer/autumn open-water period in the Chukchi Sea (Boveng *et al.*, 2013), and at least two tagged individuals used Canada Basin waters of 2100–3800 m depth, at latitudes of 76–79°N (P. Boveng, personal communication). Their diet in Canada Basin is undocumented, but based on the species food habits elsewhere, it is likely to include Arctic and polar cod.

Ribbon seals are distributed in Bering Sea and Sea of Okhotsk, and occur with three breeding aggregations, two of them in the Sea of Okhotsk (Fedoseev, 2002; Boveng *et al.*, 2008, 2013; Lowry, 2016a). Ribbon seals are associated with sea ice when they breed and moult in late winter and spring. When the ice melts in the northern Bering Sea, ribbon seals disperse to live largely pelagically in the Bering Sea region, as shown by satellite-tracking of tagged seals (Boveng *et al.*, 2013). However, a fraction of the population moves north through Bering Strait to the Chukchi Sea. As the seasonal ice retreated northward, 21 out of 72 ribbon seals (29%) which were tagged in the central Bering Sea during 2007–2010 moved to the Bering Strait, Chukchi Sea, or Arctic Basin (Boveng *et al.*, 2013). Ribbon seal distribution is described to extend out in Canada Basin north to nearly 80°N, but it is presumed that only a small number of individuals extend this far north.

Ribbon seal is a deep diver, to a maximum depth of 600 m or more (Boveng *et al.*, 2013). Its diet in the pelagic habitat is not so well known due to limited sampling, but is assumed to include pelagic and demersal fish, cephalopods, and crustaceans (Boveng *et al.*, 2013).

The total population of ribbon seal is estimated to be about 365 000 individuals, and it is listed by the IUCN as a species of Least Concern (Lowry, 2016b).

#### 10.2.6 Harp seal (*Pagophilus groenlandicus*)

Harp seals ([Figure 10.7](#)) occur with two recognized subspecies (*groenlandicus* and *oceanicus* for individuals breeding in the Northwest Atlantic and the White Sea, respectively; Rice, 1998) and three populations: Northwest Atlantic, Greenland Sea, and White Sea populations (Lavigne, 2009; Kovacs, 2015). It is a numerous species, with a total population of about 9 million individuals, with estimates of 7.5 million, 0.6 million, and 1.4 million for the Northwest Atlantic, Greenland Sea, and White Sea populations, respectively (ICES, 2013; Hammill *et al.*, 2014; Øigård *et al.*, 2014; Kovacs, 2015). Two of the populations are increasing (Northwest Atlantic and Greenland Sea), and harp seal is listed by the IUCN as a species of Least Concern (Kovacs, 2015).



Figure 10.7. Harp seals on ice floes in the northern Barents Sea. Photo: Kjell-Arne Fagerheim, IMR.

The Greenland Sea population of harp seals has whelping areas in the outer (eastern) part of the drifting pack ice, commonly located between 70 and 75°N in the western and central Greenland Sea (Sergeant, 1991; Øritsland and Øien, 1995; Haug *et al.*, 2006). The seals disperse after breeding in March, and aggregate again 1–2 months later (late April–May) to moult on sea ice somewhat north of the whelping areas (Sergeant, 1991; Lavigne, 2009). Tagged harp seals from the Greenland Sea stock have been found to migrate northward along the marginal ice zone in the Greenland Sea to Fram Strait, and to continue eastward into the northern Barents Sea during summer and autumn (Øien and Øritsland, 1995; Folkow *et al.*, 2004). Harp seals from the White Sea population whelp and moult on the ice at the entrance to the White Sea in late winter and spring (Sergeant, 1991; Haug *et al.*, 1994; Potelov *et al.*, 2003). After moulting, the harp seals migrate along the ice edge westward to feed in the central and western Barents Sea

in the first part of summer, and later disperse over the northern and northeastern Barents Sea and into adjacent parts of the northern Kara Sea (Haug *et al.*, 1994; Nordøy *et al.*, 2008).

Harp seals of the Greenland and White Sea populations may follow the ice edge into the western and central Nansen Basin and forage there for some time during late summer and autumn (Folkow *et al.*, 2004; Kovacs and Lydersen, 2006; Nordøy *et al.*, 2008; Kovacs, 2015; Haug *et al.*, 2017). Pelagic and ice amphipods are assumed to be the main prey sought by harp seals in these northern waters, as well as krill advected with north-flowing water. Polar cod under sea ice may also be a potential prey. In the shallow Barents Sea, harp seals feed mainly on small fish and pelagic crustaceans, with krill, amphipods (*Themisto* spp.), capelin, polar cod, and herring being predominant prey (Nilssen, 1995; Nilssen *et al.*, 1995, 2000; Lindstrøm *et al.*, 1998b, 2013; Wathne *et al.*, 2000; Bogstad *et al.*, 2015). Harp seals in the Greenland Sea pack ice have been found to feed predominantly on pelagic crustaceans, mainly the amphipod *Themisto libellula*, but krill and polar cod also contribute to their diet there (Potelov *et al.*, 2000; Haug *et al.*, 2004).

How large a fraction of the two harp seal populations moves into the western Nansen Basin to feed in summer is unknown. However, it is expected that the numbers will increase as sea ice retreats and seawaters becomes more open (Haug *et al.*, 2017).

### 10.2.7 Hooded seal (*Cystophora cristata*)

The hooded seal ([Figure 10.8](#)) is a deep-diver, capable of diving to 1000 m or more (Folkow and Blix, 1999; Kovacs, 2009; Andersen *et al.*, 2013). It occurs with three commonly recognized breeding stocks: Gulf of Saint Lawrence and the Front stock on the east coast of Canada, Davis Strait stock, and the West Ice stock in the Greenland Sea (Lavigne and Kovacs, 1988; Kovacs, 2009, 2016b). The total population is estimated to be around 675 000 individuals, although this is uncertain due to lack of recent data for the Northwest Atlantic stock components. The species is listed as Vulnerable in the IUCN Red List, mainly due to a long-term declining trend in the West Ice population. Retrospective models for this population indicate a dramatic decline from ~1.3 million individuals in 1945 to ~200 000 in 1980 and ~84 000 in 2012 (Øigård *et al.*, 2014).

The West Ice or Greenland Sea population has its whelping and moulting areas on pack ice in the western Greenland Sea (Øritsland and Øien, 1995; Folkow *et al.*, 1996; Folkow and Blix, 1999; Haug *et al.*, 2006). Recent publications have shown the location of the moulting area in the Northeast Water region in western Fram Strait, at about 78–82°N (Coltman *et al.*, 2007; Frie *et al.*, 2012). Outside the breeding and moulting periods in March and July, hooded seals disperse widely and live much of the time pelagic in open waters, where they conduct long feeding excursions (Folkow and Blix, 1995, 1999; Folkow *et al.*, 1996).

Hooded seals are seen in the slope waters north of Svalbard (Folkow *et al.*, 1996; Kovacs and Lydersen, 2006; Kovacs, 2016b; Vacquie-Garcia, 2017). The extent to which hooded seals move to these northern waters is not well known, but out of 15 adult animals (5 males and 10 females) tagged July 1992, one (male) went north of Svalbard and stayed there until tag-loss in January 1993 (Folkow *et al.*, 1996). Among 10 adult animals (9 females) tagged after breeding in 2008, two (females) went through the East Greenland rift basin and into Fram Basin (Vacquie-Garcia *et al.*, 2017). Hooded seal diets in the northeast Atlantic are mainly known from digestive tracts collected in pack ice areas during breeding and moulting. These samples were dominated by the squid *Gonatus fabricii* and polar cod (Potelov *et al.*, 2000; Haug *et al.*, 2004, 2007; Enoksen *et al.*, 2017). Out of the breeding and moulting seasons, redfish, Greenland halibut, capelin, and sandeel have also been found in samples from East Greenland (Haug *et al.*, 2007). This is more similar to diets reported from the Northwest Atlantic, which are dominated by various benthopelagic and demersal fish species (Hammill and Stenson, 2000; Tucker *et al.*, 2009). Diving and distribution patterns throughout the year also suggest that species like herring and blue whiting (*Micromesistius poutassou*) could be important prey items in some parts of the Norwegian Sea



(Folkow and Blix, 1999). *Gonatus*, Greenland halibut, redfish [especially beaked redfish (*Sebastes mentella*)], and polar cod are all found in the slope region of the western Nansen Basin (Haug *et al.*, 2017) and represent a potential prey base for hooded seals in this area.



Figure 10.8. Hooded seal on sea ice in the Greenland Sea. Photo: Michael Poltermann, IMR.

### 10.2.8 Atlantic and Pacific walrus (*Odobenus rosmarus*)

Walrus occurs with two subspecies: Atlantic walrus (*Odobenus rosmarus rosmarus*) and Pacific walrus (*O. rosmarus divergens*; [Figure 10.9](#)). A third subspecies, Laptev walrus (*O. rosmarus laptevi*) used to be recognized (Rice, 1998), but is now generally considered to be part of the Pacific subspecies (Kastelein, 2002; Lindqvist *et al.*, 2009; Lowry, 2016b). Pacific walrus is about tenfold more numerous than Atlantic walrus, with estimated abundances of > 200 000 vs. > 25 000 individuals, respectively. Laptev walrus is thought to number 3000–5000 individuals (Belikov and Boltunov, 2005; Speckman *et al.*, 2011; Laidre *et al.*, 2015; Lowry, 2016b). Walrus is listed as Vulnerable on the IUCN Red List, based on a likely decline in the population due to reduced habitat quality from loss of sea ice and possibly increased pup mortality (Udevitz *et al.*, 2009, 2013; Garlich-Miller *et al.*, 2011; Kovacs *et al.*, 2015; Lowry, 2016b).

#### Atlantic walrus

The Atlantic walrus is found from the central part of the Canadian Arctic Archipelago (west to Bathurst Island) to the northern Kara Sea (east to Severnaya Zemlya), with possibly eight stocks (or subpopulations): five to the west and three to the east of Greenland ([Figure 10.10](#); Born *et al.*, 1995, 2001; COSEWIC, 2006b, Stewart *et al.*, 2014a, 2014b). Walruses from the stocks in the eastern Canadian Arctic and western Greenland (numbers 1-5 in [Figure 10.10](#)) do not venture north into the CAO due to the heavy ice conditions in this part of the Arctic.

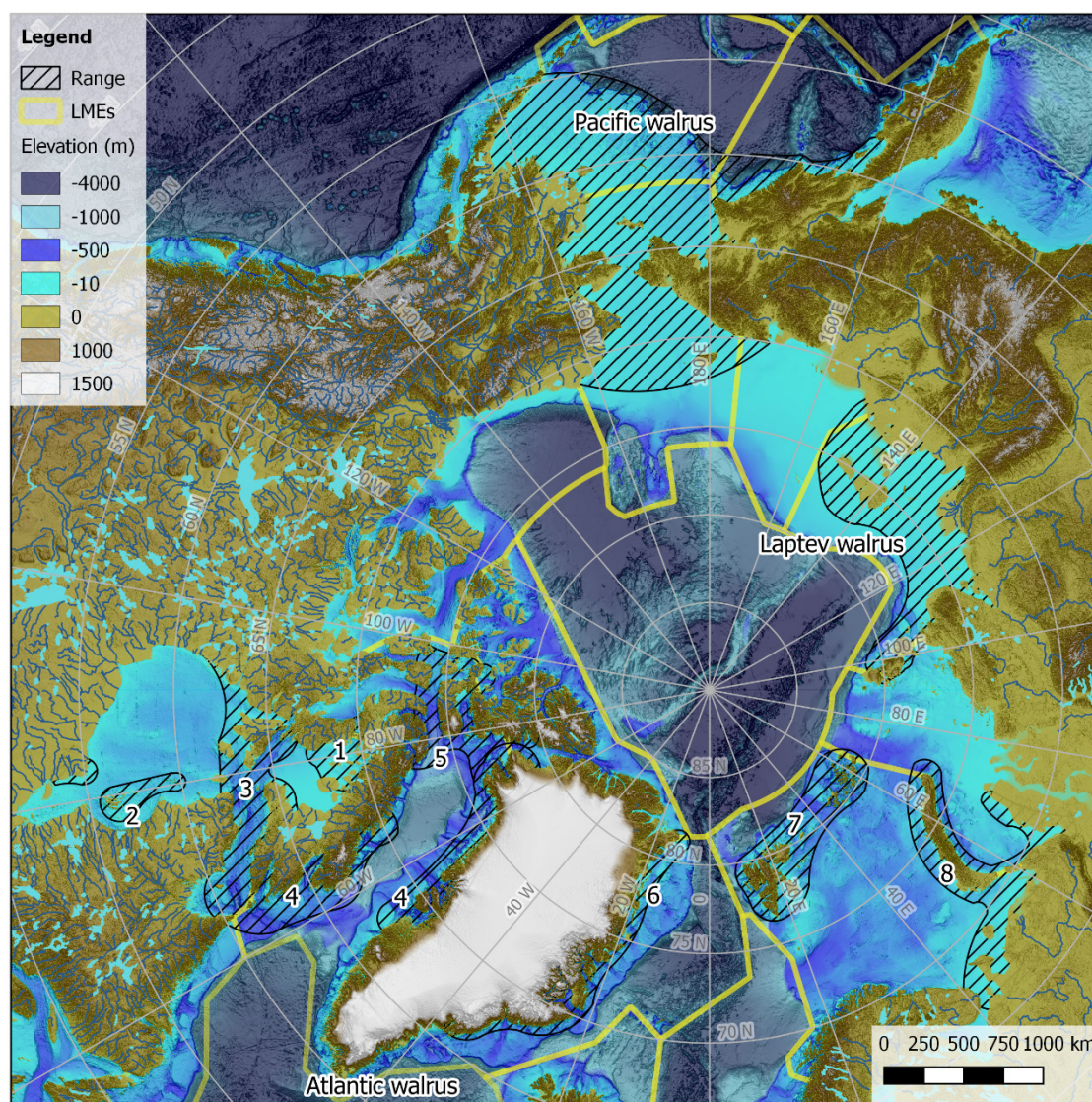
Walruses of the Eastern Greenland stock (number 6 in [Figure 10.10](#)) are distributed along eastern Greenland from about 66°N to the northeasternmost point of Nordostrundingen, at

about 81°N (Born, 1990; Born *et al.*, 1995). They haul-out mainly on ice, with at least five haul-outs on land used regularly in summer (including Sandøen in Young Sound and Lille Snenæs in Dove Bay) and several others used irregularly (Born, 2020). They winter in areas of recurrent polynyas and leads in shallow water, but can also occur farther offshore in the pack ice (Born and Knutsen, 1992). The population is estimated to be about 1400 animals and is increasing (Witting and Born, 2014). It is very unlikely that walrus of this population migrate north into the CAO, since they would have to move against the strong southward ice drift with the East Greenland Current. Their benthic feeding mode also makes this migration unlikely.



Figure 10.9. Atlantic (upper) and Pacific (lower) walrus. Photos: Kjell-Arne Fagerheim, IMR, and Anatoly Kochnev.





