ARCTIC ECOLOGY

EDITED BY DAVID N. THOMAS

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Preface

Sitting down to write this brief introduction is overshadowed by recent reports of a record highest temperature of 38 °C within the Arctic Circle. Undeniably the Arctic is warming at an alarming rate and we can foresee climate and environmental records in the whole region being routinely broken in even the short term. This book was never intended to be a book about the effects of global climate change on Arctic ecology, although we have included two fundamental chapters covering climate change in the Arctic (Chapters 2 and 3). This is not because that issue is not important, in fact it is arguably the region where change is amplified to the greatest extent. However, many statements we make about climate change effects will quickly be out of date and there are more easily and regulated updated resources than a book like this (cf. Box et al. 2019; IPCC 2019; Overland et al. 2019). Instead our aim was to produce a book that seeks to systematically introduce the diverse array of ecologies within the Arctic region, highlighting some influences of global climate change where appropriate.

The Arctic is often portrayed as being isolated, but the reality is that the connectivity with the rest of the planet is huge, be it through weather patterns, global ocean circulation, and large-scale migration patterns to name but a few. A more immediate connectivity is evident in Figure P.1. From 2008 this illustration well reflects the connectivity in terms of human populations associated with the perimeter of the Arctic Circle. It does not leave much to the imagination as to how this will change over the next decades.

This project was conceived in October 2012 and gelled during 2013. The need for this book was obvious then, but over the intervening seven to eight years its pertinence has grown immensely. Our aim, as in 2012, is that the book stimulates a wide audience to think about the Arctic by highlighting the remarkable breadth of what it means to study its ecology. The Arctic is rapidly changing and by the time a second edition of this book is published, it will be a very different place than it is today. Understanding the fundamental ecology underpinning the Arctic is paramount to understanding the consequences of what such change will inevitably bring about.

A final comment is that although we have tried to synthesize current understanding, for many habitats within the Arctic we are still only beginning to understand some key processes and mechanisms. It is hoped that this book will spur the imagination of many readers to go on to dedicate their efforts so that some of the conclusions outlined here are confirmed, or even disproven, and the many knowledge gaps filled.

David N. Thomas
Anglesey, July 2020

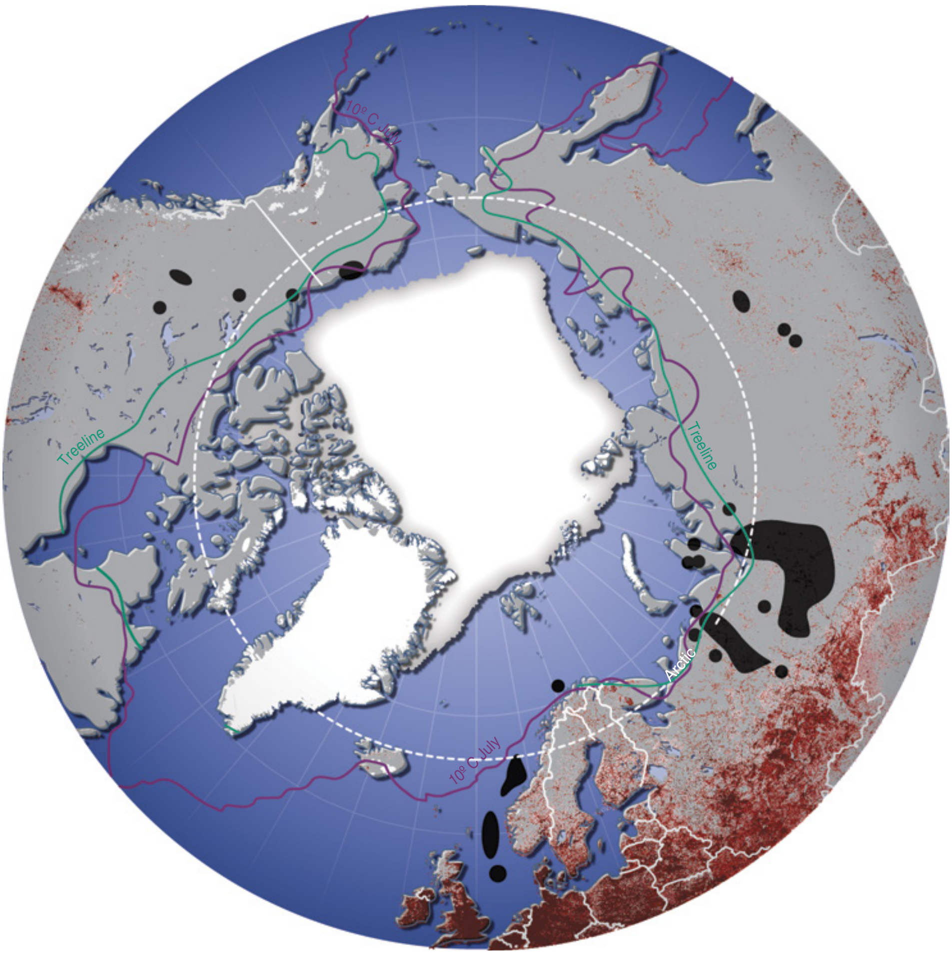

Figure P.1 A view of the Arctic showing the Arctic Circle and human population density in red and large oil fields in black. *Source:* Hugo Ahlenius, UNEP/GRID-Arendal. https://www.grida.no/resources/7143.

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1

What Is the Arctic?

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1.1 Setting the Scene

The aim of this chapter is to "set the scene" for the rest of the book. The "actors" are climate, glaciers, lakes, streams, rivers, sea ice, pelagic, benthic, plants, soil, birds, and mammals. In which ways is the Arctic different? How was it discovered and explored? How large is it? What is found there? What is the Arctic providing in terms of natural resources and ecosystem services? And finally, what are the biotic changes due to various major drivers including global climate change?

The name Arctic derives from the Greek word *Arktikós*, meaning the land of the North. It relates to *Arktos*, the Great Bear, which is the star constellation close to the Pole Star (CAFF 2013). For a long time, the Arctic has fascinated people and such intrigue extends back some three millennia according to notes and drawings in early Chinese culture. Since then the Arctic has been mapped and its landscape, biota and native people discovered and documented. Visions, bold ideas and the search for natural resources stimulated much of this endeavor. It took hundreds of years to get a reliable picture of this "unknown and mysterious" far-away land. Many of the "mysteries" are now resolved, but the immense beauty is still there, and it is safe to say that many exciting things and phenomena remain to be discovered by coming generations of Arctic explorers.

Today many of these northern realms are possible to reach within a few hours. Anyone with internet and access to global maps can "explore" even the most remote corners of the Arctic in an armchair. In addition, modern field and laboratory techniques have given us more powerful tools for certain advanced research than have ever before existed. This chapter will give a brief overview of the Arctic: Although trying to avoid generalities, some cannot be escaped – remember Aldous Huxley's (1894–1963) statement in *Brave New World* (1932) "Generalities are intellectually necessary evils."

Arctic Ecology, First Edition. Edited by David N. Thomas.

1.2 In Which Ways Is the Arctic Different?

The Arctic is situated at *high latitudes* and includes land, ice, rivers, lakes, and seas above the boreal forest and ends at the North Pole. The Arctic is to a large extent covered by *ice and snow*. Generally, it is a *cold* region of the planet with *four distinct seasons*. However, the Saami people, with a culture strongly connected to reindeer herding, divide the year into eight functional seasons. Winters and summers are cold, but the summer can be 30–50 °C warmer than the winter. For much of the Arctic there is a continuous winter night at mid-winter, but at mid-summer the sun shines both day and night. In spring, the bright light demands sunglasses. Many artists have stressed how different the light is in the Arctic compared with what is found elsewhere. The Arctic is generally silent except during a few weeks in spring and fall when the migrating birds arrive and leave.

