Chapter 4

Ecological Characteristics of the Arctic

Contents

4.1. Introduction

Polar ecosystems exist under extreme environmental conditions, including cold temperatures, large seasonal fluctuations in incoming solar radiation, extensive snow and ice cover, and short growing seasons. These conditions affect the productivity, species diversity, wildlife behavior (e.g., migration), and food chain characteristics of Arctic and subarctic ecosystems. These effects have implications on contaminant transfer and storage in Arctic biota, and on the sensitivity of Arctic ecosystems to contaminants and other stressors. This chapter describes ecosystems of the Arctic terrestrial, freshwater, and marine environments as a background for discussion in later chapters on contaminants and their effects in these ecosystems. It is not intended as a comprehensive coverage of the ecology of the Arctic. Animal species which are of special interest, for example, those important in the diets of Arctic peoples, such as caribou/reindeer, some fish, and marine mammals, are described in greater detail.

4.2. Physical-geographical characteristics affecting Arctic ecosystems

4.2.1. Recent glaciations

Over the last 1.8 million years, since the start of the Pleistocene era, polar regions have undergone numerous glaciations. The most recent of these occurred approximately 20 000 years ago, during which time many Arctic and subarctic areas were covered with ice. Some regions of the Arctic have been deglaciated for only 3000 years whilst others are still glaciated. Due to these recent glaciations, Arctic ecosystems, in general, are relatively young compared to those farther south (Bliss 1981a, Stonehouse 1989). Despite this short timespan for ecosystem development, Arctic ecosystems, including soils and biota, appear to be stable and in equilibrium with the current northern climate (Bliss 1981a).

4.2.2. Cold

The Arctic is synonymous with cold temperatures. In the coldest regions, air temperatures fall below –60°C in winter and reach averages of only 4°C in July (Barry and Hare 1974). Low temperatures slow down chemical reactions and biological processes.

Weathering rates and production of dissolved chemicals in Arctic soils are reduced by cold. This is compounded by the presence of permafrost, whereby soils are frozen for most of the year, with only a shallow upper layer of thawed soil during the brief summer. Thus, Arctic soils are immature and low in nutrients (Stonehouse 1989).

The most important factor for the development of life in the Arctic is the length of the growing season (Chernov 1985), which ranges from three to four months in the Low Arctic to as little as one to two and a half months in the High Arctic (Bliss 1981b). This gives little time for growth of plants and represents a short timespan during which herbivores have access to quality forage. In addition, the summer provides a short window during which poikilothermic (cold-blooded) animals can develop.

Low temperatures result in extensive ice cover of Arctic freshwater and marine habitats. This results in reduced light penetration and therefore reduced photosynthesis. In some lakes and ocean areas, ice cover lasts year-round and productivity is very limited.

There is a large variety of physiological and behavioral adaptations of Arctic biota to cold. Important among these is the metabolic use of lipids as stored energy and as a source of energy. This has implications for contaminant levels in Arctic wildlife and is discussed further in chapter 6, section 6.3.1.1.

4.2.3. Low light levels

The region north of the Arctic Circle receives one-third to one-half of the annual solar radiation compared to that reaching temperate and equatorial latitudes. During the Arctic summer, this radiation is received 24 hours a day, resulting in a relatively large amount of incoming solar energy (Fridriksson 1986, Odum 1983 in Freedman *et al.* 1994). However, much of this energy is used to melt ice and snow, and over 50% of the total annual radiation is received prior to completion of spring melt, which usually occurs in June. Thus, the growing season typically begins when solar radiation levels are already declining (Courtin and Labine 1977, Fridriksson 1986, Etkin and Agnew 1992). Furthermore, on average, about 90% of the incoming radiation is reflected back to space due to the high surface albedo resulting from snow and ice cover and limited vegetation cover (Stonehouse 1989).

In the marine environment, sea ice and snow cover further limit energy input. However, there is some light penetration before all the ice is melted, allowing spring production to begin before the water is open.

4.2.4. Water availability

Arctic ecosystems generally receive little precipitation and much of this is received in the form of snow. Studies have shown that 80-90% of the annual runoff in the Arctic can occur in just two to three weeks during snowmelt, followed by an abrupt shift to low runoff during the growing season (Bliss *et al.* 1984, Bliss 1986). Due to low levels of evaporation under the cold conditions, and the presence of permafrost acting as a barrier to subsurface drainage, the moisture provided by snowmelt and rainfall is largely retained. This is especially evident in the Low Arctic tundra with its numerous wetlands (Chernov 1985, Stonehouse 1989). However, in the polar desert regions of the High Arctic, where the levels of precipitation are extremely low and snowmelt is the key contributor to water budgets, the cessation of runoff following snowmelt can result in very low availability of moisture during the growing season (Bliss *et al.* 1984, Bliss 1986).