**Figure 10.10.** Distribution of Atlantic, Pacific and Laptev walrus. The numbers denote identified populations of Atlantic walrus: 1 – Foxe Basin, 2 – South and East Hudson Bay, 3 – Northern Hudson Bay-Davis Strait, 4 – Western Greenland, 5 – Baffin Bay-Eastern Canadian Arctic, 6 – Eastern Greenland, 7 – Svalbard-Franz Joseph Land, 8 – Kara Sea-Southern Barents Sea-Novaya Zemlya. Pacific and Laptev walrus occur with one population each.

Walruses in the northern Barents and Kara seas are considered one population, the Svalbard–Franz Josef Land population (number 7 in [Figure 10.10](#)). It is centered around the northern and eastern Svalbard and the Franz Josef Land archipelagos, with the distribution extending farther east in the northern Kara Sea, possibly to northern Severnaya Zemlya (Born *et al.*, 1995; NAMMCO, 2006). The concept of one population in this area has been confirmed by results from satellite-tracking of tagged individuals and genetics (Wiig *et al.*, 1996; Andersen *et al.*, 1998; Lydersen and Kovacs, 2014). The population is sexually segregated, with most of the males summering in Svalbard and most of the females, calves, and immature individuals summering at Franz Josef Land (Born, 1984; Gjertz and Wiig, 1994; Born *et al.*, 1995; Wiig *et al.*, 1996). The Svalbard–Franz Josef Land population of walrus was hunted to the brink of extinction, with an estimate of only a few hundred animals remaining when protection was given in 1952 and 1956 (Reeves, 1978; Born, 1984; Gjertz and Wiig, 1995). The population has been recovering in recent decades. A survey of terrestrial haul-out sites at Svalbard in August 2006, combined with data from satellite-tagging to estimate proportion of walruses not hauled out (0.75), gave an estimate

of about 2600 individuals (mostly males; Lydersen *et al.*, 2008). Assuming an equal proportion of females summering at Franz Josef Land, this suggested a total population of over 5000 walrus (Lydersen *et al.*, 2008).

As a benthic feeder, walrus are generally found in areas of shallow water (< 80 m) with a suitable bottom substrate that can support a productive bivalve community within reasonably close proximity to suitable haul-out areas (Kovacs *et al.*, 2009). Recent surveys and observations have recorded walrus commonly in two of the historical areas with terrestrial haul-outs at Svalbard: southern Edgeøya and Tusenøyane on the southeastern side, and northern Nordaustlandet and Kvitøya in the northeast (Gjertz and Wiig, 1994, 1995; Lydersen *et al.*, 2008). Walrus have also been recorded regularly in Hinlopenstredet and at Moffen north of Spitsbergen (Lydersen *et al.*, 2008). There are also terrestrial haul-outs at Franz Josef Land, with important summering areas across the archipelago (Gjertz *et al.*, 1992; Born *et al.*, 1995; Gavrilov, 2010, 2017; Gavrilov and Martynova, 2017), as well as on Victoria Island (Gavrilov, 2008).

Satellite-tracked walrus (mostly males) have been recorded moving across the northern Barents Sea, between Svalbard and Franz Josef Land (Gjertz and Wiig, 1993; Knutsen, 1993; Wiig *et al.*, 1996). A recent study with 17 tagged males showed that they remained near coastal feeding areas in summer, and used terrestrial haul-outs at Svalbard (Freitas *et al.*, 2009; Lydersen and Kovacs, 2014). In winter they moved into areas of high ice concentration (> 90%) in pack ice in the northern Barents Sea, between Svalbard and Franz Josef Land. This coincides with their breeding period (January–March). The males were found to have low diving activity to the seabed, suggesting low feeding activity when they are breeding (Freitas *et al.*, 2009). The male walrus moved at relatively high speed across the ice (up to 670 km in 10 days) to specific areas where they would remain for an average of four months, presumably to breed. Subsequently, the males returned, with high fidelity, to coastal summering areas at Svalbard (Freitas *et al.*, 2009).

The winter areas of walrus in the northern Barents Sea are located over the northern shelf, with individual movements north to the slope region beyond 82°N (Freitas *et al.*, 2009). In the projected warmer climate, with little or no winter ice in the northern Barents Sea, wintering and breeding areas for walrus of the Svalbard–Franz Josef Land population may shift north or northeast into Nansen Basin of the CAO. The summer feeding areas are in shallow waters in the archipelagoes, where the walrus use terrestrial haul-outs. Other than occasional vagrants, walrus would not be expected to move out into Nansen Basin with the seasonal retreat of sea ice.

The Kara Sea–Southern Barents Sea–Novaya Zemlya population (number 8 in [Figure 10.10](#)) of walrus is distributed in winter in the Pechora Sea area, in leads and polynyas off the fast ice, where males and females with calves are observed in groups of different sizes (Born *et al.*, 1995; Zyryanov and Vorontsov, 1999; Goryaev *et al.*, 2006; Svetochnev and Svetochneva, 2008). Walrus remain in the Pechora Sea during summer, with known haul-out sites located on Vaigach, Matveev, and Dolgiy islands, and on small islands off the southern tip of Novaya Zemlya (Boltunov *et al.*, 2010; Lydersen *et al.*, 2012; Glazov *et al.*, 2013; Semenova *et al.*, 2015, 2019). Some walrus also move into the southern Kara Sea and north along eastern Novaya Zemlya or northeast to northern Severnaya Zemlya (Semenova *et al.*, 2019). The population structure for walrus in this region is not clear and requires further study (Kovacs *et al.*, 2009; Lydersen *et al.*, 2012). An aerial survey along the coastline of the Pechora Sea in August 2011 counted nearly 1000 walrus on haul-outs, giving an estimate of about 4000 individuals after correction for walrus at sea (Lydersen *et al.*, 2012). The animals were males, with no female walrus and calves being observed. Another aerial survey conducted in April 2014 provided an estimate of slightly over 3000 animals (Semenova *et al.*, 2015).



The walrus of this population use mainly the southeastern Barents Sea and southwestern Kara Sea. However, a walrus was observed that travelled all the way from the Pechora Sea to the northernmost Severnaya Zemlya (Semenova *et al.*, 2019), suggesting that some individuals from this stock can move into the CAO. Walrus have been observed recently with haul-outs on islands in the northeastern Kara Sea (Gavrilo, 2010; M. Gavrilo, unpublished observations). The origin and population connectivity of these animals need to be established.

### **Pacific walrus**

The Pacific walrus (subspecies *divergens*) is distinctly different, genetically and anatomically, from Atlantic walrus. It occurs in the Bering and Chukchi seas, with a summer range extending into the East Siberian and western Beaufort seas (Fay, 1982). Pacific walrus in the Bering and Chukchi seas are considered to make up one large migratory population. They winter in the pack ice of the northern Bering Sea, with two core areas in the late winter breeding season, one in the Gulf of Anadyr and the other in the southeastern Bering Sea from south of Nunivak Island extending into northwestern Bristol Bay (Angliss and Outlaw, 2008). Genetic studies did not reveal any clear separation between individuals of the two core breeding areas (Schribner *et al.*, 1997). There is a clear sexual segregation of the population for most of the year. Females, calves, and subadults move north to the Chukchi Sea in summer, while most males remain to summer in the ice-free eastern and northern Bering Sea, with coastal haul-outs in Bristol Bay and Gulf of Anadyr (Fay, 1982; Jay and Hills, 2005).

The shallow Chukchi Sea and eastern East Siberian Sea serve as the main feeding grounds for the bulk of the Pacific walrus population in summer and autumn (Kochnev, 2004). The main feeding areas extend from the Bering Strait, north in the western Chukchi Sea off the Chukotka coast and north to the area around Wrangel Island, and in the northeastern Chukchi Sea from north of Cape Lisburne to Barrow (Ray and Hufford, 1989). The feeding areas are located in relatively shallow waters on each side of the deeper Hope Valley. Traditionally, walrus tended to concentrate in areas of unconsolidated pack ice and move north as the ice retreated seasonally. By July, large groups were found along the edge of the pack ice between Icy Cape and Point Barrow, while by August, the largest concentrations might occur northwest of Barrow in the area around Hannah Shoal (MMS, 2007). When pack ice is not available, walrus will rest on land, with traditional haul-out sites located on Cape Thompson, Cape Lisburne, and Icy Cape in the eastern Chukchi Sea (MMS, 2007). In the northwestern part of the sea, Wrangel Island is a very important area, where up to 125 000 walrus have been estimated to use coastal haul-outs in late summer (Kochnev, 2004). There are also 10–13 haul-out sites that are used regularly in summer and autumn on the north coast of Chukotka.

The retreating pack ice across the Chukchi shelf has offered walrus feeding opportunities over wide shallow areas, with the ice providing haul-out platforms where the animals could rest between feeding bouts. This is particularly important for the calves and young animals still dependent on care by their mothers. When the edge of the pack ice moves north of the Chukchi shelf edge, the deep water prevents feeding by walrus, and the ice is no longer a favorable habitat. The recent trend of earlier and more extensive retreat of the sea ice represents a major challenge to the Pacific walrus population (Tynan and DeMaster, 1997). Recent observations of motherless calves on ice floes over deep water off northwest Alaska could indicate the difficulties that the walrus is having under the warming climate in the Chukchi Sea (Cooper *et al.*, 2006).

With less summer sea ice and a more northerly distribution of the ice, walrus have become more dependent on coastal haul-outs ([Figure 10.11](#)). This limits their feeding opportunities, as they are restricted to feed in the vicinity of haul-outs, thereby leading to more competition and presumably local depletion of their benthic food. Large numbers of walrus aggregated at coastal

haul-outs leads to increased mortality, particularly of young animals, due to stampede. This is aggravated by the presence of polar bears, brown bears, and wolverines, which cause disturbances and mortalities at the colonies. Human harvest is an additional disturbance, and food limitation leads to lean and weakened walrus that are more susceptible to stress and diseases. All these factors have probably contributed to lower pup survival in recent years and an apparent decline in the Pacific walrus population (Fay *et al.*, 1997; Kochnev, 2004; MMS, 2007; Garlich-Miller *et al.*, 2011; Kovacs *et al.*, 2015; Lowry, 2016b). The size of the population is not known with high accuracy, which makes the documentation of trends difficult (Garlich-Miller and Jay, 2000; Garlich-Miller *et al.*, 2011; Lowry, 2016b). However, based on underlying mechanisms, it is anticipated that the Pacific walrus population will continue to decline under a warming climate and the further loss in sea ice (Jay *et al.*, 2011; MacCracken, 2012; Kovacs *et al.*, 2015; Lowry, 2016b). The Pacific walrus population is considered to number at least 200 000 individuals, but their status is listed as Data Deficient on the IUCN Red List (Lowry, 2015).

The distribution of Pacific walrus commonly extends north to the shelf edge of the Chukchi Sea (Garlich-Miller *et al.*, 2011). They have been observed on ice in the Chukchi Borderland area, north to 76°N (Harwood *et al.*, 2005). It appears that most of the walrus dissociate from the ice as it recedes north of the shelf edge, where they can no longer feed, and move to coastal haul-outs in northwestern Alaska, Wrangel Island, and northern Chukotka. Walrus that remain with the pack ice over deep water may have to swim back to the shelf areas to avoid perishing. Use of habitats in the CAO by Pacific walrus is considered of low importance.



Figure 10.11. Pacific walrus aggregated at a coastal haul-out at Cape Serdtse Kamen, Chukotka. Photo: Anatoly Kochnev.

### Laptev walrus

The Laptev walrus is a separate population that lives its entire life in the Laptev and East Siberian seas. It is described as being distributed in the western Laptev Sea, along the east coast of the Taimyr Peninsula and Severnaya Zemlya, and in the eastern Laptev Sea, from the Lena



Delta to the New Siberian Islands (Chapskii, 1940; Born *et al.*, 1995; Kastelein, 2002). There is limited information on the seasonal changes in the distribution of walrus in the Laptev Sea. In winter and spring they are assumed to be distributed in the Great Siberian Polynya system located north and west of the New Siberian Islands. Wintering walruses in the Great Siberian Polynya in May 1996 were found to be mainly male individuals (numbering about 1400), suggesting that females winter in other areas (Solovieva, 2001). The extent to which Laptev walruses associate with pack ice in the CAO in the Laptev slope region is not known, but it is assumed to be low.

#### 10.2.9 Beluga whale (*Delphinapterus leucas*)

The beluga whale ([Figure 10.12](#)) has a circumpolar distribution and occurs with about 20 more or less well-defined subpopulations or stocks (Jefferson *et al.*, 2008, 2012; O’Corry-Crowe, 2009; Laidre *et al.*, 2015; Lowry *et al.*, 2017a; NAMMCO, 2018). The beluga stocks have strong geographic connections with seasonal migrations between defined wintering and summering areas (O’Corry-Crowe, 2009). Many of the stocks are found outside the near-periphery of the CAO, in the Sea of Okhotsk, Gulf of Alaska (Cook Inlet), Hudson Bay, Baffin Bay, St Lawrence Bay, and the White Sea. Six stocks are found in the Bering Sea, three of which migrate north to summering areas in the Chukchi, Beaufort, and East Siberian seas (Eastern Chukchi Sea, Eastern Beaufort Sea, and East Siberian and Western Chukchi Seas stocks; [Figure 10.13](#)). In the Barents, Kara, and Laptev seas, there is a population complex (called the Karskaya population) with an unclear structure. IWC (2000) recognized eight stocks: two with summer feeding areas in the northern Barents Sea (Svalbard and Franz Josef Land), three in the White Sea (Onezhsky Bay, Mezhenskyi Bay, and Dvinsky Bay), two in the Kara Sea (Ob Gulf and Yenesei Gulf), and one in the western Laptev Sea. At the species level, beluga is listed as a species of Least Concern by IUCN, although some stocks (e.g. Cook Inlet stock in Alaska and Cumberland Sound and Ungava Bay stocks in Canada) are recognized as being endangered (Lowry *et al.*, 2017a).



Figure 10.12. Beluga whales swimming near sea ice in the northern Bering Sea near Cape Navarin. Photo: Boris Soloviev.

### Eastern Beaufort Sea and Eastern Chukchi Sea stocks

The Eastern Beaufort Sea stock winters in the ice-covered waters of the northern Bering Sea, and migrates north in spring via the lead system along Alaska, through the Chukchi Sea, to summer feeding areas in the eastern Beaufort Sea (COSEWIC, 2004). The stock is estimated to number about 40 000 individuals (Angliss and Outlaw, 2008; Muto *et al.*, 2016). Belugas move east, through offshore and ice-covered waters of the southern Beaufort Sea, toward the Canadian Beaufort Sea, where they are observed off the west coast of Banks Island and Cape Bathurst in late May and early June (Fraker, 1979; Moore and Reeves, 1993). The belugas of this stock move into the Mackenzie estuary around the time of ice breakup in late June and early July (Harwood and Smith, 2002). Satellite-tagging has shown that whales move offshore in the eastern Canada Basin in late summer, with many (particularly males) moving into Viscount Melville Sound (Richard *et al.*, 2001; Paulic *et al.*, 2009). The summer home range area (in July and August) for the belugas of this stock is in the eastern Canada Basin (between about 130 and 120°W) extending north to about 78°N (Hauser *et al.*, 2014; [Figure 10.14](#)).

The belugas of the Eastern Beaufort Sea stock start the autumn migration in late August or early September, and quickly move east to waters of the western Canada Basin and the northwestern Chukchi Sea (Richard *et al.*, 2001; Hauser *et al.*, 2014). Here, they disperse northwards in the Chukchi Borderland region to around 78°N. In October and November, they move south through the Chukchi Sea to wintering grounds in the northern Bering Sea (Hauser *et al.*, 2014).