In the Arctic ice dominates as icebergs, glaciers, ice sheets, ice-covered lakes, rivers, seas, and oceans as well as the frozen subsoil, the permafrost (Figure 1.1). The land is without trees and is generally divided into two major vegetation zones, polar desert and tundra. There are peculiar geometric patterns on the ground as well as heap-like structures with an ice core. Winds and waters transport nutrients, pollutants, living plants, and animals from the south and so the Arctic is not isolated in the way that the Antarctic is. Human communities and settlements are small and most of the Arctic is not populated but if it is, only sparsely.

The Arctic is changing now but always has been. The most dramatic time was when the Arctic was formed by rotation and migration of tectonic plates. During the ice ages it was totally covered by ice and snow. Between these cold periods there were warmer times with steppes and forests inhabited by mammoths, tigers, and rhinoceros. Today there is intense discussion about how serious the changes we have noted in modern times really are, and sometimes some of this controversy depends upon what is studied, where and for which

Figure 1.1 Iceberg in spring. Devon Island. *Source:* Photo: Kjell Danell.

Table 1.1 Some Arctic explorers and expeditions up to 1900.

Years	Travelers	Area
c. 330 BCE	Pytheas of Massilia	The waters north of Scotland
c. 879 CE	Floki Vilgerdarson	Iceland
983	Erik the Red	Greenland
1000	Leif Eriksson	Newfoundland
1000–1200	Novgorodians	White Sea
1594–1597	Willem Barents	Spitzbergen, Novaya Zemla
1615–1616	William Baffin and Robert Bylot	Hudson Bay, Baffin Bay
1725–1734	Vitus Bering	Kamchatka
1825–1827	John Franklin	Coronation Gulf – Prudhoe Bay
1845	John Franklin	Northwest Passage
1878–1879	Adolf Nordenskiöld	Northeast Passage
1888	Fridtjof Nansen	Greenland
1893–1895	Fridtjof Nansen	Arctic Ocean

time period. However, beyond this, there are without doubt many alarming observations of significant deviations from normal, and which demand our attention and action. Science and gathering traditional knowledge help us to understand what is going on, and perhaps may help us mitigate serious unwanted changes.

1.3 How Was the Arctic Discovered?

The Arctic was discovered tens of thousands of years ago by small groups of humans who migrated to it. During the last centuries many Arctic expeditions carved their names into the Arctic history (Table 1.1). The first true discoverers of a given area are often difficult or impossible to determine (Levere 1993; Liljequist 1993).

The Greek, Hippocrates (c. 460–370 BCE) never visited the Arctic, but he drew a map of the northern land where the Hyperboreans lived. They were too far away to be reached by anyone. Another Greek, the sailor Pytheas (c. 380–310 BCE), was the first Arctic explorer as far as we know. Around 325 BCE he sailed to search for tin, which was used for the production of bronze and he found it in Cornwall, and during the voyage he was told about the mysterious northern land of Thule. Pytheas sailed north and after a week he reached a frozen sea. He reported polar bears and what could have been the Aurora Borealis and the midnight sun. Unfortunately, the exact route he sailed is not known.

The Vikings were early Arctic explorers of North America, Iceland, Greenland, and eastern areas too. The Pomors, Russian settlers and traders at the White Sea, started exploration of the Northeast Passage as early as the eleventh century. In 1553, Russians founded the Pechenga Monastery on the northern Kola Peninsula, from which the Barents Region, Spitzbergen, and Novaya Zemlja were explored. A settlement on Yamal Penisula was

Table 1.2 Some examples of the different bases for defining the extension of Arctic.

1)	Arctic Circle, 66.3°N
2)	Mean summer temperature of no more than 10 °C
3)	Permafrost
4)	Lakes and sea ice-covered
5)	Absence of trees
6)	Vegetation zones
7)	National borders
8)	Practical solutions

established in the early sixteenth century and Russians reached the trans-Ural as well as northern Siberia. It is not possible to describe the exploration of all Arctic lands here, but there are many fascinating stories to read (e.g. John Franklin's travel on the Northwest Passages in 1845 and Salomon August Andrée's polar expedition by balloon in 1896–1897).

In 1878 the Finnish–Swedish explorer Adolf Erik Nordenskiöld (1832–1901) managed to sail through the Northeast Passage with his ship *Vega*. The Northwest Passage was also traversed in 1906 by the Norwegian Roald Amundsen (1872–1928) on the herring boat *Gjøa*. The first undisputed sighting of the Pole was made in 1926 from the airship *Norge* by Roald Amundsen and others.

More recently of significant importance for the exploration of the Arctic has been the International Polar Years. During the first one, 1882–1883, 12 meteorological stations were established. Fifty years thereafter, the Second International Polar Year took place and among other activities, 94 arctic meteorological stations were set in place. The Fourth International Polar Year, 2007–2008, involved more than 10 000 scientists from more than 60 countries engaged in over 170 research projects (Allison et al. 2007).

1.4 How Large Is the Arctic?

Because of the many different definitions of the Arctic (Table 1.2) various figures for its size are given. Commonly, around 10 million km^2 for the land between the closed boreal forest and the Arctic Ocean is used (The Millennium Ecosystem Assessment 2005). The Arctic Ocean is larger, 14 million km^2. However, some of the map projections mislead us and make the Arctic seem much larger on the map. This is especially true when the drawings do not take into account that the distances between the latitudes get smaller toward the north. The circumference of the Equator is around 40 000 km and the 70°N parallel is only about 13 750 km (Nuttall and Callaghan 2000).

1.5 What Is in the Arctic?

1.5.1 Arctic Haze and Ice Fog

During winter, the Arctic receives air masses with pollution from mid-latitudes due to emissions from the burning of fossil fuel and industrial processes; this is called Arctic haze. Ice fog is more local and occurs around −30 °C and during situations with significant temperature inversions. Water vapor from for example trucks and heating systems condense into droplets which supercool or freeze (Nuttall and Callaghan 2000; AMAP 2003, 2011a).

1.5.2 Aurora Borealis

The Arctic as well as the Antarctic have "windows" to space. The atmosphere of the sun and our atmosphere are brought into contact by the earth's magnetic field (Nuttall and Callaghan 2000). In the Arctic, the Aurora Borealis is most common in the zone 20°–25° from the Magnetic Pole, which is not exactly the same as the geographic North Pole. An explanation for the phenomenon is that high energy electrons and protons are accelerated down the magnetic field lines to collide at 70–200 km height with our neutral atmosphere and release numerous electrons and ionizing atoms and molecules. When these are transformed back to their ground states, various colors of light are emitted and we see the Aurora.

Under extreme conditions in the atmosphere there are many optical and acoustic phenomena due to microscopic ice crystals suspended in the air which change how light and sound travel. Under such conditions, conversations between humans can sometimes be heard up to three kilometers away. Further, snow, ice, and layers of air with different characteristics produce illusions. Together, these conditions form a base which may account for many "Arctic mysteries."

1.6 Climate and Weather

The climate is what happens over a longer time period, for example 30 years. Weather is the short-term variations and is what we experience when outside during a day. The climate and weather of the Arctic are extreme, and the limited sunlight makes these environments inhospitable for most plants, animals, and humans. The snow-free seasons are short and range from one to three months. The warmest month, often July, has a mean temperature below 10–12 °C in many places. Winters are cold and temperatures can go down to −60 °C or more in continental parts. The difference in temperature between the coldest and the warmest months is at extremes 80 °C or more (CAFF 2013).