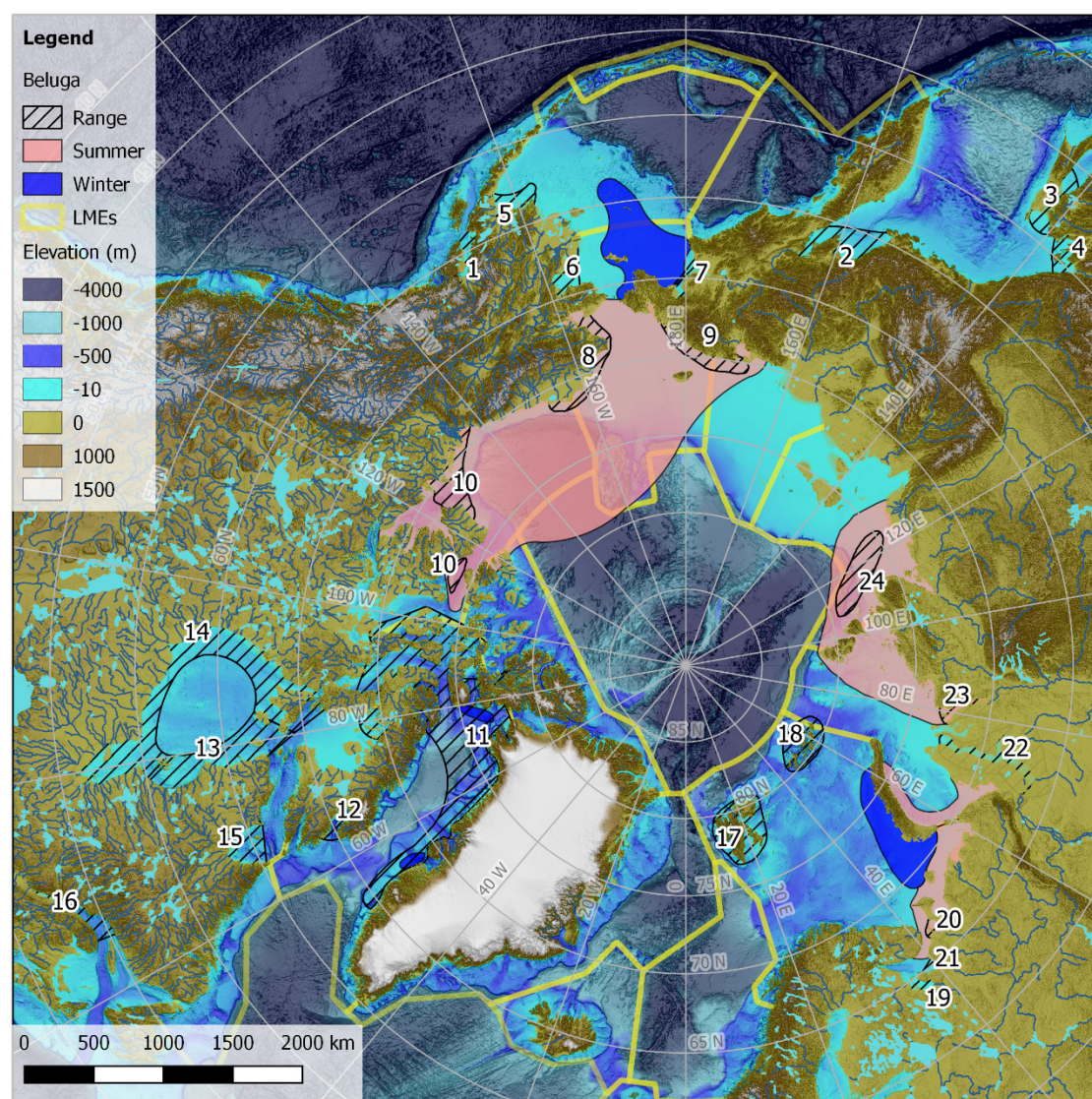
The Eastern Chukchi Sea stock of belugas also winters in the northern Bering Sea, apparently with a spatial (and partly temporal) separation from wintering areas of other beluga stocks that winter in the same general area (Citta *et al.*, 2017). These belugas move into coastal waters of the eastern Chukchi Sea at ice breakup in spring, when they go into the Kotzebue area and later Kasegaluk Lagoon (Frost and Lowry, 1990; Frost *et al.*, 1993; Huntington *et al.*, 1999). Satellite-tagging has shown that belugas from Kasegaluk Lagoon can move north at high speed through pack ice to beyond 80°N in Canada Basin (Suydam *et al.*, 2001, 2005). Three males migrated 700 km through ice of > 90% coverage at about 3 km h<sup>-1</sup>, or 60–70 km per day (Suydam *et al.*, 2001). A summary of tagging results (from 1998–2007) shows that the Eastern Chukchi belugas mainly occupied the southern Beaufort Sea and the shelf edge region in July ([Figure 10.14](#)), and then moved north and east to the eastern Canada Basin, replacing the belugas of the Eastern Beaufort stock, which by then had moved west (Hauser *et al.*, 2014). The Eastern Chukchi belugas migrated west through the southern Beaufort Sea in October, and south through the Chukchi Sea in November (Hauser *et al.*, 2014). In the recent decade, the autumn migration for this stock has been delayed by 2–4 weeks with the later freeze-up, while this has not been the case for the Eastern Beaufort stock of belugas (Hauser *et al.*, 2017a).

The size of the Eastern Chukchi Sea stock was until recently estimated to be about 4000 individuals (Angliss and Outlaw, 2008; Laidre *et al.*, 2015). This estimate was adjusted upwards to about 20 000 whales based on combined results from aerial surveys (Clarke *et al.*, 2013a) and satellite-tagging (Hauser *et al.*, 2014; Lowry *et al.* 2017a, 2017b).

The diving behavior (analysed with time–depth recorders) of belugas of both stocks in the Beaufort Sea revealed maximum dives of up to > 900 m, but the most frequent dive depths were down to 200–300 m (Hauser *et al.*, 2015). This coincides with the depth where polar cod is most frequent in slope waters, which suggests that this fish was the primary prey for the belugas (Parker-Stetter *et al.*, 2011; Hauser *et al.*, 2015). A habitat modelling study, based on satellite position data for belugas of both stocks, found that bathymetric features were the primary drivers for habitat selection, being more important than ice conditions (Hauser *et al.*, 2017b). The Eastern Chukchi belugas predominantly used areas near Barrow Canyon and the slope region of the Beaufort Sea in summer. Females of the Eastern Beaufort stock were predominantly found within 200 km of the shore and in relatively light ice conditions (0–40%



ice cover) whereas males selected higher ice concentrations (> 40%) than the females. However, males were also more likely to be found in slope waters, along both the southern rim of the Beaufort Sea and the Chukchi slope (Hauser *et al.*, 2017b).



**Figure 10.13.** Distribution of beluga whale populations or stocks in the circumpolar Arctic seas. Numbers refer to identified stocks, or core summer areas for the Russian Arctic. Summer and winter areas are shown for two of the populations in the Pacific Arctic: the Eastern Chukchi Sea (No. 8) and Eastern Beaufort Sea (No. 10) stocks, wintering in the Bering Sea and summering in the Chukchi and Beaufort seas, and for the Karskaya population (No. 24, and possibly including No. 22 and 23), wintering in the southeastern Barents Sea and summering in the Kara and Laptev seas. Other stocks described in the text are the Western Chukchi Sea/Eastern East Siberian Sea stock (No. 9), Svalbard stock (No. 17), and Franz Joseph Land stock (No. 18).

Satellite-tagging of belugas of the two stocks show that they concentrate in slope regions in summer, but some individuals disperse in Canada Basin north to 78–80°N (Figure 10.14; Richard *et al.*, 2001; Suydam *et al.*, 2001; Hauser *et al.*, 2014, 2017a, 2017b). Aerial surveys have revealed the same general pattern of distribution and seasonal movements (Moore, 2000; Moore *et al.*, 2000a; Asselin *et al.*, 2011). The larger Eastern Beaufort stock (40 000 individuals) concentrates its summer feeding (July–August) in the eastern Beaufort Sea, while the somewhat smaller Eastern Chukchi stock (20 000 individuals) concentrates in the Barrow Canyon region of the southwestern Beaufort Sea. Diving behavior suggests that they target polar cod, which is



found in the Atlantic layer at 200–400 m depth (Logerwell *et al.*, 2011, 2015; Parker-Stetter *et al.*, 2011; Benoit *et al.*, 2014). The population structure of polar cod is not well known, but there are probably two stocks, one in the eastern Beaufort Sea and another in the Chukchi Sea (see [Section 8.5.1](#)). The Beaufort stock is likely to be large (possibly more than 1 million t; Benoit *et al.*, 2008) and supported by high productivity in the Amundsen Gulf region. Arctic cod, which we know very little about, may occur in Canada Basin (see [Section 8.5.2](#)) and could be what the belugas are seeking when they venture into this area in summer.

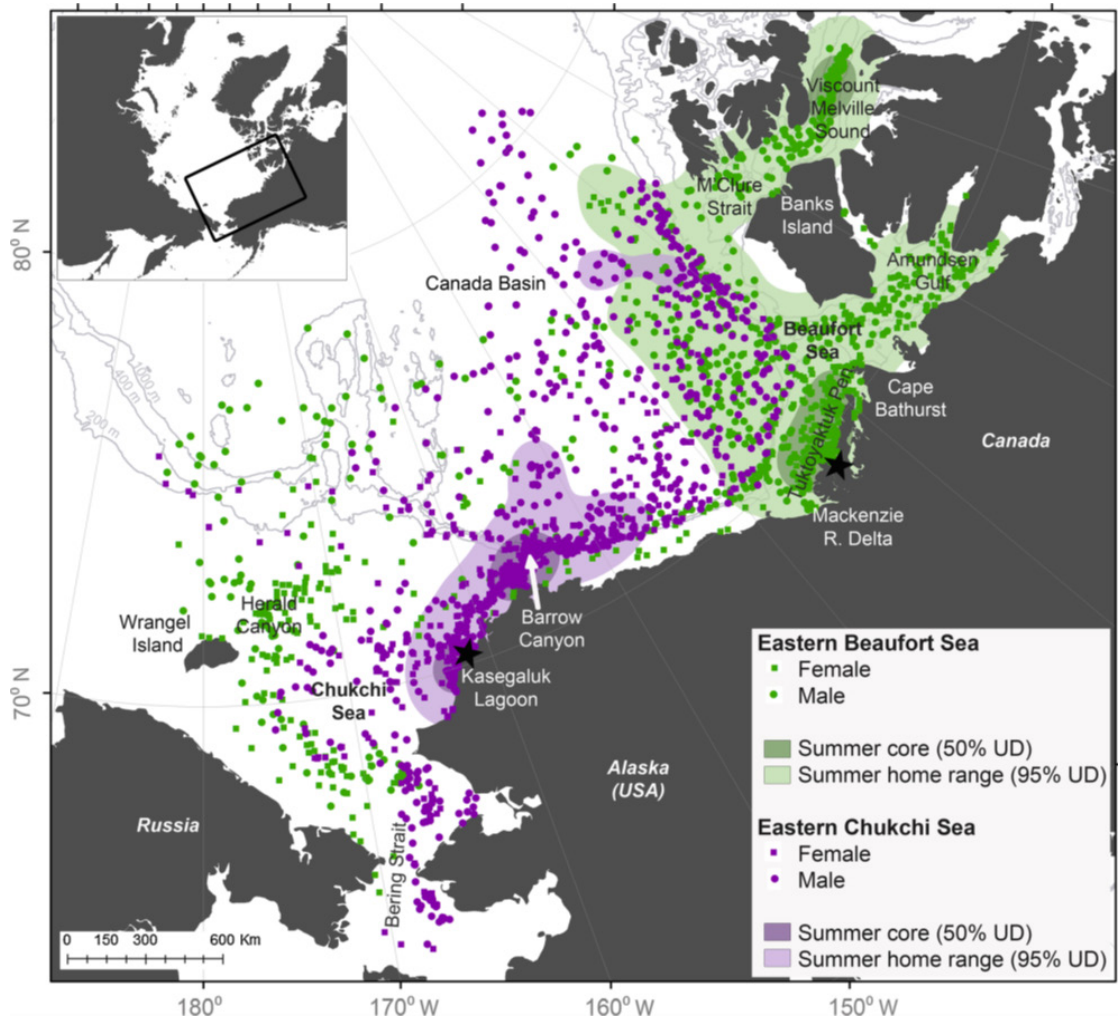


Figure 10.14. Summer distribution of two beluga whale stocks (Eastern Beaufort Sea and Eastern Chukchi Sea stocks) in the Beaufort Sea based on satellite records of tagged individuals. Reproduced with permission from Hauser *et al.* (2014).

#### Western Chukchi Sea/Eastern East Siberian Sea stock

Belugas of the Western Chukchi Sea/Eastern East Siberian Sea stock winter in the northern Bering Sea off eastern Chukotka (IWC, 2000; Belikov and Boltunov, 2002). This stock moves north through the Bering Strait in spring and continues west along the north coast of Chukotka. In summer, it is distributed off the coast, as far west as Chaunskaya Bay in the East Siberian Sea (Kleinenberg *et al.*, 1964; Mymrin *et al.*, 1999; Belikov and Boltunov, 2002). There is limited knowledge of this stock, but it is believed to number a few thousand individuals (IWC, 2000). To what extent they migrate into the CAO is not known. Sightings from aircrafts in the Soviet period showed belugas in offshore regions of the western Chukchi and East Siberian seas (Belikov and Boltunov, 2002). However, these whales might have been from the Eastern



Beaufort stock, which satellite-tagging has shown move west to this area in autumn before returning south for wintering (Hauser *et al.*, 2014).

### **Barents, Kara, and Laptev seas stocks**

In the Atlantic sector, there are possibly three stocks of belugas that are found adjacent to, and might migrate into, the CAO ([Figure 10.13](#)). The stock structure of belugas in the Barents, Kara, and Laptev seas is not clear. Boltunov and Belikov (2002) recognized two populations, each consisting of several stocks, with one population in the White Sea (estimated to number about 6000 animals; Solovyev *et al.*, 2012) and a larger migratory population (the Karskaya population) in the Barents, Kara, and Laptev seas. IWC (2000) recognized five stocks in this larger region based on summer feeding areas: Svalbard, Franz Josef Land, Ob Gulf, Yenisey Gulf, and western Laptev Sea.

### **Svalbard and Franz Joseph Land stocks**

The Svalbard stock of belugas has been found to be genetically distinct (O’Corry-Crowe *et al.*, 2010). Satellite-tagging has shown them to occur in nearshore waters during summer and autumn, where they spend most of the time near glacier fronts (Lydersen *et al.*, 2001, 2014; Vacquié-Garcia *et al.*, 2017). With sea-ice formation in late autumn, the Svalbard belugas are displaced offshore where they winter in drifting pack ice at ice concentrations of up to more than 90% (Lydersen *et al.*, 2002). However, they do not move far and stay in the same general area, which is consistent with them being an isolated stock (Lydersen *et al.*, 2001; Kovacs and Lydersen, 2006). The size of the Svalbard stock is not known, but it has been suggested that it could be in the low thousands (IWC, 2000).