In the Arctic there are two main types of climate, maritime and continental. There are large variations in time and space. The Arctic is part of the global circulation patterns of the atmosphere and oceans. The drivers are the sun and the difference in temperature between the Equator and the poles. Large amounts of solar energy are received in the equatorial regions and much of it is transported by air masses and oceans north- and southwards. From the poles, energy goes back to space. On the other hand, cold water current and air masses from the poles go to warmer regions (The Millennium Ecosystem Assessment 2005). "Arctic" temperature conditions can occur at relatively low latitudes (e.g. at 52°N in eastern Canada), but on the other hand forestry and agriculture is practiced north of the Arctic Circle in Fennoscandia.

1.7 Ice and Snow

There are many types of ice and snow on land and water in the Arctic. The land ice sheets cover 50 000–100 000 km^2 and can be up to several thousand meters thick. The ice can flow in all directions from the center. Within the Arctic, the Greenland Ice Sheet is the largest and represents about 15% of the total area of all glaciers in the world. Its mean thickness is around 1500 m with a maximum of 3200 m. It has been estimated that the age of the base is over 100 000 years old. This is the reason for drilling in this unique frozen archive to collect information on past events. Glaciers are smaller ice masses, often less than 8000 km^2.

The average cover of sea ice varies between $6.5 \times 10^6\,km^2$ in September and $15.5 \times 10^6\,km^2$ in March (Figure 1.2). It controls the exchange of energy and mass between the atmosphere and ocean (Chapter 10; AMAP 2011b; Laybourn-Parry et al. 2012; Thomas 2017).

1.8 Permafrost, Polygons, Pingos, and Palsas

There is continuous permafrost in the Arctic, and it is present under all land and even below the continental shelves. Permafrost is a substrate which has been at or below 0 °C for at least two years in a row (The Millennium Ecosystem Assessment 2005).

Figure 1.2 Sea ice in spring. Kent Peninsula. *Source:* Photo: Kjell Danell.

The annual freezing and thawing processes result in repeated expansions and contractions of soils. During freeze–thawing from the top, the larger particles move upwards and the finer ones move down. This sorting may produce circles and polygons, often of very striking orthogonal or hexagonal patterns on the ground (Figure 1.3). Such processes also form more distinct landform, for example boulder fields, pingos, and palsas. A pingo is a continuous frost mound which can be several tens of meters in height, has a massive ice core and is covered with soil and vegetation. A palsa is similar and occurs in peaty, permafrost-dominated material. Its height ranges from 0.5 to 10 m and it has a width of over 2 m.

Most of the Arctic permafrost is found on Greenland; 80% of Alaska and about 50% of Russia and Canada are covered. There is little information on the thickness of permafrost, but it reaches 400–1000 m. The thickness decreases southwards in parallel with an increase in the depth of the active layer, which ranges from 0.3 m in the High Arctic to over 2 m in the southern parts. The top three meters of permafrost soils contain more than twice the amount of carbon as the atmosphere (CAFF 2013), so thawing permafrost may further influence global warming.

1.9 Animals, Plants, and Fungi

The Arctic biota contains more than 21 000 species of mammals, birds, fish, invertebrates, plants, and fungi with lichens included. In addition, there are numerous known and unknown endoparasites and microbes. Some of the Arctic species have become icons, e.g.

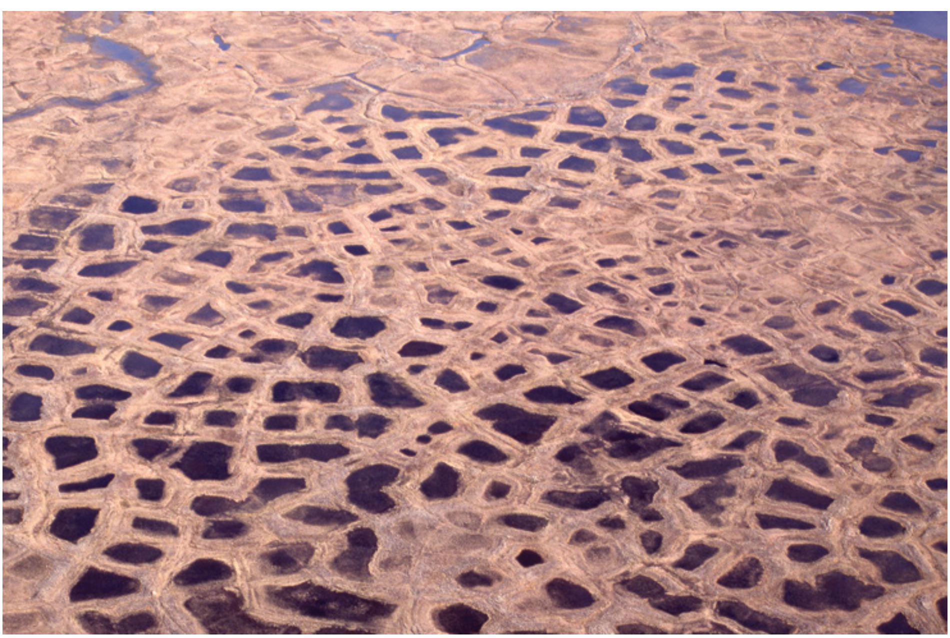

Figure 1.3 Wetland polygons. Chatanga. *Source:* Photo: Kjell Danell.

Arctic fox, caribou/reindeer, muskox, narwhal, walrus, ivory gull, and snowy owl (Figure 1.4; Blix 2005; Pielou 2012; CAFF 2013; Crawford 2014).

Mammals: About 70 terrestrial and 35 marine species are found in the Arctic, which represents 1 and 27%, respectively, of the global species pool of approximately 4000 species; in all 2%. Out of the totals, 19 terrestrial and 11 marine mammalian species are predominantly Arctic (CAFF 2013). The species richness is generally higher in the Low Arctic than in the High Arctic. The highest numbers of species are found in areas which were not glaciated during the last ice age, for example Beringia. For the marine mammals, species richness is highest in the Atlantic and Pacific sectors.

Examples of human translocations of mammals are bison, muskox, and muskrat. Human-induced global extinctions include Steller's sea cow and populations of Atlantic gray whale and Northeast Atlantic northern right whale. Local extinctions have occurred in many places, but some such as walrus, beluga whale, and large terrestrial predators are now recovering from heavy hunting. Significant northern range expansions during the last decades are shown by moose, snowshoe hare, and red fox. An endangered mammalian species, according to the International Union for Conservation of Nature (IUCN) criteria, is the Pribilof Island shrew (CAFF 2013).

Birds: About 200 bird species occur regularly in the Arctic, which is about 2% of the global total but only a handful of these birds stay year-round. Approximately one fourth of the total bird species are marine. Focusing on the Arctic, we can regard about 80 as freshwater and terrestrial birds, and about 25 as marine birds. The majority of the Arctic species are waterfowl, shorebirds, and seabirds. The Arctic is now the home for 30% of the world's shorebird species and two thirds of the global numbers of geese (CAFF 2013). Highest species richness

Figure 1.4 Reindeer antlers. Northwestern Taymyr Peninsula. *Source:* Photo: Kjell Danell.

is found in the Bering Strait region. In general, Arctic birds are more long-lived and often more specialized feeders than birds in other areas. Most Arctic seabirds nest in colonies, often in spectacular numbers. There are nine avian raptor species and two owls which are often partly dependent upon the abundance of lemmings and voles for good reproduction (Chapter 14). The great auk is extinct, the Eskimo curlew is probably extinct, and the spoon-billed sandpiper is close to extinction. Threatened species are the lesser white-fronted goose, red-breasted goose, bristle-thighed curlew, and Siberian crane (CAFF 2013).

Amphibians and reptiles: Only five amphibians and one reptile, a lizard, are found in the low Arctic. All species are considered to be stable.

Fish: There are about 250 marine and 127 anadromous and freshwater fishes in the Arctic. Together they constitute about 1% of the global fish pool with no difference between the groups. Of the first mentioned group there are about 80 species classified as mainly Arctic and of the second group about 60. The highest species richness is found in the Arctic gateways to the Atlantic and Pacific Oceans. There are no clear examples of extinct Arctic fish species. The IUCN status of the Arctic fish fauna has not yet been evaluated (CAFF 2013). Many fish species have been translocated, especially salmonids.