Belugas are also found in the Franz Josef Land area, where there could be a separate stock wintering in polynyas associated with this archipelago (Martin and Cavalieri, 1989). This remains speculative, but it is plausible considering the degree of stock separation for belugas which exist in other geographical areas, such as the Bering Sea and the Canadian Arctic ([Figure 10.14](#)).

A survey conducted aurally from helicopters and from ships (with polar bears as the main target) in the western Nansen Basin in summer 2015, observed no belugas in waters north of Svalbard (Vacquié-Garcia *et al.*, 2017). In contrast, many bowhead and narwhals were observed in the pack ice during this survey (see species accounts in [sections 10.2.10](#) and [10.2.11](#), respectively). At the time of the survey north of Svalbard, many belugas were sighted in coastal waters at Svalbard (Vacquié-Garcia *et al.*, 2017). This suggests that the Svalbard belugas remain coastal and do not migrate north to feed in the adjacent Nansen Basin of the CAO in summer.

### **Karskaya stock**

Belugas of the Karskaya stock are thought to winter in the southeastern Barents Sea (Boltunov and Belikov, 2002). From there they migrate in May and June into the northern Kara Sea, north of Novaya Zemlya, using networks of leads, channels, and cracks to move through the still ice-covered waters (Belikov and Boltunov, 2002). Recent observations of beluga whales travelling north along leads in closed pack ice in northeastern Kara Sea already in April (Gavrilo, 2018) suggest that there might also be wintering grounds in the Kara Sea. A considerable component of the beluga stock appears to continue its migration into the western Laptev Sea (Belikov and Boltunov, 2002). There is a population of polar cod in the Laptev Sea (see [Section 8.5.1](#)), which is presumably what the Laptev belugas target when they come to summer in this area. The total abundance of the migratory Karskaya population is not known, but it has been suggested to be 15 000–20 000 belugas (Boltunov and Belikov, 2002, citing Ognetov and Stepakhno, 1997).

Belikov and Boltunov (2002) presented observations of belugas (also narwhal and bowheads) from more than 40 years of aerial surveys of ice conditions in the Russian Arctic, supplemented with information from the North Pole ice-drift stations and other opportunistic sightings, during 1958–1995. Belugas were observed in Nansen Basin, north of the Kara Sea and the Severnaya Zemlya archipelago. The northernmost observation was at more than 86°N (at 60°E), and there were several observations at about 84°N. Most of the beluga sightings in the Laptev Sea were from the slope region in the western part, at about 82–83°N. There were also sightings in the central and southern Laptev Sea, but no records north of the New Siberian Islands in the eastern Laptev. There was also a noticeable gap with no sightings in the East Siberian Sea, between the areas for Laptev and Pacific belugas, which were sighted west to about 167°W (at 80°N, north of Chaun Bay; Belikov and Boltunov, 2002). The Laptev belugas of the Karskaya population appear to move as far east as the Indikirka River estuary, while Pacific belugas move west to the Kolyma River estuary (Solovyev *et al.*, 2012).

#### 10.2.10 Narwhal (*Monodon monoceros*)

The narwhal ([Figure 10.15](#)) is found in the Atlantic sector of the Arctic, where it occurs with about 12 more or less distinct subpopulations or management stocks (Palsbøll *et al.*, 1997; Heide-Jørgensen, 2009; Heide-Jørgensen *et al.*, 2013; Lowry *et al.*, 2017c). The total population is estimated to be more than 170 000 individuals, with most of them occurring in the Baffin Bay area (Lowry *et al.*, 2017c). Narwhals are assessed as a species of Least Concern on the IUCN Red List, downlisted from Near Threatened in 2012 (Lowry *et al.*, 2017c).



**Figure 10.15.** Narwhals swimming at the surface in the Canadian Arctic, photographed by using drone. Photo: Fisheries and Oceans Canada.

Narwhals in the Baffin Bay region consist of eight stocks with different summering areas in the Lancaster Sound region (Somerset Island, Admiralty Inlet, Eclipse Sound), northern Baffin Bay (Jones Sound, Smith Sound, Inglefield Bredning, Melville Bay), and Eastern Baffin Island (Heide-Jørgensen *et al.*, 2013; Lowry *et al.*, 2017c). The narwhals of these stocks migrate south to winter in pack ice in central and southern Baffin Bay (Dietz *et al.*, 2001, 2008; Heide-Jørgensen *et al.*, 2003, 2015; Laidre *et al.*, 2003, 2004; Laidre and Heide-Jørgensen, 2005a, 2011; Heide-Jørgensen, 2009). There is no evidence that narwhals from the Baffin Bay region move north into

the CAO, and it is thought that heavy ice conditions combined with a low productivity deters them from going there.

There are possibly three or more stocks of narwhal in the Northeast Atlantic sector of the Arctic: East Greenland, Northeast Greenland, and Svalbard–Russia (Lowry *et al.*, 2017c). The East Greenland stock is found mostly between 64 and 72°N in summer, when they are commonly seen in Scoresby Sound and Kangerlussuaq fjord (Dietz *et al.*, 1994; Heide-Jørgensen *et al.*, 2010). The Northeast Greenland stock is found in summer in Young Sound at 74°N and along the coast as far north as Nordøstrundingen at 82°N (Dietz *et al.*, 1994; Boertmann *et al.*, 2009). The separation of these two stocks is not clear, and their abundance is uncertain (Lowry *et al.*, 2017c). Laidre *et al.* (2015) gave an estimate of about 6000 narwhals for East Greenland.

There is limited knowledge of the narwhal stock (or stocks) in Svalbard and the western Russian Arctic, and how it relates to the Northeast Greenland narwhals. Gjertz (1991) reviewed information on narwhals in the Svalbard area from historical and scientific literature, reports, logbooks from sealers, and opportunistic interviews. Most of the records of narwhals were from the Fram Strait area between 78 and 80°N, in what was known as the Northern Whaling Ground during the former large-scale bowhead whaling that took place from 1611 (see [Section 10.2.11](#)). In contrast, there were few records from the waters on the east side of Svalbard. Observations of narwhals were reported from ice-covered waters north of Svalbard by early explorers including Parry, and Nansen during the Fram expedition (Gjertz, 1991). Fram encountered narwhals at 83°45'N, 12°50'E in May 1896 (Nansen, 1897). Subadult narwhals tagged at Svalbard and tracked for up to 46 days, spent some time in Spitsbergen fjords before they moved north and east to deep offshore waters north of 80°N (Lydersen *et al.*, 2007).

Gray (1931) described seasonal migration routes of bowheads and narwhals in the Greenland Sea and Fram Strait area. Narwhals were seen as forerunners for the appearance of bowheads at the Northern Whaling Ground, and both were found associated with green and productive waters (due to spring growth of algae) rather than blue waters (Gray, 1931). It was believed that narwhals migrated from the Greenland Sea through Fram Strait in spring (April–May), and then further east to waters north of Franz Josef Land. The observations by Parry, Nansen, and others (e.g. Kristoffersen, 1982) demonstrated the presence of narwhals in the ice in western Nansen Basin. During the aerial survey for polar bears in summer 2015, a total of 58 narwhals were sighted, giving an estimate of nearly 1000 whales within the surveyed area of about 50 000 km<sup>2</sup> (Vacquié-Garcia *et al.*, 2017). The narwhals were sighted deep into the ice at about 82–83°N. A recent study of narwhals, detected by passive acoustic monitoring in western Fram Strait at 78°50'N, demonstrated that narwhals were present in that region throughout the year (Ahonen *et al.*, 2019).

Russian observations of narwhals are mostly from the Franz Josef Land area, and are summarized by Kondakov and Zyryanov (1994), Belikov and Boltunov (2002), and Gavrilov and Ershov (2010). Nansen (1897) observed groups of narwhals as he approached Franz Josef Land from the north, and narwhals were also observed during a Fram anniversary cruise 100 years later (Wiig and Boltunov, 1997). Narwhals have been observed from ice-drift stations and from airplanes in the eastern Eurasian Basin, at about 84–85°N, 70–85°E (Belikov and Boltunov, 2002). Narwhals are occasionally observed farther east in waters north of Alaska and as vagrants in the Chukchi and Bering seas (Rice, 1998).

The ice-covered waters of Nansen Basin are clearly a habitat for narwhals. The stock structure is unclear (Lowry *et al.*, 2017c), but there is a possibility that there are two stocks, with summering areas in western Fram Strait off Northeast Greenland and in western Nansen Basin, respectively.

Fish, squid, and shrimp are the main prey types for narwhal, including Greenland halibut, polar cod, and Arctic cod (Hay and Mansfield, 1989; Laidre and Heide-Jørgensen, 2005b; Heide-Jørgensen, 2009; Heide-Jørgensen *et al.*, 2015). Greenland halibut is found along the slope north of the Barents and Kara seas and could be a food source for deep-diving narwhals in this area. The squid *Gonatus fabricii*, which is abundant in the Norwegian Sea (Bjørke and Gjørseter, 2004), is another potential prey organism for narwhals in this area.

#### 10.2.11 Bowhead whale (*Balaena mysticetus*)

The bowhead or Greenland right whale ([Figure 10.16](#)) is a true Arctic resident, well adapted to life in the ice-covered waters of the high Arctic (Rugh and Sheldon, 2009). It occurs with four populations: Bering/Chukchi/Beaufort seas, East Canada/West Greenland, Okhotsk Sea, and East Greenland/Svalbard/Barents Sea (Rugh *et al.*, 2003; Reilly *et al.*, 2012a; Cooke and Reeves, 2018a). Two of the four stocks are found in the CAO: the Bering/Chukchi/Beaufort seas stock, and the East Greenland/Svalbard/Barents Sea stock (see more details below).



**Figure 10.16. Bowhead whale swimming at the surface in Greenland waters. Photo: Anders Mosbech.**

It was formerly believed that there were two stocks in Davis Strait/Baffin Bay and Hudson Bay/Foxe Basin, but evidence from genetic and satellite-tracking studies indicated that they are not separate stocks (Postma *et al.*, 2006; Heide-Jørgensen *et al.*, 2006). Therefore, the East Canada/West Greenland stock is the only stock recognized in that area (IWC, 2008; COSEWIC, 2009; Cooke and Reeves, 2018a). Whales of this stock are not likely to move into the CAO due to the heavy ice conditions in the northernmost part of the Canadian Arctic. However, it is possible, that under a warming climate some individuals may migrate through the Northwest Passage and meet bowheads of the Bering/Chukchi/Beaufort seas stock (Heide-Jørgensen *et al.*, 2012).



Bowhead whales were downlisted by IUCN in 2008 to the Least Concern category, from a Vulnerable status in the 1990s, and an Endangered status in the 1980s (Reilly *et al.*, 2012a). The reasons for this downlisting have been the steady and substantial increase of the Bering/Chukchi/Beaufort seas stock to about 17 000 whales (Muto *et al.*, 2016), and a large estimate adjustment and likely an abundance increase for the East Canada/West Greenland stock to a conservative estimate of over 6000 whales (COSEWIC, 2009; IWC, 2009). In contrast, the East Greenland/Svalbard/Barents Sea (Spitsbergen) stock was, until recently, assessed as Critically Endangered (Reilly *et al.*, 2012b), and is currently assessed as Endangered (Cooke and Reeves, 2018b).

### Bering/Chukchi/Beaufort seas stock

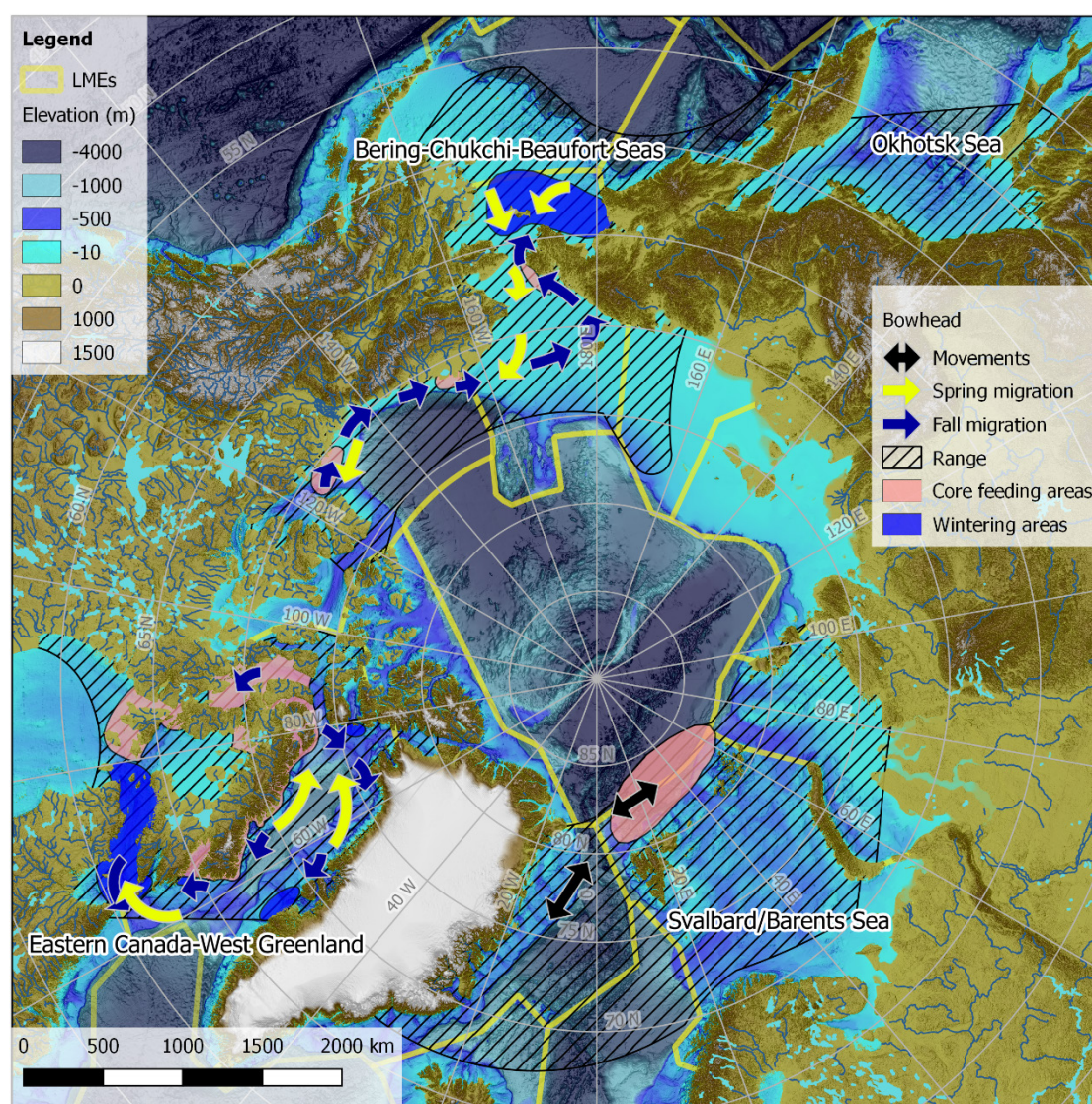


Figure 10.17. Distribution and seasonal migrations of bowhead whales of the Bering/Chukchi/Beaufort stock, East Canada/West Greenland stock, and East Greenland/Svalbard/Barents Sea stock. There is limited information on the latter stock which was depleted almost to extinction and was until recently considered Critically Endangered. It has now been downlisted by IUCN to Endangered.