Terrestrial and freshwater invertebrates: There are upwards of 4750 species of terrestrial and freshwater invertebrates in the Arctic, but many additional species certainly remain to be described. The most species-rich groups are amoebae, rotifers, water bears, water fleas and copepods, ostracods, enchytraeid worms, eelworms, spiders, springtails, mites, and insects. For example, springtails are more common in the Arctic than expected and insects are less common. Endemism varies greatly between groups. For example, it is 31% for one group of mites and 0% for stoneflies (CAFF 2013). A group of insects which summer travelers cannot avoid are the mosquitos.

Marine invertebrates: About 5000 species of marine invertebrates are found in the Arctic, microbes excluded. Several areas are under-sampled, so estimates are uncertain. Around 90% of the fauna known today are benthic and compared with other marine areas in the world, the Arctic has an intermediate species richness. There are few endemic species. One of the invasive species is the red king crab from the Barents Sea (CAFF 2013).

Plants: Of the vascular plants about 2200 species are Arctic, about 1% of the global number. About 5% of the Arctic flora is constituted of non-native species, endemic species account for about 5% (CAFF 2013). No native species are known to have gone extinct due to human activities. The number of bryophytes is around 900; 6% of the global total. For terrestrial and freshwater algae more than 1700 species are reported, estimates for marine algae are of more than 2300 species.

Fungi: The total number of fungi in the Arctic is about 4300; 2030 macrofungi and 1750 lichens. This corresponds to about 4% for the total number of fungi in the world and c. 10% of the global lichen pool. Most species seem to occur throughout the Arctic and there are few species classified as endemic (CAFF 2013).

1.10 Arctic Ecosystems

The Arctic is situated around a mainly ice-covered ocean, the Arctic Ocean. It is connected to the Atlantic by a wide passage, and a narrow opening to the Pacific Ocean by the Bering

Strait (Sakshaug et al. 2009). On one side of the Arctic Ocean, there is the northern part of Eurasia with a long and relatively straight shoreline with few peninsulas and islands. On the other side, there is North America with a more fragmented shoreline. One fifth of the world's total coastline, about 177 000 km, is found in the Arctic (CAFF 2013). The Arctic represents a wide variety of landscapes with mountains, glaciers, plains, rivers, lakes, wetlands, and polar deserts (Figure 1.5). Different seascapes occur from the shallow coastal areas to the deep ocean reaching a depth of about 5 km.

Here, we divide the Arctic ecosystem into terrestrial, freshwater, and marine ecosystems. There are productive and species-rich habitats between these major ecosystems, e.g. tidal flats. However, we should always keep in mind that the Arctic is an integrated ecosystem. During the Quaternary Period, the Arctic ecosystem was profoundly molded by climate during more than 20 cycles of glacial advances and retreats in parallel with changes in sea-ice cover (CAFF 2013). Still, it is a young ecosystem.

1.10.1 Terrestrial Ecosystems

The Arctic land covers about 5% of the global land surface (CAFF 2013). The main landforms are mountains and plains or plateaus. At coasts dominated by mountains we can find dramatic fjord landscapes. Sharp mountain peaks characterize young mountain ranges such as the Canadian Rockies, while the older Urals have more rounded peaks. Active volcanos are mainly located in Beringia and Iceland. The plains/plateaus are covered by deposits of glacial, alluvial, and marine origin.

Figure 1.5 Polar desert. Ellef Ringnes Island. *Source:* Photo: Kjell Danell.

Table 1.3 Ecosystem types in the Arctic, in million km^2.

Ecosystem types	Total	Canada	USA	Greenland	Eurasia
Ice	2.50	0.25	0.10	1.95	0.20
Barrens	3.01	1.90	0.11	0.12	0.88
Tundra	5.06	1.14	0.80	0.07	3.05

Source: Hassan et al. (2005, p. 720).

Ice covers a minor part of the Arctic (Table 1.3 and Figure 1.6). Barrens are partly free from vegetation in contrast to the tundra. The tundra is the largest natural wetland of the world and covers almost half of all the Arctic land (The Millennium Ecosystem Assessment 2005).

The tundra vegetation type is not unique for the Arctic because it also occurs in the upper boreal zone as well as in alpine areas (CAFF 2013). The high latitude tundra is found in the High Arctic, Low Arctic, and Sub-Arctic where they are inhabited by somewhat different functional groups of plants. For most Arctic plant taxa, the species richness is low. This is explained by the relatively young age of the ecosystem (around three million years), low solar energy influx, extreme climatic variability and decreasing biome area with increasing latitude (CAFF 2013). Many of the northern species have a circumpolar distribution and occur in a wide range of habitats. Particularly the temperature is responsible for the composition of the biota. All this leads to a rather uniform biota in the Arctic, which becomes more diverse closer to the tree line. The topographic variation between lowlands and

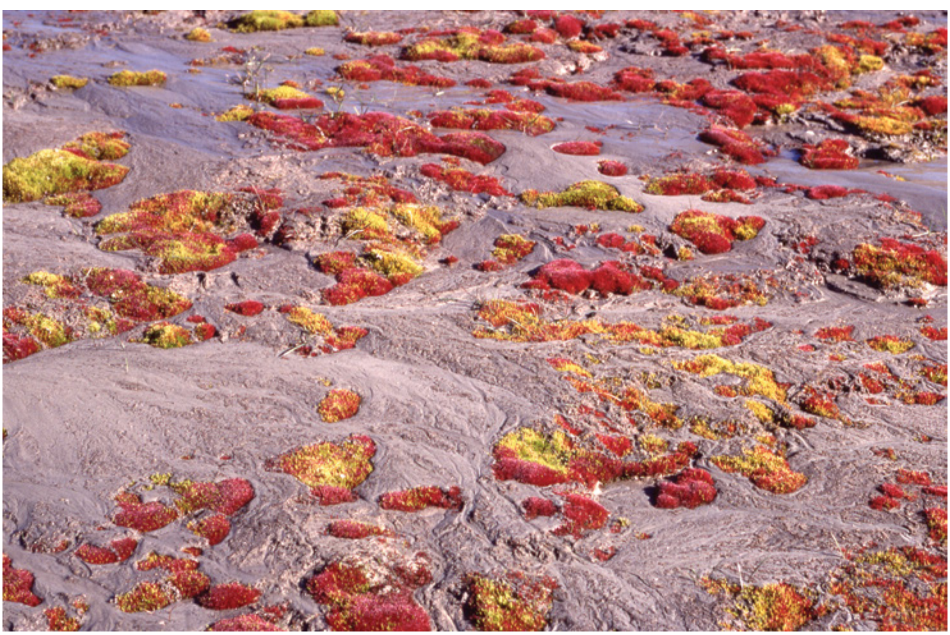

Figure 1.6 Mosses near the ice front. Melville Island. *Source:* Photo: Kjell Danell.

mountain adds more biodiversity to the landscape (Nuttall and Callaghan 2000). In the rather uniform landscapes, we can notice greener patches when the composition of nutrients, water, and light are optimal. On a much smaller scale, such green patches occur around things such as a carcass of a muskox (Figure 1.7).

There is a short productive summer season, low primary productivity and low biomass per area compared with southern latitudes. However, a large proportion of underground biomass is often found in the Arctic. Plants and fungi are often small and compact and have slow growth, asexual reproduction, furry or wax-like coatings, and long life cycles. At low temperatures, their photosynthesis is higher than respiration.