The Bering/Chukchi/Beaufort seas stock winters in the ice-covered parts of the northern Bering Sea. In spring (April and May), they migrate north through Bering Strait and eastern Chukchi Sea, following the shore-lead system along western Alaska, past Barrow, to summer feeding

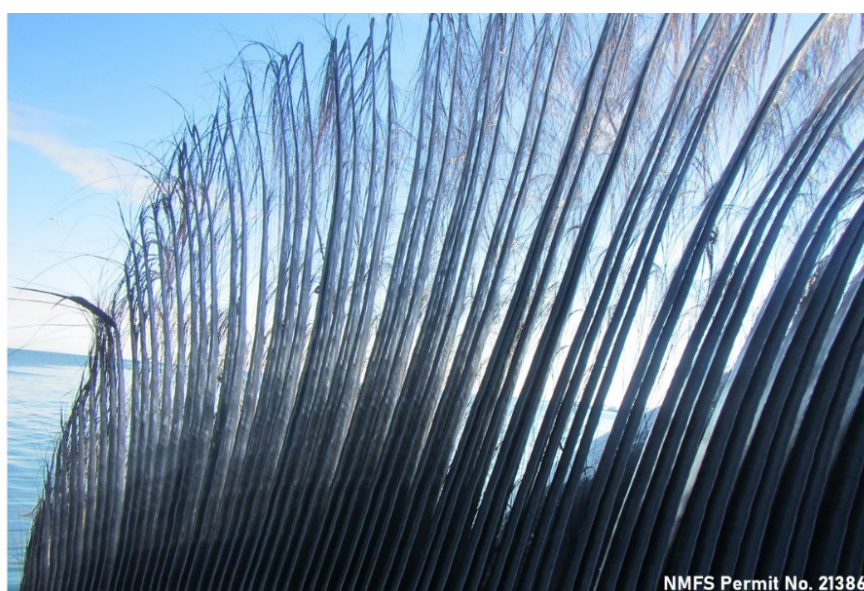
areas in eastern Beaufort Sea ([Figure 10.17](#); Moore and Reeves, 1993; Harwood *et al.*, 2010; Citta *et al.*, 2015). The spring migration across western Beaufort Sea occurs through offshore ice leads, generally from mid-April to mid-June, depending on ice conditions (Moore and Reeves, 1993). Bowhead whales summer in the Amundsen Gulf region, with core-use areas in Cape Bathurst Polynya and Mackenzie Shelf off Tuktoyaktuk Peninsula, based on results from satellite-tagged whales (Citta *et al.*, 2015). There were extensive aerial surveys in the 1980s that confirmed these core use areas and, in addition, showed a third area along the Yukon coast and around Herschel Island (Moore and Reeves, 1993; Harwood and Smith, 2002; Cobb *et al.*, 2008).

Bowheads tend to stay offshore in the Amundsen Gulf area in early summer (May and June) and move closer to shore in July. Bowheads segregate by age and size, with subadults moving into coastal and nearshore waters, while adults tend to spend more time in deeper waters in Amundsen Gulf (Cubbage and Calambokidis, 1987; Koski and Miller, 2008). Bowheads typically occur in smaller groups of up to 10 animals, but can form larger groups where ocean conditions concentrate prey, such as along the shelf break, in marine canyon areas, and where there is upwelling (Moore and Reeves, 1993; Harwood and Smith, 2002; COSEWIC, 2009; Citta *et al.*, 2018b). Bowheads start moving westward out of eastern Beaufort Sea in late August, when they tend to migrate along the shelf and slope waters (Moore, 2000; Moore *et al.*, 2000a). They swim westward through nearshore waters of the Beaufort Sea, past northern Alaska and Point Barrow, from where they proceed west and south through the Chukchi Sea and Bering Strait to wintering quarters in the northern Bering Sea (Moore and Reeves, 1993; Quakenbush *et al.*, 2010). The westward movement is largely over the Beaufort shelf, with the axis of autumn migration over water depths of 20–40 m (Moore *et al.*, 1989; Moore and Clarke, 1990; Moore and Reeves, 1993). Juvenile whales tagged in Mackenzie Bay in early September stayed most of the time in shallow waters, but several individuals made excursions out beyond the shelf into deep water (Mate *et al.*, 2000). The autumn distribution is influenced by ice conditions, with more whales migrating farther offshore in years with heavy ice than in light ice years (Moore, 2000; Moore *et al.*, 2000a). Near Point Barrow is a core-use area where bowheads aggregate to feed in autumn (September–October; Ashjian *et al.*, 2010; Moore *et al.*, 2010; Okkonen *et al.*, 2011; Citta *et al.*, 2015). Many of the whales continue west to the area around Wrangel Island before they move south through the western Chukchi Sea. Satellite-tagging has revealed another core-use area for bowheads along the north coast of Chukotka in late autumn, before the whales continue south to the Bering Sea (Citta *et al.*, 2015, 2018b). Some bowheads move west along Chukotka during the spring migration and remain in the Chukchi Sea during summer (Melnikov and Zeh, 2007; Citta *et al.*, 2012).

Satellite-tagged bowhead whales (in 2006–2012) moved into the deep water of Canada Basin, but they were generally not found beyond 72–73°N in the Beaufort Sea or north of 73–74°N in the Chukchi Borderland region (Quakenbush *et al.*, 2012; Citta *et al.*, 2015). Sightings from aerial surveys (in 1982–1991) showed the same general pattern, with bowheads concentrating in the shelf and slope regions and no whales seen north of 72 or 73°N in the Beaufort and Chukchi seas, respectively (Moore, 2000; Moore *et al.*, 2000a). Bowheads can move through pack ice, as demonstrated by the spring migration east through the ice-covered southern Beaufort Sea (Moore and Reeves, 1993). A tagged juvenile bowhead moved about 4000 km from the eastern Beaufort Sea to the northwestern Chukchi Sea in about a month, at an average speed of 5 km h<sup>-1</sup>, with most of the route in heavy ice (> 90%; Mate *et al.*, 2000). Some tagged bowheads moved farther north to about 75°N along western Banks Island and into M'Clure Strait and Viscount Melville Sound (Heide-Jørgensen *et al.*, 2012; Quakenbush *et al.*, 2012, 2013). Another tagged whale moved north to about 78°N north of Wrangel Island in July 2012 (Quakenbush *et al.*, 2013). Russian aerial surveys in the Soviet period also observed baleen whales (presumably bowheads) north of Wrangel Island to about 76°N (Belikov and Boltunov, 2002).



Bowheads have fine-meshed baleen ([Figure 10.18](#)) and are specialized in feeding on Arctic zooplankton by swimming slowly with their mouth open, filtering water through the fine filaments of their baleen (Simon *et al.*, 2009). The main prey are copepods, dominated by *Calanus* species, and krill, where they are available in subarctic or low Arctic areas (Lowry, 1993; Finley, 2001). In the Beaufort Sea, where most of the studies of bowhead feeding have been carried out, *Calanus hyperboreus* and *C. glacialis* were the dominant copepods, while *Thysanoessa raschii* was the predominant krill species, taken mainly in the western Beaufort Sea off Barrow (Lowry and Frost, 1984; Lowry, 1993; Lowry *et al.*, 2004). Bowheads may also feed close to the bottom in shallow water on aggregations of epibenthic organisms such as mysids and gammarid amphipods (Lowry, 1993; Würsig and Clark, 1993; Lowry *et al.*, 2004). The core-use areas identified for bowheads in the Beaufort and Chukchi seas were interpreted to be sites where *Calanus* copepods would be concentrated by topography and oceanographic features (Citta *et al.*, 2015). The feeding area near Barrow also involves mechanisms that concentrate krill, thought to be advected north with currents through the Chukchi Sea (Ashjian *et al.*, 2010; Moore *et al.*, 2010; Okkonen *et al.*, 2011).



**Figure 10.18.** Baleen of bowhead whale forming a fine-meshed filter allowing retention of calanoid copepods such as *Calanus hyperboreus* in the Arctic Ocean. Photo provided by the Alaska North Slope Borough (Nicole Kanayurak).

Bowheads of the Bering/Chukchi/Beaufort stock use the deep areas of the CAO in Canada Basin, but apparently to a limited extent, with most whales staying in shelf and slope waters. The areas where they have been observed farthest north is in the eastern Beaufort Sea west of Banks Island and in the Chukchi Borderland region, where a tagged whale moved north to 78°N (Quakenbush *et al.*, 2012, 2013). In the east, bowheads move into M'Clure Strait and Viscount Melville Sound, where there might possibly be an advection-driven productivity feature associated with the exit flow of Pacific water through this part of the Northwest Passage. In the Chukchi Borderland, copepods may be transported in Pacific water flowing north through the Chukchi Sea, as well as *Calanus* species associated with the Atlantic water flowing east from the Laptev Sea.

### **East Greenland/Svalbard/Barents Sea stock (or Spitsbergen stock)**

The East Greenland/Svalbard/Barents Sea stock (or Spitsbergen stock; [Figure 10.17](#)) of bowheads was probably the largest of the stocks historically, but it was severely depleted by

large-scale whaling during 1611–1911 (Woodby and Botkin, 1993). Over 100 000 whales were harvested during the 300-year period of whaling, with about half of them taken during a 100-year period from the 1650s to the 1750s (Hjort, 1902; Allen and Keay, 2006). At the peak of the whaling, there were as many as 400–500 vessels annually in the Spitsbergen area, manned by thousands of people and resulting in harvests of more than 1000 bowheads per year (Ruud, 1937; Ross, 1993; Hacquebord, 1999, 2001). Whaling declined to low levels during the 1800s before ending in 1911, when virtually no whales were left (de Jong, 1983; Ross, 1993).

The distribution area of the stock was (and possibly still is) the Greenland Sea, Fram Strait, northern Barents and Kara seas east to Severnaya Zemlya, and adjacent parts of Nansen Basin (Ruud, 1937; Christensen *et al.*, 1992a; Moore and Reeves, 1993; Wiig *et al.*, 2007; Cooke and Reeves, 2018b). The seasonal migration of bowheads has been interpreted from observations during the whaling period (Scoresby, 1820, 1823; Southwell, 1898; Gray, 1931; Ross, 1993; Moore and Reeves, 1993; Shelden and Rugh, 1995; Hacquebord, 1999, 2001). The whales were believed to winter in the marginal ice zone in the southern Greenland Sea and Denmark Strait, and possibly also along southeastern Greenland (Figure 10.19). The bowheads would migrate north in spring, along the ice edge, to the areas along western Spitsbergen, where they arrived in April or May. In summer, bowheads moved west and south in the marginal ice zone in the western Greenland Sea in a anticlockwise migration pattern around the Greenland Sea. There was likely size and sex segregation within the population, reflected in catch compositions in different areas (Scoresby, 1823; Southwell, 1898; Gray, 1931; de Jong, 1983; Moore and Reeves, 1993; Hacquebord, 1999).

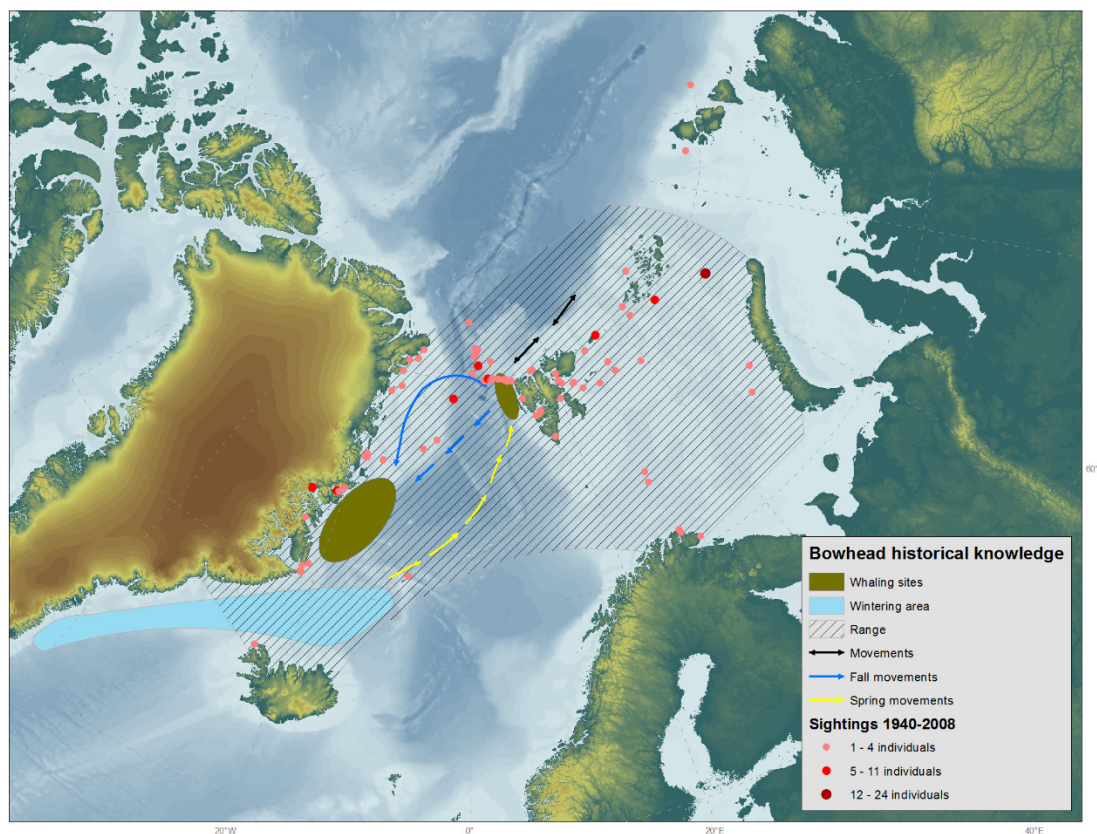


Figure 10.19. Distribution, seasonal migration, and former whaling sites of bowhead whales of the East Greenland/Svalbard/Barents Sea stock based on observations in the historical whaling period. Redrawn from Southwell (1898). Also shown are sightings of bowhead whales in the period 1940–2008, based on Boertmann *et al.* (2009) and Wiig *et al.* (2010).



Historical whaling started in bays and inshore waters along western Spitsbergen, in what was called bay whaling, before it shifted from about 1650, because of the depletion of whales, to pelagic whaling in the Greenland Sea and Fram Strait. Whaling was concentrated in the marginal ice zone in what was called ice whaling (de Jong, 1983; Ross, 1993). The northern whaling ground was located in eastern Fram Strait off northwestern Spitsbergen between about 78 and 80°N, where the WSC of relatively warm Atlantic water keeps the water open and accessible, in the so-called Whaler's Bay (Reeves, 1980; Sanger, 1991; Ross, 1993). There was also whaling north of Spitsbergen, in an eastward extension from the northern whaling ground, when sea ice conditions allowed. After bowheads became scarce in the Svalbard area, a southern whaling ground located off East Greenland, at about 72–75°N, was used from around 1815 (Scoresby, 1823; Southwell, 1898; Gray, 1931; Moore and Reeves, 1993; Ross, 1993).

Historical bowhead whaling took place during the cold climatic period of the Little Ice Age. There were climatic fluctuations and shifts during this period, which probably affected the distribution and migration of the whales (Sanger, 1991; Hacquebord and Leinenga, 1994; Hacquebord, 1999, 2001). In cold years with heavy ice conditions, bowheads concentrated along the ice edge of the Whalebay off northwestern Spitsbergen. In this situation, they were particularly vulnerable to whaling since they could not escape into the ice. Therefore, climatic conditions played a contributing role in the very heavy impact of whaling, which led to the near extinction of the Spitsbergen bowhead stock (Hacquebord, 1999, 2001). Catches declined during the 1800s, but whaling continued until nearly the last whale for two main reasons: (i) whaling was combined with, and subsidized by, the harvest of other species, including walrus, polar bear, narwhal, bottlenose whale, and harp and hooded seals (Reeves, 1980); and (ii) baleen had a very high value, which meant the expenses of an expedition could be nearly covered by the catch of one bowhead whale (Ruud, 1937).

After whaling ended in 1911, the stock was initially considered extinct. Moore and Reeves (1993) provided a summary of sightings of bowheads from the former range of the Spitsbergen stock in the Greenland, Barents, and Kara seas, from 1940 to 1990. This included 12 records from the Greenland Sea and Fram Strait area, and about 20 records from the Barents Sea area, most of them from the northeastern part around Franz Josef Land. Since 1990, there has been an increase in the number of sightings from the Greenland and northern Barents seas. Gilg and Born (2005) compiled a summary of 26 observations of bowhead whales from eastern Greenland between 1940 and 2004, with 16 of them since 1990. Most of the sightings were of 1–2 individuals, but three of the recent sightings were of groups of 5–10 bowheads. Boertmann *et al.* (2009) reported 13 additional sightings for three subsequent years (2006–2008), including a young juvenile. During an aerial survey in the Northeast Water Polynya area in Northeast Greenland in August 2009, sightings of seven bowhead whales gave an estimate of about 100 whales in the survey area (Boertmann *et al.*, 2015). Later surveys in March and August–September 2017 gave higher estimates of about 300 bowheads in the Northeast Water Polynya area (Annex D in Boertmann *et al.*, 2020a).

Wiig *et al.* (2010) summarized sightings of bowheads in the Svalbard area since 1940, with 35 out of a total of 46 sightings after 1990, and 33 of them in 2000 or later. Many of the recent sightings have been from cruise ships operating in the area in summer, and some have been from whaling vessels (hunting for minke whales). During a dedicated survey in spring (April) 2006, eight sightings of a total of 17–20 bowheads were made (Wiig *et al.*, 2007, 2008). Most of the recent sightings from the Svalbard area have been of single individuals, but seven sightings are of groups of 3–7+ bowheads. One sighting of 20 individuals from a whaling vessel in 2000 is considered a possible, but unconfirmed, observation (the sighting was supposedly photographed, but has not been verified; Wiig *et al.*, 2010).

In the waters around Franz Josef Land there are many sightings of bowheads, including larger groups of up to nearly 70 bowheads (Ivashin, 1988; Belikov *et al.*, 1989; de Korte and Belikov, 1994; Belikov and Boltunov, 2002). Bowheads are observed in polynyas near Franz Josef Land in late winter, and a total of 20 animals were recorded there in April 2010 (Gavrilo and Ershov, 2010). The earlier records include two late-winter sightings of relatively large groups near Franz Josef Land in 1981 ("several 10s of individuals") and in 1983 ("about 66 animals"; Belikov *et al.*, 1989). There are also records of larger groups in summer from this part of the Barents Sea (> 24 individuals in drift ice between Franz Josef Land and Novaya Zemlya in August 1981, and about 15 at Franz Josef Land in September 1983; Ivashin, 1988; Belikov *et al.*, 1989; Moore and Reeves, 1993). Seven bowhead whales were observed at Franz Josef Land in September 1990 (Wiig, 1991). Important summer feeding grounds have been observed south of Franz Josef Land, as well as in the western deep-water part of the archipelago (Gavrilo, 2013, 2015). Satellite-tagging has shown considerable movements of bowhead whales in the marginal ice zone along East Greenland, and between this area and Franz Josef Land, with one out of 12 whales tagged in East Greenland moving east to Ushakov Island in the northern Kara Sea (Lydersen *et al.*, 2012; Annexes C and D in Boertmann *et al.*, 2020a).

The relatively consistent and regular sightings of bowheads in the Greenland Sea, Fram Strait, and around Svalbard and Franz Josef Land suggest that the stock is likely to number some 100 individuals. An aerial survey (primarily targeting polar bear) in August 2015 made 15 sightings of a total of 27 individual bowheads in the marginal ice zone of western Nansen Basin, at around 82°N between 15 and 30°E (Vacquié-Garcia *et al.*, 2017). These counts translate into an estimate of about 350 bowhead whales. De Boer *et al.* (2019) reported sightings of around 225 bowhead whales on 85 occasions during annual wildlife ship expeditions to western Fram Strait in early summer over four years (2015–2018). A large aggregation of 84 bowhead whales was encountered in 2015, while 104–110 whales were sighted during a systematic and effort-corrected survey in 2018. With this new information, the East Greenland–Svalbard–Barents Sea stock of bowheads was downlisted from Critically Endangered (Reilly *et al.*, 2012b) to Endangered in 2018 (Cooke and Reeves, 2018b).

The Spitsbergen, or now East Greenland–Svalbard–Barents Sea, stock of bowhead whales possibly consisted of different stock components, subpopulations, or tribes, although this issue remains unresolved (Reeves, 1980). Zorgdrager (1720) suggested that the whales killed in Storfjorden in southern Spitsbergen (at the southward fishing station, and called south-ice whales) differed from the whales caught in the Greenland Sea (called west-ice whales). The south-ice whales had thinner and softer yellow blubber and a different appearance with a "more even back", when compared to the west-ice whales. Scoresby (1820) also noted differences among subpopulations or tribes, with different summer grounds and migration routes. However, it is unclear how much of the noted differences were due to size and age segregation within the larger stock (Eschricht and Reinhardt, 1866; Reeves, 1980).

There is limited information on the former feeding of this stock in the Greenland Sea, although there are indications that euphausiids were important prey (Ruud, 1937; Christensen *et al.*, 1992b). The Greenland Sea and eastern Fram Strait area, where the northern whaling ground was located, must have had a high production and abundance of plankton to support a bowhead whale population of 25 000 or more individuals. It is likely that northward advection of *Calanus finmarchicus* and krill species (*Meganycetiophanes norvegica*, *Thysanoessa inermis*) from the Norwegian Sea with the WSC, along with circulation of *C. hyperboreus* in the Greenland Sea basin, contributed to rich feeding grounds for bowheads. Whalers in former times had noticed a connection between the colour of the water and the occurrence and migration of bowhead whales. Scoresby (1820) noted that the water varied in colour from ultramarine blue to olive green, and that the whales avoided the clear blue waters and congregated in the green waters. He also noted that whales were found in waters with an abundance of zooplankton including

small crustaceans and pteropods. The more turbid and discoloured green water was interpreted to reflect spring growth of diatoms which would then nourish the growth of "animalcules" or plankton, which formed the food for the bowheads (Gray, 1931). Gray (1931) mentioned specifically the herbivorous copepod *C. finmarchicus* as the main food for the bowheads.

### 10.2.12 Blue whale (*Balaenoptera musculus*)

Blue whale ([Figure 10.20](#)) occurs with three recognized subspecies: Antarctic or true blue whale (subspecies *intermedia*), North Atlantic blue whale (nominate *musculus*), and pygmy blue whale in the southern Indian Ocean (*brevicauda*; Reilly *et al.*, 2008a). The North Pacific blue whale is considered the same as the North Atlantic blue whale (nominate *musculus*), but could be a different subspecies. The subspecies taxonomy of the blue whale is still open and requires more study (Reilly *et al.*, 2008a). Blue whales were hunted to low levels by modern whaling, which started in the Barents Sea in the 1860s and continued in the Antarctic in the first part of the 20th century. Most stocks appear to be slowly recovering, but the blue whale as a species is assessed as being Endangered on the IUCN Red List due to the previous decline, with a total population (for all subspecies) now estimated at 10 000–25 000 individuals (Reilly *et al.*, 2008a; Cooke, 2018a).

The North Atlantic blue whale is distributed in summer from the Scotian Shelf in the west and Spain in the east, north to Davis Strait, Denmark Strait, Jan Mayen, Svalbard, and the southern Barents Sea. Two populations (or management stocks) are generally recognized for the western and central, and the eastern North Atlantic, respectively (Sears, 2002; Sears and Calambokidis, 2002; Sears and Perrin, 2009). The eastern population occurs around Iceland and farther east in the Northeast Atlantic. It is estimated to number around 1000 animals, and is thought to have increased by about 5% per year during the 1970s and 1980s (Reilly *et al.*, 2008a; Pike *et al.*, 2009).

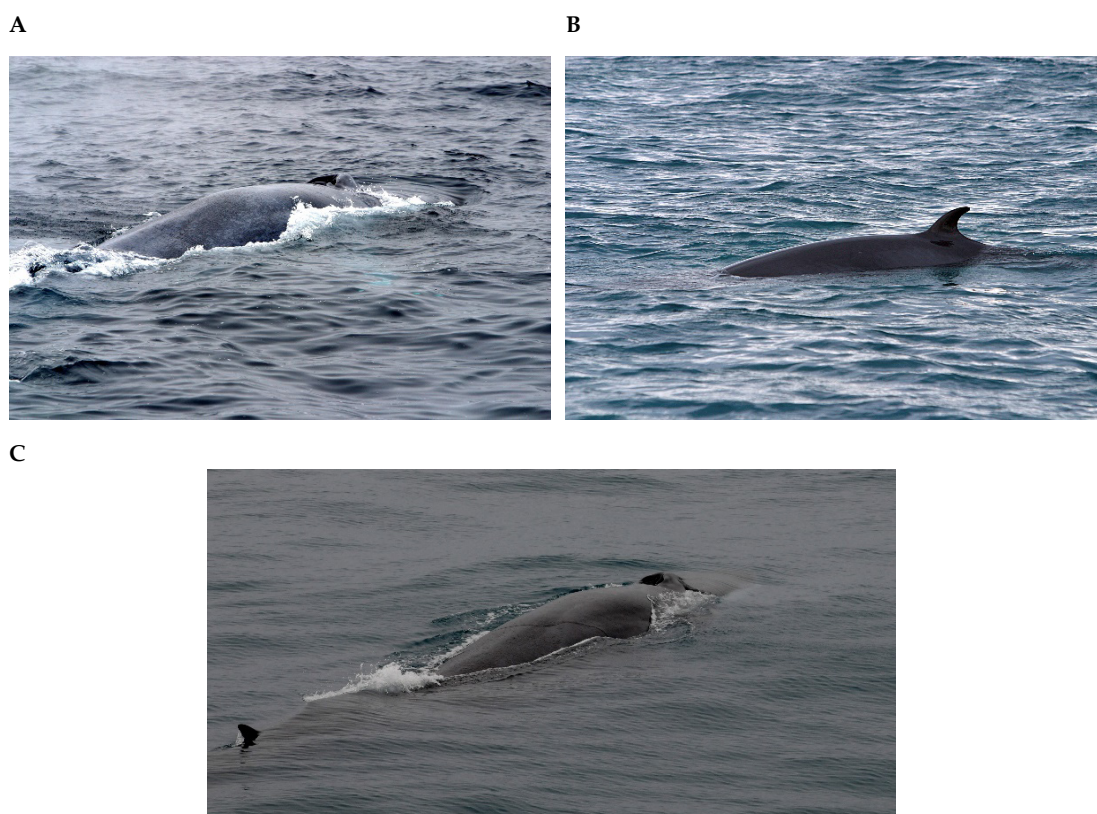


Figure 10.20. Photos of (A) blue whale, (B) minke whale, and (C) fin whale breaching the water surface to breathe in the Norwegian Sea. Note the large blow holes (nostrils) on the photos of the blue and fin whales. Photo credits: Kjell-Arne Fagerheim (A and C) and Leif Nøttestad (B), IMR.

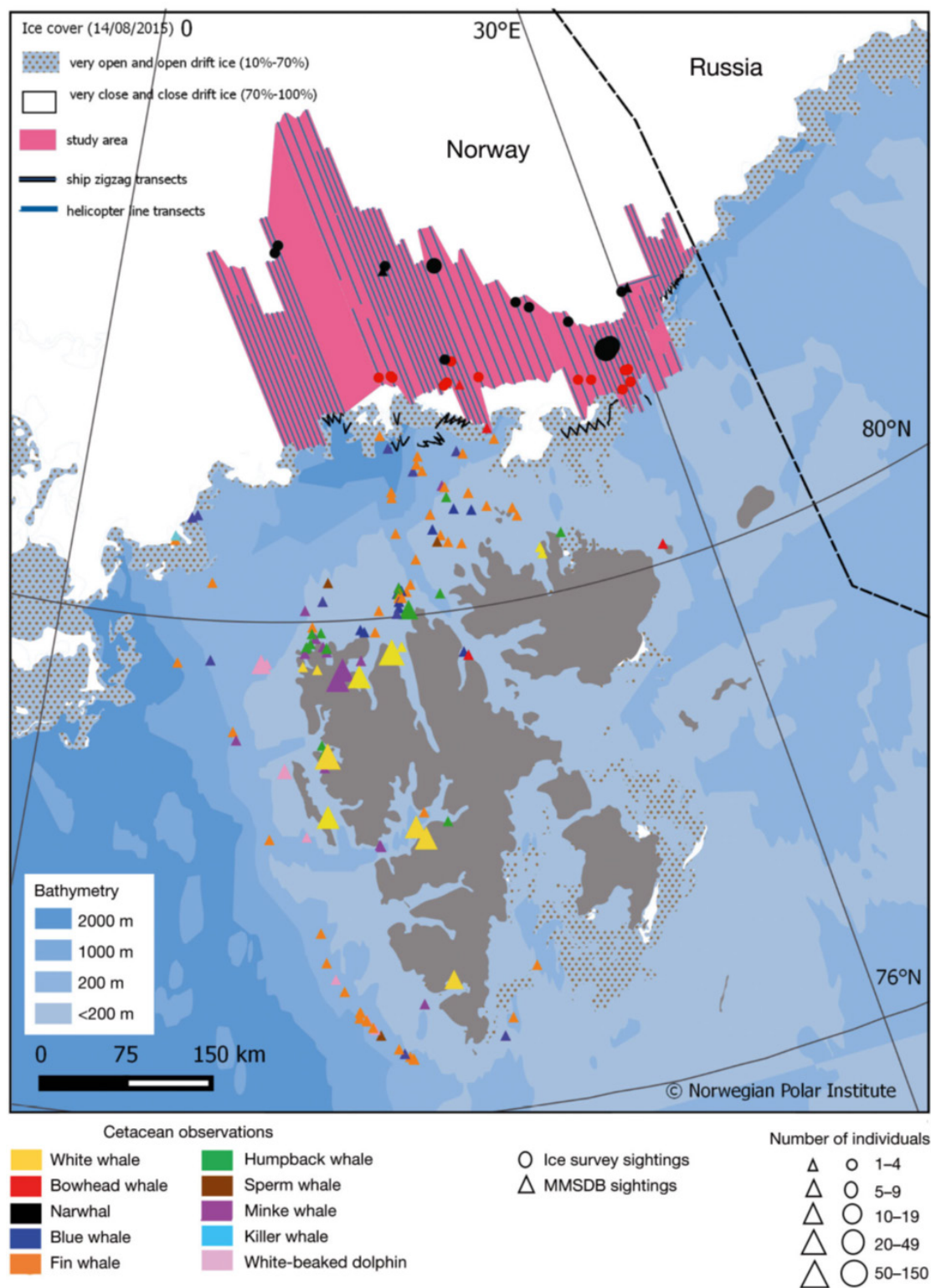


Figure 10.21. Sightings of whales in the waters around Svalbard and in Nansen Basin north of Svalbard based on helicopter surveys and observations from ships during late summer 2015. From Vacquie-Garcia *et al.* (2017).