Invertebrates have small average body size. Migratory birds visit the Arctic to breed and feed intensively during the summer burst of productivity, both on land and on sea. Many of the birds spend more than half of the year outside the Arctic. Wintering areas occur in all parts of the world, even in Antarctica. Mammals show often short extremities, winter whiteness, insulation by fur and fat, freeze tolerance, hibernation, and stay under snow. Many mammals fluctuate dramatically in numbers between years (CAFF 2013).

1.10.2 Freshwater Ecosystems

Arctic freshwater ecosystems are of three main types: flowing water (rivers, streams), permanent standing water (lakes, ponds), and wetlands (fens, marshes). The large, north-flowing rivers from the interior of the continents transport heat, water, nutrients, contaminants, sediment, and biota into the Arctic Ocean. The Arctic Ocean Watershed covers 16 million km^2 and contains four of the largest rivers on Earth: the Lena, Ob and

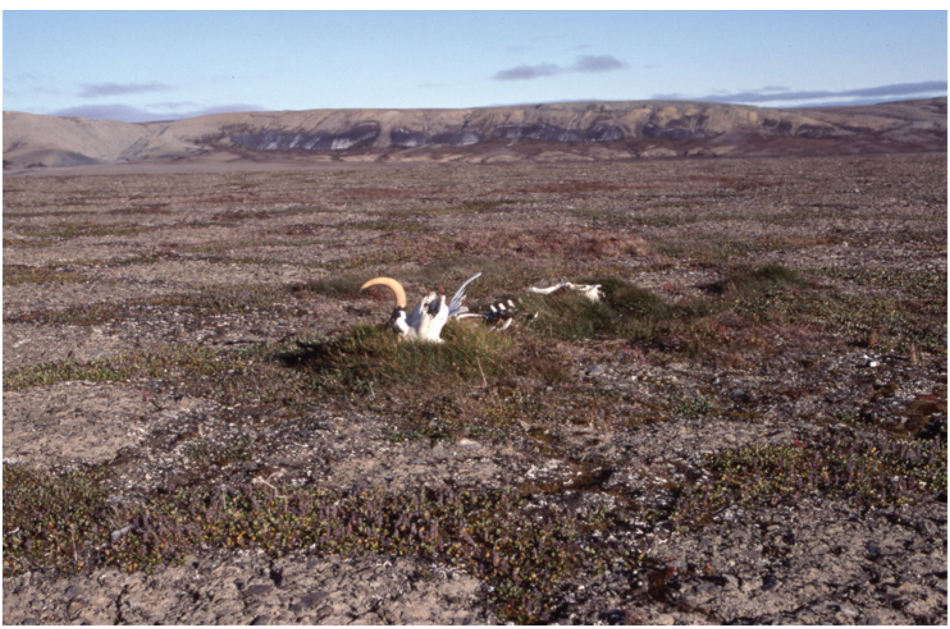

Figure 1.7 A dead muskox creating a green patch on the nutrient-poor tundra. Melville Island. *Source:* Photo: Kjell Danell.

Yenisei in Siberia, and the Mackenzie in Canada. They flow through a variety of boreal and arctic landscapes. About 25% of the world's lakes are situated in the Arctic (Chapter 8). Wetlands, more common in the south, cover some 10% of the land area. They are almost all created by the retention of water above the permafrost. Together with lakes and ponds, arctic wetlands are summer homes to abundant populations of migratory birds which utilize the abundant food resources of invertebrates during spring and summer (Figure 1.8; Vincent and Laybourn-Parry 2008).

The systems are characterized by high seasonality and are in many cases ephemeral (CAFF 2013). The permanent standing water ranges from large and deep lakes to shallow tundra ponds that freeze to the bottom in winter. The species richness of freshwater species and their productivity decrease northwards. Zooplankton species are few or even absent in some arctic lakes because of low temperatures and low nutrient availability. The fish fauna is generally of low diversity, ranging from 3 to 20 species, with Arctic char, pike, trout, and salmon important as human food resources.

Adaptations of the Arctic freshwater species include diapause and resting stages, unique physiological mechanisms to store energy, an ability to grow and reproduce quickly under short growing seasons, and they often have extended life spans. Migrations are common. A special kind of migration is shown by diadromous fish which spend each summer in the sea to fatten up, or live there for most of their lives before going up to rivers to reproduce (CAFF 2013).

Figure 1.8 Brent geese. Pechora Bay. *Source:* Photo: Kjell Danell.

1.10.3 Marine Ecosystems

The Arctic Ocean is the smallest among the oceans (CAFF 2013). The continental shelves less than 200 m deep around the deep central basin occupy slightly more than half of the ocean. These shelves constitute about 30% of the global total shelf area. The maximum recorded depth is 5441 m. The deep-sea Arctic benthos is less well known, but the few available studies from the central Arctic Ocean report extremely low benthic species biomass and richness compared with the shallow shelves. Over 90% of the known Arctic marine invertebrate species live at the seafloor and are regarded as benthic. Sediment type, adequate attachment sites, and bottom current flows are important factors for the distribution and abundance of the fauna. In general, heterogeneous bottom sediments harbor a higher benthic diversity and production. The most species rich taxon in the Arctic seas are crustaceans, especially amphipods, and after that it is polychaetes with about 500 species (Chapter 12).

The Arctic Ocean differs in several respects from other oceans. It is dominated by a seasonally formed ice cover, and in the central area there is a multi-year pack ice. The ice greatly affects light conditions for organisms in the water below, but it also plays an important role in heat exchange between water and atmosphere, which is vital for global circulation. Ice is also a habitat for seals and polar bears (Figure 1.9). At the edge of the pack ice, polynyas, there is a high production of phytoplankton and ice algal blooms develop providing energy and material to zooplankton and higher trophic levels including fish (CAFF 2013).

Figure 1.9 Polar bear during ice break-up. Cape Bathurst. *Source:* Photo: Kjell Danell.

The two ocean gateways facilitate interchanges with the Atlantic and Pacific Oceans. Several rivers transport freshwater, nutrients, and pollutants into the Arctic Sea. In addition, freshwater is added from melting sea ice. This results in a stratification of the sea water with the least salt water on top. The stratification limits nutrient transport upwards from the nutrient-rich deep waters, and as a consequence depresses primary production in the upper water column (CAFF 2013).

Arctic sea ice provides a unique habitat for a diverse biological community of e.g. viruses, bacteria, algae, and meiofauna. The ice offers resting and breeding spaces for marine mammals and birds as well as a feeding ground and refuge to escape predation for larger invertebrates and fish (Chapter 10).

In general, the Arctic marine ecosystems are simple and with relatively low productivity and biodiversity and the species here are often long-lived and slow growing (Figure 1.10). Some arctic marine areas, however, have very high seasonal productivity, and the subpolar seas have among the highest marine productivity in the world. In the Bering and Chukchi Seas, for example, the nutrient-rich upwelling areas support large concentrations of migratory seabirds and diverse communities of marine mammals. The Barents and Bering Seas hold some of the world's richest fisheries.

1.10.4 Humans

Humans are a part of the Arctic ecosystem since at least the last ice age, but the history of northern humans is still unclear and controversial. Remains older than 12 000 years have been collected in northern Fennoscandia, Russia, and Alaska. In the eastern European Arctic, Paleolithic settlements have been dated to about 40 000 years ago. In Eurasia and

Figure 1.10 Mussel shells and seaweeds on the seashore, Kent Peninsula. *Source:* Photo: Kjell Danell.

across the North Atlantic, groups of humans have sailed northward over the past several centuries, colonizing new lands such as the Faroe Islands and Iceland and encountered colonized areas elsewhere.

The Arctic people are adapted to the harsh environments, keeping life in synchrony with the seasonal changes and the great migrations of fish, birds, and mammals (Figure 1.11. The carrying capacity of the Arctic cannot support dense human populations. However, a recent population growth has taken place due to integration with southern economies and societies, modern medicine, and technology. One example is Greenland, where the population has increased 10-fold since contact with Europe about 300 years ago (CAFF 2013).

The human population of the Arctic is now two to four million depending upon how the Arctic borders are drawn. These people include indigenous peoples and recent arrivals, herders and hunters and city dwellers. During the twentieth century, immigration increased dramatically. Non-indigenous persons came to outnumber indigenous ones in many regions. These immigrations were driven by search for natural resources, for example fish, fur, gold, whales, oil, and gas. This resulted in social, economic, and cultural conflicts between groups of people. Indigenous claims to land and resources have been addressed to some extent in land claim agreements. Some largely self-governed regions within states have been formed and discussions continue. Over the past decade, the human population has increased significantly only in three areas: Alaska, Iceland, and the Faroe Islands.

Figure 1.11 Nomads at Kamchatka in summer. *Source:* Photo: Kjell Danell.

Rapid declines in population have taken place across most of northern Russia, but lesser declines or modest increases are recorded in other parts of the North.

1.11 Which Natural Resources and Ecosystem Services does the Arctic Offer?

Natural resources have been the backbone for the exploration of the Arctic. The first explorers discovered a high abundance of whales, seals, furbearers, fish, and birds which could be harvested and sold in markets further south. In the twentieth century, more minerals and deposits of oil and gas were discovered and exploited. The Arctic also became an important strategic military area and bases and facilities were established. All these new activities provided employment and affected the distribution of humans and other animals. In recent decades, tourism has added another sector to the economies of many communities in the Arctic. The public sector, including government services and transfer payments, is also a major part of the economy in nearly all areas of the Arctic and are responsible in some cases for over half the available jobs. In addition to the cash economy of the Arctic, the traditional subsistence and barter economies are major contributors to the overall well-being of the region, producing significant value that is not recorded in the official statistics.

Agriculture: Agriculture is a relatively small industry in high-latitude regions and consists mostly of forage crops, vegetables, and small grains. Further, there is the raising of traditional livestock (cattle, sheep, goats, pigs, and chickens) and the herding of reindeer. Major climate limitations include short growing seasons, and the long and/or unfavorable winter can limit the survival of many perennial crops. Grasses often do better than grains. On the other hand, products of high quality can be produced. In the north there are generally low numbers of pathogens which favors production of, for example, seed potatoes for export to southern areas. In addition to limitations by climate, agriculture is also limited by infrastructure, a small and older population base, remoteness from markets, and lack of temporary workers.

Cooling the Earth: The Arctic plays an important role in cooling the Earth. This is done by reflecting incoming radiation by ice and snow and by radiating back to the atmosphere heat transported by wind and water streams from warmer areas. The heat loss from the polar regions is more than twice the solar input per square meter. When snow and ice disappear, and reflection (albedo) is reduced, the annual energy absorption increases. If the tundra is replaced by forests, heat absorption increases even more. Thus the ecosystem feedbacks are sensitive, complex, and difficult to predict (The Millennium Ecosystem Assessment 2005).

Harvestable animals: Fish, birds and mammals were harvested by the indigenous people for millennia. Some animals, e.g. bears, were harvested less often because of their great symbolic value. The limited and sporadic availability of edible native plants and poor conditions for agriculture made the Arctic cultures highly dependent upon hunting and fishing. For humans, the Arctic offers generally fewer food alternatives than the boreal forests. Further, longer periods of extreme weather can make hunting and fishing difficult. During such severe conditions, whole cultures may have disappeared as suggested by archeological findings, for example in Greenland and the Canadian Arctic (CAFF 2013).

The wave of incoming people from the south, particularly during the seventeenth century and later, increased pressure on harvestable wildlife on land and water. During the whaling era, some whale species were driven to, or near, extinction. The presence of land predators in the Arctic forced the flightless great auk to the margins of the Arctic and on islands where polar bears, wolves, Arctic foxes, and humans were few. When European mariners reached their breeding grounds a few centuries ago, the great auk was driven to extinction (CAFF 2013).

The marine ecosystems of the Arctic provide a range of ecosystem services that are of fundamental importance for the sustenance of inhabitants in the coastal areas. Some of the richest fisheries on Earth are found here, particularly along the sub-Arctic fringes. These fisheries contribute to more than 10% of global marine fish catches by weight and 5% of the crustacean harvest, but the harvest of other species is small (CAFF 2013).

Many arctic animals are migratory and often aggregate and follow distinct migration routes. Their occurrence at a given area and time is therefore highly predictable. For example, caribou and salmon often occur in large numbers and are easy to shoot or catch. Furthermore, the migrants have often accumulated fat reserves which make them even more valued as food.

Reindeer herding supports many people in the north. The total number of domesticated reindeer is more than two million and the majority of them are found in Russia. The numbers in Fennoscandia are about 640 000, and in Greenland about 2000–3000. In North America there is about 10 000 in Alaska and 3000–4000 in the Northwest Territories. In the different regions the numbers have changed considerably over time and in different directions. Ecological and political reasons have been the main drivers. For example, reindeer was introduced into Alaska in 1892 by Saami herders and by about 1930 there were some 600 000 (CAFF 2013).

Mineral, oil, and gas: The Arctic has large mineral reserves, ranging from gemstones to fertilizers. Russia extracts the greatest quantities of these minerals, including nickel, copper, platinum, apatite, tin, diamonds, and gold, mostly on the Kola Peninsula but also in Siberia. Canadian mining in the Yukon and Northwest Territories and Nunavut is for lead, zinc, copper, diamonds, and gold. In Alaska, lead and zinc deposits are found in the Red Dog Mine, which contains two-thirds of the US zinc resources; gold mining continues. The mining activities in the Arctic are an important contributor of raw materials to the world economy. The Arctic has huge oil and gas reserves. Russia has large oil resources in the Pechora Basin, gas in the lower Ob Basin, and other potential oil and gas fields along the Siberian coast. Canadian oil and gas fields are mainly in the Mackenzie Delta/Beaufort Sea region and in the Arctic Islands. In Alaska, Prudhoe Bay is the largest oil field in North America. Other fields are located at Greenland's west coast and in Norway's arctic territories. With a greater access to areas previously blocked by permanent sea ice, further mineral deposits and oil and gas fields may become economically possible to extract.

Tourism: In the Arctic there are many attractions for tourists in all seasons. The winter sports, hiking, biking, canoeing, nature observations, photography, hunting, fishing, and the picking of berries and mushrooms are popular activities. Polar tourism can be divided into five segments: (i) mass tourism which is attracted to sightseeing in comfort, (ii) sport fishing and hunting, (iii) nature; (iv) adventure, and (v) culture and heritage (CAFF 2013).

Tourism is increasing in the Arctic, especially through more cruise ships. Such tourism can increase environmental awareness and support for nature conservation, but if not carefully managed it can lead to disturbance of animals and vegetation (CAFF 2013). Sustainable issues have to be addressed more firmly in tourism, and also in all the various forms of extraction of natural resources.

1.12 Biotic Changes in the Arctic

The Arctic, as well as other biomes, is subject to the effects of global climate change. The list of abiotic changes is long, e.g. increasing land and water temperatures, reduced and collapsing permafrost, glaciers and sea ice, changes in concentrations of greenhouse gases such as carbon dioxide and methane, acidification, eutrophication, and rise in sea level. The Arctic is part of global circulation systems, so significant changes in other parts of the world can be noted here and vice versa. The abiotic changes are described in detail in many of the following chapters. Therefore, the focus here is to give a short overview of some of the observed biotic changes in northern areas.

Distribution of species: invasive and non-invasive: We have noticed northward range extensions of several plant and animal species in recent time. Boreal species move into the Low Arctic, and Low Arctic species move into the High Arctic. Over a longer period, the High Arctic species will lose suitable habitats and become extinct. They can survive in the coldest areas at high elevation or in deep sea for some time. As humans have become more and more mobile, the transfer of species, as well as diseases, beyond their native ranges has increased. In addition, shipping and resource development corridors increase spread northwards, but to a lesser extent southwards (Figure 1.12; CAFF 2013).