Whales from this population migrate north to the Svalbard area in summer. Previously, they used to arrive there from their southern wintering areas in May before they moved southeast into the Barents Sea, where they were known to feed on krill in the Varangerfjord (Sars, 1874; Hjort and Ruud, 1929; Christensen *et al.*, 1992a, 1992b). Blue whales have been seen regularly in



the Svalbard area in recent years, particularly on the western and northern sides ([Figure 10.21](#); Vacquié-Garcia *et al.*, 2017). Sightings have been made in waters north to the ice edge in Fram Strait, and north of Svalbard to beyond 81°N (Vacquié-Garcia *et al.*, 2017). Therefore, blue whales are recorded in western Nansen Basin of the CAO. Considering the previous migration of blue whales to the Svalbard area in summer (Christensen *et al.*, 1992a), the Whaler's Bay region north of Svalbard may be an important area for blue whales of the eastern population in the North Atlantic.

The North Pacific blue whale is widely distributed across the North Pacific, from Japan to Kamchatka on the western side, across to the Gulf of Alaska, and south to Central America on the eastern side. It occurs with possibly five or more subpopulations, including a western subpopulation in the area from northern Japan to the Kuriles and Kamchatka, and a central subpopulation from Hawaii to the Aleutians (Reeves *et al.*, 1998). Blue whales of the western and central subpopulations move only to a limited extent into the Bering Sea. No blue whales were taken in the earlier Japanese whaling in the Bering Sea (Nasu, 1974). Blue whales from the Pacific side are, therefore, not expected to move north through Bering Strait and into the CAO.

### 10.2.13 Fin whale (*Balaenoptera physalus*)

The fin whale ([Figure 10.20](#)) occurs with two (or possibly three or four) subspecies: nominate *physalus* in the northern hemisphere, and subspecies *quoyi* in the southern hemisphere (Aguilar, 2009; Reilly *et al.*, 2013). Fin whales in the North Pacific may be a different subspecies than the North Atlantic fin whale, but this needs further study. Fin whales were, like blue whales, severely depleted by whaling in the former century, particularly in the Antarctic. It is currently listed as Vulnerable on the IUCN Red List, due to the previous strong decline caused by whaling (Cooke, 2018b).

#### North Atlantic fin whale

North Atlantic fin whales are distributed north to Davis Strait and Baffin Bay in the western part, and to Svalbard and the Barents Sea in the east. It is likely that there are 2–4 breeding stocks (IWC, 2007). The total population of fin whales in the North Atlantic was estimated to be about 53 000 individuals, with the largest numbers in the waters around Iceland (about 25 000) and about 6000 in the Norwegian and Barents seas (IWC, 2007; Vikingsson *et al.*, 2009; Reilly *et al.*, 2013). The migration of fin whales in the North Atlantic is apparently complex, and many whales remain in northern waters during winter, e.g. in the Norwegian and Barents seas (Christensen *et al.*, 1992b; Clark, 1995).

Fin whales are commonly observed in Arctic waters of the northern Barents Sea shelf in autumn surveys, where they appear to target krill and capelin as their main prey items (Skern-Mauritzen *et al.*, 2011; Ressler *et al.*, 2015). They are also found in the slope region west and north of Svalbard, where sightings extended north to the marginal ice zone at nearly 82°N in 2015 ([Figure 10.21](#); Skern-Mauritzen *et al.*, 2009; Vacquié-Garcia *et al.*, 2017). Therefore, fin whales are present in the southwestern Nansen Basin in the Whaler's Bay region, like blue whales.

#### North Pacific fin whale

The North Pacific fin whale is widely distributed across the North Pacific (Perry *et al.*, 1999). The population structure is uncertain, but there appears to be at least two migratory stocks (in the northeastern and northwestern areas), as well as several non-migratory resident groups on both sides of the ocean (Mizroch *et al.*, 2009; Angliss and Outlaw, 2008). Fin whales of the western and eastern migratory stocks appear to arrive in the Bering Sea in summer (Mizroch *et al.*, 2009). There is no current estimate of the total fin whale population abundance in the North Pacific (Reilly *et al.*, 2013). Recent estimates give an abundance of 5700 fin whales in the Bering

Sea, the Aleutian Islands, and Gulf of Alaska (Moore *et al.*, 2002; Zerbini *et al.*, 2006). Information from previous whaling records suggests that the fin whales arriving in the waters north of Unalaska Island, in the eastern Aleutians, used to split into two groups (Nasu, 1974). Some whales, including high percentages of young immature individuals and lactating females with calves, remained in the area of the southeastern Bering Sea during summer. Another group, consisting of older whales, migrated north along the shelf break towards Cape Navarin. Whaling on these northern grounds took place in July and August (Nasu, 1974).

The large copepod *Neocalanus cristatus* and the krill *Thysanoessa inermis* were the dominant prey for fin whales in the eastern Bering Sea, with a seasonal progression from copepods to krill during the summer season (Nemoto, 1959; Frost and Lowry, 1981). Some of the larger and older whales used to move north to feed in the southwestern Chukchi Sea during the period of commercial whaling in the mid-part of the former century (Nasu, 1974). The distribution extended west to north of Kolyuchinskaya Bay, and seemed to follow the distribution of Anadyr water (AnaW), where the whales were probably feeding on dense concentrations of advected prey such as *Neocalanus* copepods and krill (Nasu, 1974; Mizroch *et al.*, 1984). Fin whales were seen north to the ice edge near Wrangel and Herald Islands at about 71°N (Sleptsov, 1961, cited in Mizroch *et al.*, 2009).

Commercial whaling decimated the fin whales in the North Pacific (an early estimate suggested a decrease from around 45 000 individuals to down to 17 000; Perry *et al.*, 1999; Mizroch *et al.*, 2009; Reilly *et al.*, 2013). After whaling stopped in the 1970s, there appears to have been very few fin whales migrating into the southern Chukchi Sea (Ljungblad *et al.*, 1988; MMS, 2007; Mizroch *et al.*, 2009). No fin whales have been observed in aerial surveys of the northeastern Chukchi Sea or the southern Beaufort Sea (Ljungblad *et al.*, 1988; Moore *et al.*, 2000a). Also, on the Russian side, no fin whales were seen in the Chukchi Sea on whale-sighting cruises from 1979 to 1992 (Vladimirov, 1994). Thus, while the southern and southwestern Chukchi Sea was earlier part of the summer range of fin whales when the stock was larger, this appears to no longer be the case. There are no documented sightings off the Chukchi shelf edge, and the North Pacific fin whale is, therefore, not a subspecies occurring in the CAO, in contrast to the North Atlantic fin whale.

#### 10.2.14 Humpback whale (*Megaptera novaeangliae*)

The humpback whale has a cosmopolitan distribution, with no subspecies recognized (Clapham, 2009; Bettridge *et al.*, 2015). It is generally migratory, with subpopulations moving between mating and calving grounds in tropical waters, and feeding grounds in productive colder waters in temperate and high latitudes, typically in coastal and shelf environments (Clapham, 2009). The total population numbers > 60 000 animals, and humpback is assessed as a species of Least Concern on the IUCN Red List (Reilly *et al.*, 2008b; Cooke, 2018c).

##### North Atlantic subpopulations

In the North Atlantic, humpback whales have their main wintering, calving, and breeding areas in the West Indies, with smaller numbers wintering around the Cape Verde Islands (Reilly *et al.*, 2008b). There are six major summer feeding grounds: Gulf of Maine, Gulf of St Lawrence, Newfoundland and Labrador, western Greenland, waters around Iceland and the Iceland Sea, and the Barents Sea (Stevick *et al.*, 2003, 2006; Reilly *et al.*, 2008b). There is a high degree of fidelity to the feeding grounds, with individual whales returning each spring to their own areas. The Barents Sea group (or subpopulation) appears to target the Barents Sea capelin stock as a main prey, but they are also known to feed on krill and other food, such as herring (Figure 10.22). Humpbacks appear around Svalbard in early summer, where they feed mainly on krill. Later, in summer and autumn, they may be distributed farther north and east, in the waters

between Svalbard, Franz Josef Land, and Novaya Zemlya, where they feed on capelin (Christensen *et al.*, 1992a, 1992b). This subpopulation has been estimated to be about 1500 individuals (Øien, 2009).

Sightings from autumn surveys in the Barents Sea (2003–2007) found most of the humpback whales north of the polar front, with concentrations of sightings east of Svalbard (Skern-Mauritzen *et al.*, 2011). Reported sightings from the Svalbard area in 2015 showed humpbacks to be present north of Svalbard, occurring generally close to the coast (Figure 10.21; Vacquié-Garcia *et al.*, 2017). The northernmost record was at the shelf edge at about 81°N. This suggests that humpback whales are more restricted to the Barents shelf than blue and fin whales, and occur to a lesser extent in slope waters of Nansen Basin north of Svalbard (Vacquié-Garcia *et al.*, 2017).



Figure 10.22. Feeding humpback whale surfacing in the Barents Sea amid black-legged kittiwakes. Photo: Nils Øien, IMR.

### North Pacific subpopulations

In the North Pacific, humpback whales are distributed north to the Bering Sea and into the Chukchi Sea. Three main subpopulations are recognized in the eastern, central, and western North Pacific (Calambokidis *et al.*, 2001, 2008; Reilly *et al.*, 2008b; Fleming and Jackson, 2011; Allen and English, 2013). The eastern subpopulation summers off the US Pacific coast, the central subpopulation (which winters around Hawaii) summers in the Gulf of Alaska, and the western (or Asian) subpopulation summers off Kamchatka, along the Aleutians, and in the Bering Sea. The western subpopulation is the smallest one, with about 1000 animals (Calambokidis *et al.*, 2008; Reilly *et al.*, 2008b; Allen and English, 2013). The central and eastern subpopulations are estimated to be about 7000–10 000 and 6000–7000 individuals, respectively, based on counts on their wintering grounds (Reilly *et al.*, 2008b; Allen and English, 2013). The total population in the North Pacific was estimated to be about 18 000 humpback whales (Calambokidis *et al.*, 2008; Reilly *et al.*, 2008b). In addition to the three subpopulations mentioned, there may be a fourth with wintering grounds around the offshore Revillagigedo



Islands (Mexico), which are located about 700 km off the Mexican mainland (Urban-Ramirez *et al.*, 2000). The summer areas for these whales are not well known, but some of them are seen in the Bering Sea and Gulf of Alaska (Allen and English, 2013).

In the Bering Sea, humpbacks are most frequently seen in the eastern Aleutian Islands and along the southeastern Bering Sea shelf edge north to the Pribilof Islands. These whales are probably mainly from the central subpopulation, although whales from the western subpopulation and the Revillagigedo wintering area may also be found there (Allen and English, 2013). Sighting surveys in summer 1999 and 2000 on the central and southern Bering shelf gave an estimate of a few hundred humpbacks, observed mainly in the middle shelf domain (Moore *et al.*, 2002). Humpback whales move commonly north to Anadyr Gulf and Bering Strait, where they were known to feed on the mysid *Mysis occulata*, the arctic amphipod *Themisto libellula*, and shrimps (*Eualus gaimardii* and *Pandalus goniurus*; Tomilin, 1957; Wolman, 1978).

Humpback whales move north through Bering Strait into the Chukchi Sea, where there were catches taken in the 1930s (Muto *et al.*, 2016). Humpback whales were seen in the southern Chukchi Sea in vessel and aerial surveys in 2009–2012 (July–September). A total of 51 sightings of 108 whales were made, mostly of adults, but also of some calves and juveniles (Clarke *et al.*, 2013 a, 2013b). There have also been scattered sightings in the northeastern Chukchi Sea and westernmost Beaufort Sea in recent years (2007–2012; Clarke *et al.*, 2013a, 2013b). Humpback whales were not seen in aerial surveys in the Chukchi Sea in the 1980s (Moore and Clarke, 1992), suggesting that there has been a more recent expansion of the range into these northern waters. On the Russian side, there also seems to have been an increase in humpback whales along the coast of Chukotka (Mel'nikov *et al.*, 1999; Mel'nikov, 2000). Earlier in the 1930s, humpback whales were seen west of Vankarem and north to Long Strait (between Wrangel Island and the mainland; Mel'nikov *et al.*, 1999). Humpbacks that migrate to the Chukchi Sea could be of the western, central, or Revillagigedo (wintering) stocks. They could possibly move north to the shelf edge of the Chukchi Sea, but humpback whales have not yet been observed in the slope region of the CAO.

### 10.2.15 Minke whale (*Balaenoptera acutorostrata*)

The minke whale (or common or northern minke whale; [Figure 10.20](#)) is the smallest of the baleen whales (typically 8–9 m in length; Perrin and Brownell, 2009). It occurs with three recognized subspecies: nominate *acutorostrata* in the North Atlantic, subspecies *scammoni* in the North Pacific, and dwarf minke whale (not yet given a Latin name). A separate minke species can be found in the southern hemisphere, the Antarctic minke whale (*Balaenoptera bonaerensis*; Rice, 1998; Perrin and Brownell, 2009). Common minke whale is assessed as a species of Least Concern on the IUCN Red List (Reilly *et al.*, 2008c; Cooke, 2018d).

#### North Atlantic minke whale

The North Atlantic minke whale is widely distributed and occurs with four recognized stocks: Northeast Atlantic, Central North Atlantic, West Greenland, and Canadian East Coast (IWC, 2004a). The Northeast Atlantic (Barents and Norwegian seas) and Central North Atlantic (Iceland–Jan Mayen) are the largest stocks, each with 80 000–90 000 animals (IWC, 2004a; Reilly *et al.*, 2008c). Minke whales of the Northeast Atlantic stock are distributed north to Svalbard and the northern Barents Sea in summer and autumn. There is segregation according to sex and size, and minke whales observed off western Spitsbergen in early summer have been mainly pregnant females (Haug *et al.*, 2011). A large fraction of the stock migrates seasonally into the Barents Sea where they play a large ecological role, feeding primarily on capelin, herring, and krill (Haug *et al.*, 1995, 2002; Folkow *et al.*, 2000; Bogstad *et al.*, 2015). The whales have a wide distribution in the open-water season, being associated with aggregations of capelin, herring,



and krill (Skern-Mauritzen *et al.*, 2009, 2011). They are found commonly along western and northern Svalbard, where they are seen mostly in coastal and shelf waters (Kovacs and Lydersen, 2006; Vacquié-Garcia *et al.*, 2017). There are limited sightings in the slope waters north of Svalbard, and minke whale is apparently less prone to move into western Nansen Basin compared to the larger species of baleen whales, notably blue and fin whales (Figure 10.21; Vacquié-Garcia *et al.*, 2017).