Invasive species are intentionally or unintentionally human-introduced alien species that are likely to cause economic or environmental harm or harm to human health. At present, there are relatively few such species in the Arctic, but more species most likely will come with warming. All introduced plant and animal species are not classified as invasive. Over a dozen terrestrial non-native plant species occur in the Canadian Arctic and such species constitute 15% of the flora of Svalbard. An invasive plant species is the Nootka lupine occurring on disturbed sites on Iceland and southwest Greenland, but without spreading to the tundra vegetation so far. Other well-known examples of invasive species are the American mink and muskrat introduced into Europe for fur production; they have spread into the Eurasian Arctic and other regions.

Red king crab is a native species in the Bering Sea where it supports a high value commercial fishery. In the 1960s, it was introduced into the Barents Sea, and now supports a productive commercial fishery there. The crabs are expanding eastwards into Russia and westwards along the Norwegian coast and are expected to spread southwards. There is concern on its ecological impacts on the marine ecosystem because it feeds on a wide range of benthic organisms and may negatively affect recruitment of some fish species through predation. Numerous introductions of fish, mainly salmonids, into inland waters have occurred over hundreds of years to increase fishing for sport and subsistence. Fish prey, e.g. crustaceans, are introduced into new waters in order to increase fish production (CAFF 2013).

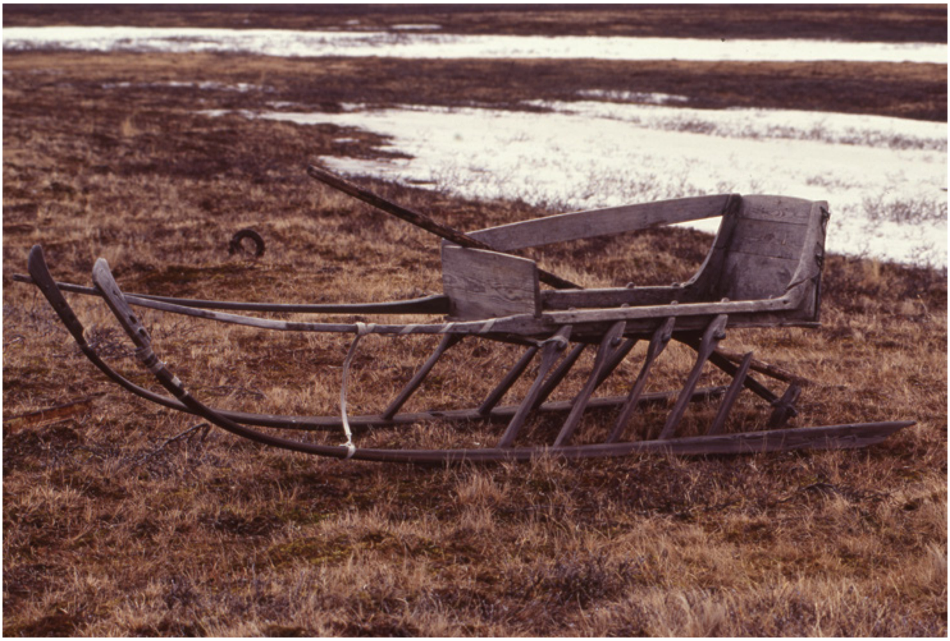

Figure 1.12 Reindeer sledge made only of wood. Western Yamal Peninsula. *Source:* Photo: Kjell Danell.

Harvestable animal species: Climate will improve conditions for a few animal species, have minor importance for others, and be negative for yet others. Many of these effects will not be obvious until later. Hooded seals and narwhal are regarded as most at risk, and ringed seals and bearded seals as least sensitive. The response of polar bear subpopulations varies geographically, but data are mostly lacking. In general, reduced sea ice causes lower body condition, reduced individual growth rates, lower fasting endurance, and lower reproductive rates and survival (IPCC 2014).

The decline in wild reindeer and caribou populations in some regions of about one third over the last decades may have been the result of both climate and human impact. Some of the large North American wild herds have for example declined by more than 75%, while other wild herds and semi-domestic herds in Fennoscandia and Russia have been stable, or even increased. More frequent rain-on-snow icing events and thicker snow-packs may restrict feeding of Arctic ungulates IPCC (2014).

Warming influences the complicated interplay between freshwater and marine systems, for example timing, growth, run size and distribution of several Arctic freshwater and anadromous fish. Some fisheries have shifted from harvesting one resource to another. For example, the fish landings in western Greenland and other parts of the North Atlantic have shifted from a strong dominance of Atlantic cod to northern shrimp. Significant changes in the Barents Sea have also taken place (CAFF 2013; IPCC 2014).

Freshwater ecosystems: Freshwater ecosystems are important trans-ecosystem integrators because they link terrestrial, freshwater and marine environments. They are undergoing significant change in response to the influence of both environmental and anthropogenic drivers (CAFF 2013). One such example is the increase in flow as well as shift in flow timing. Further, the surface-water temperature of large water bodies has warmed during the last 20 years, particularly for mid and high latitudes. Some of the consequences are delayed freeze-up, advanced break-up, thinner ice and changes in structure, increased water temperature, and earlier and longer-lasting summer stratification. The freshwater ecosystems are undergoing change because of increasing acidification, eutrophication, warming and pollution from local and remote sources, building of dams and other infrastructure, water withdrawal and over-fishing (CAFF 2013; IPCC 2014).

Marine ecosystems: The relative simplicity of arctic marine ecosystems, together with the specialization of many of its species, makes them potentially sensitive to environmental changes. During recent decades, scientists have noted a trend toward earlier phytoplankton blooms in about 10% of the area of the Arctic Ocean IPCC (2014). In general, the oceans have absorbed about one third of the anthropogenic carbon dioxide released to the atmosphere and the increased concentration of carbon dioxide contributes to acidification (CAFF 2013). Sea level rise has caused erosion in coastal areas and increased the input of organic carbon into the coastal waters, especially during storms (The Millennium Ecosystem Assessment 2005).

However, the earlier over-exploitation of some marine resources has in many cases stopped and resulted in increased stocks due to harvest restrictions and proper management (CAFF 2013).

The Northern Sea Route across the top of Eurasia has been used by icebreakers and ice-strengthened ships since the 1930s, primarily for transport within Russia. A regular ice-free summer season would make the route even attractive for shipping between East Asia and Europe. An ice-free Northwest Passage will similarly facilitate transit shipping (CAFF 2013).

Terrestrial ecosystems: Warming of the terrestrial ecosystems will cause drying of substrate and an earlier snowmelt (CAFF 2013). A significant effect of increased/decreased temperature is apparent in most Arctic terrestrial ecosystems, but not all. Therefore, the phenological responses vary from area to area. It has been estimated that vegetation seasonality has shifted about 7° toward the Equator during the last 30 years and plant flowering has advanced up to 20 days during one decade in some areas. As a result, primary productivity and vascular plant biomass have increased rapidly – “greening of the tundra” in some areas. The abundance and biomass of deciduous shrubs and grasses and grass-like plants have increased substantially in certain parts of the Arctic tundra but remained stable or decreased in others. These changes in the plant communities lead to functional changes of the ecosystem with reduced albedo, increased soil temperature, higher ecosystem respiration, and release of trace gases. Other changes are regional collapses of lemming and vole cycles, human-induced overabundance of ungulates and geese, and phenology-driven trophic mismatches (CAFF 2013; IPCC 2014). The increased local and regional abundances of keystone herbivores, such as reindeer/caribou and other ungulates, geese and herbivorous insects sometimes counteract the increase in plant productivity (CAFF 2013). Many Arctic waterbirds are highly dependent upon a network of staging and wintering areas in wetlands in many parts of the world. Especially important are the wetlands in the Arctic. So far, no dramatic changes have been reported having significant impact on such areas.

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2

Arctic Ecology – A Paleoenvironmental Perspective

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2.1 Introduction

In the absence of measured climate and ecological data records, paleoecology, and paleoclimatology provide unique opportunities to examine ecological and climatic conditions across long timescales and provide much needed long-term context. For example, are recent climate trends unique and are they trending outside the natural range of variability? Has vegetation been stable for millennia or has it been changing? And if so, why? A paleoenvironmental perspective also allows us to reconstruct trends in other environmental data that we did not measure in the past (e.g. contaminants). Thus, paleoenvironmental data collected from a variety of different sources functions much like a history book, allowing us to turn the pages and look back in time to assess how climate, biota, and ecosystems have varied in the past, before and after anthropogenic impacts. Most importantly, a paleoenvironmental perspective permits a more comprehensive examination of ecological and climatic trends and allows researchers to assess if conditions during recent times are now exceeding previous ecological and climate thresholds.

Across the Arctic there are numerous ecological problems affecting the biota and landscapes of this environmentally sensitive region. Climate change is chief amongst these. A warming climate during the twentieth and twenty-first century, which has occurred at rates and magnitudes in the Arctic that exceed those in most other parts of the world due to Arctic amplification (Serreze and Barry 2011), has led to cascading impacts throughout Arctic ecosystems. For example, warming during the twentieth century is now appearing below ground in the permafrost (the frozen ground beneath most Arctic landscapes), where temperatures at 10–20 m depth have increased significantly in most regions throughout the world where continuous permafrost occurs (Biskaborn et al. 2019). As climate changes and this warming propagates deeper into the permafrost, geomorphic disturbances, such as retrogressive thaw slumps and active layer detachments, are becoming more frequent (Lantz et al. 2009) (Figure 2.1). These disturbances often impact water chemistry of nearby aquatic systems (Kokelj et al. 2013), can alter

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Figure 2.1 A large retrogressive thaw slump on the Peel Plateau near the border between the Yukon and Northwest Territories, Canada. The lake in the bottom left is approximately 140 m across. *Source:* Photo: Michael Pisaric.

microclimatic and soil nutrient conditions in terrestrial environments leading to substantial vegetation change (Lantz et al. 2009), and even disrupt Arctic freshwater carbon cycling (Zolkos et al. 2018).

Unfortunately, our knowledge and understanding of these important environmental problems is limited both temporally and spatially throughout the Arctic. Temperature, for example, has only been recorded continuously using instruments in most Arctic locations during the latter half of the twentieth century, and in only very few stations. Snapshots of past Arctic climate conditions can be gleaned from Norse settlements established on Greenland a millennium ago and the travels of Arctic explorers plying the waters of the Canadian archipelago in search of the fabled Northwest Passage. These accounts, while valuable, are only snapshots in time and do not provide a continuous record of environmental and climate change.

The remainder of this chapter will examine the changing ecology of the Arctic from a paleoenvironmental perspective. The Earth System offers many biotic and abiotic archives that can be used to reconstruct how the Arctic environment has developed throughout geologic time. We will introduce a number of these, including ice cores, dendrochronology (the study of tree rings), paleontology, and paleolimnology (the study of allochthonous and autochthonous materials preserved in lake sediment). Each of these archives provides important opportunities to study the changing ecology of Arctic systems, but each also provides different challenges. Using examples from studies throughout the circumpolar Arctic, the changing ecology of the Arctic will be examined across longer timescales than typically considered in ecological studies.

2.2 The Distant Past

Given the overall focus of this book is on Arctic ecology, this chapter will concentrate on the recent past, and so most of our examples examine ecological change over the last few centuries. Moreover, we also focus on the time periods that overlap with significant human impacts. It is important to remember, however, that some of the most striking illustrations of natural environmental change come from paleoecological studies in the High Arctic, where, for example, ancient forests covered parts of Axel Heiberg Island about 45 million years ago (Basinger 1991; Jahren 2007). Extraordinarily well-preserved remains of the lush forests of the middle Eocene epoch can still be seen on the frozen tundra at a latitude of about 80°N and about 1500 km north of the modern tree line (Figure 2.2).

Paleobotanical evidence shows that these ancient forests were dominated by dawn redwoods (*Metasequoia*), reaching 30 m height, with diameters exceeding 1 m. Mummified remains of other trees adapted to a warm temperate climate, including species of fir (*Abies*), pine (*Pinus*), cypress (*Taxodium*), walnut (*Juglans*), and ginkgo (*Ginkgo*), with an understorey of alder (*Alnus*) and birch (*Betula*), have also been recovered, as has fossil leaf litter and other woody debris. Clearly, polar regions were much warmer in the Eocene even

Figure 2.2 One of many mummified tree-stumps preserved in a 45 million-year-old fossil "forest" on Axel Heiberg Island, in the High Arctic of Canada. *Source:* Photo: John Smol.

though they still experienced a prolonged period of polar darkness, with estimated summer temperatures of about 12 °C (as opposed to 5–6 °C now), with even winter temperatures above freezing. An interesting zoological history, represented by fossil teeth and bones of warm-climate animals (such as turtles and alligators, as well as a variety of mammals and birds), confirms the paleoecological and climatic inferences made from the botanical data.

Clearly the Arctic has not always had the same climate regime that we associate with it now. The dramatic climatic and ecological change of the Eocene has continued in the more recent past as well. For example, some of the longest paleoclimatic records that are available for study come from ice cores from the Greenland and Antarctic ice sheets (see Box 2.1). These long-term, highly resolved records suggest climatic and ecological change in Arctic regions is typical of Arctic systems and not just limited to the Eocene warm interval. Even during the Quaternary period (the past 2.6 myr), extreme climatic and ecological variability has characterized the Arctic.

2.2.1 Bones, DNA, and Megafauna

When traveling throughout the Arctic today, you would likely encounter fewer than 20 different species of mammals, with only a few likely to be considered large mammals. Perhaps you would be fortunate to experience the seasonal migration of the porcupine caribou (*Rangifer tarandus granti*) herd as they migrate between the northern Yukon Territory and northern Alaska, or perhaps muskox (*Ovibos moschatus*) while traveling through the Canadian Arctic or northern Greenland. Such low diversity of large mammals has not always been the case though. During the Pleistocene epoch, for example, parts of the Arctic supported a much higher diversity and density of large mammals.

As summarized in Box 2.1 on ice cores and elsewhere in this chapter, during the Quaternary the climate has fluctuated between cold glacial conditions and warmer than present interglacials every 100 kyr or so, driven by changes in the orbit of the Earth. These changes in climate had equally dramatic impacts on the biota of the Arctic. The cold glacial conditions of the late Pleistocene epoch, which terminated at the onset of warmer conditions during the Holocene, encouraged the development of unique biota in parts of the Arctic including the steppe tundra of Beringia, the ice age landmass that connected Eurasia and North America when sea level was much lower. The Beringian environment was home to an impressive number of large ice age mammals that have since become extinct (Barnosky et al. 2004).

The area that today is the Bering Strait between Siberia and Alaska was, in the late Pleistocene, a treeless land bridge that remained unglaciated. Sea level was 100–150 m lower than at present, allowing for the formation of the Bering land bridge and a unique assemblage of plants and animals that no longer exist today. The expansive nature of Beringia led to desert-like levels of precipitation preventing the development and expansion of glaciers in this part of the world. As a result, many unique animals and plant assemblages survived the ice age in Beringia. Today, the remains of these plants and animals are still being discovered throughout these unglaciated regions of Yukon Territory, Alaska, and eastern Siberia.