### North Pacific minke whale

The North Pacific minke whale has a summer distribution across the North Pacific, from about 30°N to the Aleutians, Bering Sea, and into the southern Chukchi Sea (Moore *et al.*, 2002a; Zerbini *et al.*, 2006; Reilly *et al.*, 2008c). Three management stocks are recognized by IWC (2004b): the “J stock” in the Yellow Sea, East China Sea, and Sea of Japan, the “O stock” in the Okhotsk Sea and West Pacific west of 180°W, and a “remainder stock” for the eastern North Pacific (Donovan, 1991; Reilly *et al.*, 2008c). The remainder stock is complex and has been split in two components: an Alaska stock that migrates in summer to the Bering Sea, and a resident California/Washington/Oregon stock (Muto *et al.*, 2016).

Ship surveys of the eastern Bering Sea shelf (1999–2010) showed minke whales to be widespread across the shelf and slope regions, with abundance estimates of up to a few thousand animals (Moore *et al.*, 2000b, 2002; Friday *et al.*, 2012, 2013). Minke whales are generalist feeders, and have been found to eat krill and various small fish such as herring, Pacific sand lance, capelin, and polar cod in the northern Bering Sea (Nemoto, 1959; Frost and Lowry, 1981). Some minke whales move north of Bering Strait to the Chukchi Sea in summer. However, they were the least common baleen whale in ship and aerial surveys in 2009–2012, seen mostly as single animals in the southern Chukchi Sea (Clarke *et al.*, 2013b). Minke whales are seen along Chukotka, depending on ice conditions, most commonly south of Bering Strait, but they were also recorded in the Chukchi Sea north to 68°N in 1992 (Mel’nikov *et al.*, 2001). Minke whales have also been sighted in the northeastern Chukchi Sea in recent years (Clarke *et al.*, 2013a, 2013b), as well as being recorded acoustically (Delarue *et al.*, 2013).

North Pacific minke whales, like the North Atlantic subspecies, seem to be associated mainly with coastal and shelf habitats. While they could move north to the ice edge, there have been no reported sightings of minke whales in the slope region to Canada Basin of the CAO.

### 10.2.16 Grey whale (*Eschrichtius robustus*)

The grey whale (Figure 10.23) differs from other baleen whales by being mainly a bottom feeder, eating tube-dwelling amphipods and other benthic prey (Jones and Swartz, 2009). It exists with two populations in the North Pacific: a small western and a larger eastern stock (LeDuc *et al.*, 2002; Swartz *et al.*, 2006). The western population numbers around 100 individuals and is assessed as Critically Endangered by IUCN (Reeves, 2005; Reilly *et al.*, 2008d). The eastern stock has recovered from previous whaling to a level now considered to be near carrying capacity, numbering around 20 000 individuals (Rugh *et al.*, 2005; Reilly *et al.*, 2008d). Due to the favorable status of this stock, grey whale at the species level is assessed as a species of Least Concern on the IUCN Red List (Reilly *et al.*, 2008d; Cooke, 2018e). Grey whales used to also occur in the North Atlantic, but they were extirpated some 300–400 years ago (Rice, 1998; Jones and Swartz, 2009).

The Eastern North Pacific population (or California–Chukchi population) is migratory, and moves between wintering and breeding areas in shallow lagoons and bays of western Baja California and summer feeding areas in the northern Bering and Chukchi seas (Jones and Swartz, 2009). Chirikov Basin, between St Lawrence Island and Bering Strait, was a main feeding area where most of the grey whales were seen in aerial surveys in summer (July–

August) in the 1980s (Moore *et al.*, 2000a, 2001, 2003). Here, they fed on the very rich benthic community dominated by ampeliscid amphipods, with the largest species *Ampelisca macrocephala* being particularly important as prey for grey whales (Grebmeier *et al.*, 1989; Highsmith and Coyle, 1990, 1992). Grey whales continue north to feed in the Chukchi Sea when the area becomes ice free in late summer and autumn. Sighting surveys in autumn (September–October) showed grey whales concentrated in an area southwest of Point Hope (in the northern flank of the southern Hope Valley), along the coast mainly between Icy Cape and Point Barrow, and farther offshore from Barrow towards Hannah Shoal (Moore *et al.*, 1986, 2000a; Moore, 2000). These areas have since been confirmed as being important for foraging grey whales (Bluhm *et al.*, 2007; Clarke *et al.*, 2015). Grey whales also feed in the southwestern Chukchi Sea off the coast of Chukotka, where they may distribute west into Long Strait and the East Siberian Sea, depending on ice conditions (Bogoslovskaya *et al.*, 1981; Miller *et al.*, 1985; Belikov and Boltunov, 2002).



**Figure 10.23.** Grey whale with its head above water. Photo: Raymond VanBuskirk, USFWS.

There is evidence to suggest that grey whales depleted the amphipod food resource in Chirikov Basin, and that there was a shift to a larger proportion of the population feeding in the Chukchi Sea after the 1990s (Moore *et al.*, 2001, 2003; Bluhm *et al.*, 2007; Coyle *et al.*, 2007). Around 2000, there was an event with large numbers of stranded dead grey whales in emaciated condition, suggesting starvation was involved in the cause of mortality (Le Boeuf *et al.*, 2000; Moore *et al.*, 2001, 2003). There was also apparently a substantial decline in population size around this time, possibly from around 30 000 to 20 000 individuals (Buckland and Breiwick, 2002; Rugh *et al.*, 2005; Reilly *et al.*, 2008d). Before this event, the population had been increasing about 2% per year since the 1960s, recovering from previous overharvesting by whaling (Buckland and Breiwick, 2002). The decline followed the period with high incidence of stranding, as well as low calf production (Perryman *et al.*, 2002), and was taken to indicate that carrying capacity for

the eastern population had been reached, and perhaps overshoot (Moore *et al.*, 2001; IWC, 2003; Reilly *et al.*, 2008d). The shift to greater dependence on feeding in the Chukchi Sea was facilitated by the shift to warmer climate, with less sea ice in the recent period (Moore *et al.*, 2003).

Grey whales in the Chukchi Sea move north to the ice edge. Aerial surveys in the 1980s found them to be associated with coastal areas and shoals with open water or light ice conditions (Moore and DeMaster, 1998; Moore, 2000; Moore *et al.*, 2000a). However, they are evidently able to cope with heavier ice conditions. Grey whale calls were recorded throughout winter (2003/2004) near Barrow in the western Beaufort Sea, demonstrating that some individuals can winter in the harsh Arctic conditions of this area (Stafford *et al.*, 2007). A few grey whales were also noted moving into the eastern Beaufort Sea, where they have been observed foraging on the eastern Mackenzie Shelf (Rugh and Fraker, 1981; Conlan *et al.*, 2013; Iwahara *et al.*, 2016). An extraordinary, extraterritorial, observation of a grey whale in the Mediterranean Sea in summer 2010 (Scheinin *et al.*, 2011) possibly reflected an individual that had travelled through the Northwest Passage into the North Atlantic, or possibly the alternative route north of Russia. Since grey whales forage in shallow waters, they are not expected to use habitats in the CAO, although a few vagrants could occur there, e.g. during migration to and from the eastern Beaufort Sea.

#### 10.2.17 Killer whale (*Orcinus orca*)

The killer whale is a charismatic and emblematic species that is well known to the general public (Figure 10.24). It is, therefore, surprising that its taxonomy is far from well established. The killer whale is treated, and assessed e.g. on the IUCN Red List, as a single species. However, it is recognized to be a species complex, with different forms in the North Pacific, North Atlantic, and the Antarctic, which probably warrant recognition as separate subspecies or even species (Pitman and Ensor, 2003; Morin *et al.*, 2010; Foote *et al.*, 2009, 2013; Reeves *et al.*, 2017). The two forms of killer whales in the North Pacific (Eastern North Pacific resident and transient killer whales) are recognized by the Committee on Taxonomy of the Society for Marine Mammalogy as subspecies (yet unnamed; Reeves *et al.*, 2017).

Killer whales are highly social and cultural animals. They live in complex arrangements with matrilineal family groups that can form pods, and belong to different clans with distinct vocal dialects, which again can belong to different communities (Ford *et al.*, 2000; Ford, 2009). On the west coast of North America, three different ecotypes have been recognized, denoted residents, transients, and offshore. They are fish-eaters and mammal-hunters (Ford, 2009). Although there are limited studies, a similar specialization in eating either fish or marine mammals is believed to also occur in other geographical areas, among ecotypes which may be different subspecies or even cryptic species. Killer whale got its name not from its fish-eating habit, but from its ability to attack and kill other marine mammals. It is now well established and documented that killer whales (of the transient type) can take a wide range of marine mammals, from seals and seal pups to large baleen whales, including minke, gray, and bowhead whales (Ford, 2009). In Arctic waters, they are known to hunt beluga, narwhal, bowhead, and seals (Laidre *et al.*, 2006; Ferguson *et al.*, 2012a, 2012b; Higdon *et al.*, 2012). It is assumed that the killer whales that move into Arctic waters are of the marine-mammal-eating ecotype. The predation potential of killer whales in the Canadian Arctic was illustrated by a model estimate (based on food demand and frequencies of reported attacks) that 25 killer whales could annually kill and eat about 50 bowheads and about 500 individuals each of narwhals, belugas, and seals (Ferguson *et al.*, 2010, 2012a, 2012b).

Killer whales move north through Bering Strait to the Chukchi Sea in the summer season, presumably to feed. They have been observed attacking and killing gray whales in the eastern





**Figure 10.24. Killer whales breaching in the Norwegian Sea. Photo: Leif Nøttestad, IMR.**

Chukchi Sea, where they possibly were targeting younger individuals (George and Suydam, 1998). Bowheads are also apparently attacked, as suggested by frequent scars from killer whale bites on the flukes of bowheads landed by Alaskan Inuits (4–8% frequency; George *et al.*, 1994). Killer whales have been sighted in the southern and northeastern Chukchi Sea, in one case as a group of 30 animals (George and Suydam, 1998; Aerts *et al.*, 2013; Clarke *et al.*, 2013a). They have also been sighted along the coast of Chukotka, where they have been observed to hunt gray whale, bowhead, and beluga (Mel'nikov and Zagrebin, 2005). The killer whales that enter the Chukchi Sea have obviously been the marine-mammal-eating type. They are possibly of the the Gulf of Alaska, Aleutian Islands, and Bering Sea Transient stock, which has a minimum population estimate of 587 individuals, based on photo-identified animals (Muto *et al.*, 2016). It is not known whether killer whales from a transient stock on the Russian side could also move north to the Chukchi Sea. So far, there seems to not have been sightings of killer whales out in the slope waters of Canada Basin and the CAO. However, the potential for killer whales to move to these waters is there, particularly under light ice conditions.

Killer whales in the Baffin Bay area move north in summer, once ice conditions allow, with frequent sightings on both the Canadian and Greenland sides, and into Lancaster Sound in the Canadian Arctic Archipelago (Heide-Jørgensen, 1988; Reeves and Mitchell, 1988; Higdon, 2007; Higdon *et al.*, 2012; Ferguson *et al.*, 2012b). Killer whales have been recorded north to Smith Sound, with one sighting farther north in Hall Basin in Nares Strait, at about 82°N (Heide-Jørgensen, 1988; Higdon, 2007). The population structure of killer whales in this region is not well known, although mammal-eaters appear to be common and are perhaps the dominant type (Higdon, 2007; Higdon *et al.*, 2012; Ferguson *et al.*, 2012b). Due to heavy ice conditions, killer whales from the Baffin Bay area are unlikely to enter the CAO.

The killer whale is a common species in the Norwegian Sea, where the population may count around 5000 individuals (Nøttestad and Olsen, 2004). These killer whales are of the fish-eating type, feeding mainly on herring of the large Norwegian spring-spawning stock. They move seasonally in conjunction with the spawning and feeding migrations of herring, and exhibit complex feeding behaviours including coordinated herding of herring schools into shallow



waters where they can be stunned and eaten (Øien, 1988; Similä *et al.*, 1996; Nøttestad and Similä, 2001; Nøttestad *et al.*, 2002; Nøttestad and Olsen, 2004). Killer whales are also found in the Barents Sea and around Svalbard. The population structure of killer whales in the northeast North Atlantic is not well known, although genetic studies and photo-identification of individuals are contributing important information to this end (e.g. Foote *et al.*, 2009, 2010, 2011; Kuningas *et al.*, 2014). Killer whales are commonly seen around Svalbard, both along the western and east coasts (Kovacs *et al.*, 2009), as well as farther east in the northern Barents Sea to Franz Josef Land. Whether these are of the mammal-eating type is not known. There is evidence suggesting that some killer whales from the Norwegian Sea area are generalist feeders that, in addition to herring and mackerel, also take marine mammals like seals (Stenersen and Similä, 2004; Foote *et al.*, 2009, 2010).

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## Annex 2: List of abbreviations

ACW	Alaskan Coastal Water
AD	Arctic Dipole
AnaW	Anadyr Water
AO	Arctic Oscillation
AOO	Arctic Ocean Oscillation
BOD	Biological oxygen demand
BSAW	Bering Shelf–Anadyr Water
BSW	Bering Shelf Water
C	Carbon
CAO	Central Arctic Ocean
CBMP	Circumpolar Biodiversity Monitoring Program of the Arctic Council
CDOM	Coloured dissolved organic matter
CFC	Chlorofluorocarbons
Chl	Chlorophyll
DBO	Distributed Biological Observatory
DIC	Dissolved inorganic carbon
DOM	Dissolved organic matter
dw	Dry weight
E	Irradiance notation
$E_k$	Light saturation index notation
EA	Ecosystem approach to management
EBM	Ecosystem based management
EEZ	Exclusive Economic Zones
EP	Export production
ETS	Electron transport system
EU	European Union
FEC	Focal ecosystem component
FYI	First-year ice
GPP	Gross PP
ICES	International Council for the Exploration of the Sea
IASC	International Arctic Science Committee
IEA	Integrated ecosystem assessment



IMO	International Maritime Organization
IUCN	International Union for the Conservation of Nature
IUU	Illegal, unreported, and unregulated
k	Extinction coefficient notation
LME	Large Marine Ecosystem
MYI	Multi-year ice
N	Nitrogen
NAO	North Atlantic Oscillation
NCP	Net community production
NP	New production
NPP	Net PP
O <sub>2</sub>	Oxygen
PAME	Protection of the Arctic Marine Environment Arctic Council working group
PAR	Photosynthetically active radiation
PICES	North Pacific Science Organization
POC	Particulate organic carbon
PON	Particulate organic nitrogen
PP	Primary production
RCP	Representative concentration pathway
RP	Regenerated production
RV	Research vessel
S	Salinity
s. d.	Standard deviation
SHEBA	Surface heat budget of the Arctic Ocean
SIMBA	Sea ice model for bottom algae
T	Temperature
UN	United Nations
UNCLOS	UN Convention on the Law of the Sea
UNFSA	UN Fish Stocks Agreement
WGICA	Joint ICES, PICES, and PAME Working Group on Integrated Ecosystem Assessment of the Central Arctic Ocean
WSC	West Spitsbergen Current
ww	Wet weight