4.2.5. Anthropogenic stressors

Arctic species are generally not considered 'sensitive', since environmental tolerances of most species are broad. However, the physical environment of the Arctic is sensitive. There are numerous stressors, not directly related to chemical contamination, which do and will continue to affect the Arctic. These could change the effects of contaminants on species or ecosystems. Among these stressors are habitat destruction due to hydroelectric development, increased human settlement and activity, resource extraction, and over-harvesting (Welch 1995). The Arctic terrestrial environment is very susceptible to physical destruction. Evidence of human activity is often still visible after hundreds of years. In some cases, ecotourism has already led to habitat destruction and harassment of animals.

Nearly all populations of large Arctic mammals have been considerably reduced from historic levels. In most cases, the protected or endangered status of Arctic species is due to habitat degradation or excessive harvesting, with species at the higher trophic levels most affected. Some marine mammal stocks are harvested by more than one country, and these countries are not always in agreement about migration patterns, sustainable catches, or the rights of native peoples.

4.3. General ecological characteristics of Arctic ecosystems relevant to contaminants and other stressors

4.3.1. Low productivity

As will be discussed in sections 4.4, 4.5 and 4.6, productivity in terrestrial, freshwater, and marine environments is reduced due to limited nutrient availability, low light, low temperatures, ice cover, and short growing seasons. The low productivity in the Arctic results in slower-growing and longer-lived poikilotherms than in temperate climates. Some Arctic insects, for example, can take up to 14 years to complete their life cycle, and Arctic char up to 12 years (Remmert 1980, Kukal and Kevan 1994). Arctic mammals grow at rates similar to temperate mammals of the same size, however, the large mammals (e.g. whales) tend to take a long time to reach maturity.

4.3.2. Bioaccumulation and biomagnification

Levels of some contaminants, particularly metals, in specific tissues and organs of a number of temperate and Arctic species increase with age. This is due to bioaccumulation, i.e., increases in contaminant concentrations in biota with continued exposure over time. Some organic contaminants become further concentrated in animals with each successive step up a food chain, a process called biomagnification (see chapter 6, section 6.4, and chapter 7, section 7.4.2.1).

The burden of contaminants stored in the body of animals usually increases with age, unless they have some mechanism for breaking down or excreting the chemicals. Older animals are thus more likely to have higher levels of some contaminants. The age effect is further pronounced in the Arctic by the fact that predators, including people, are more likely to eat older animals than those that are hunted in more southern climates.

4.3.3. Cyclic annual productivity

Arctic ecosystems are highly cyclic due to seasonal fluctuations in light levels, nutrient inputs, and temperature. Nutrients and contaminants deposited on snow, ice, soil, and plants during the Arctic winter can be mobilized and assimilated very quickly in the spring when sunlight returns and temperatures rise. In freshwater systems, the spring melt carries nutrients and some contaminants into streams, ponds, and lakes. In the Arctic marine environment, a burst of primary productivity occurs under the ice when light levels become sufficiently high in the spring. At this time, nutrients and contaminants can move into, and through, food chains very rapidly.

Cyclic productivity in biota is related to many physiological and behavioral adaptations of animals to their environment. One such adaptation is to consume and store energy and nutrients when food is available, and metabolize these when food is lacking. Another adaptation is to migrate to superior overwintering, feeding or spawning habitats. Migratory species include: small birds that may migrate over two continents, foraging mammals such as caribou that move from the boreal forest to summer grazing areas on the tundra, fish that travel to find favorable spawning sites, and whales that move in search of food. This means that contaminants in some species, and also in the predators that consume them, may not relate to contaminant deposition in the Arctic, but to levels in other parts of the world.

4.3.4. Low species diversity

The low species diversity in the Arctic is a consequence of low absolute productivity and recent glaciations. In contrast, the Antarctic marine environment which has not experienced such glaciations, has considerably higher biological diversity and an accompanying higher degree of specialization (Dunbar 1986). Although listings of Arctic species may appear substantial, the number of species in any particular area is usually very limited. Because of this low biological diversity, some food chains may be very simple, for example, the lichen→caribou→wolf food chain in Arctic Canada. The complexity of food webs increases as Arctic ecosystems grade into temperate systems.

The low diversity in the Arctic is associated with opportunistic and invading species that are adapted to survive successfully under a range of conditions. Individuals of most Arctic species adjust their feeding habits, growth rates, and reproductive characteristics in response to climatic factors or the availability of food. Individuals or species in any given environment may be opportunistic feeders, and thus will not have a well-defined position in the food web. For example, freshwater *Gammarus* can be entirely herbivorous, but is carnivorous if possible; a few individuals in a population of freshwater fish may be cannibals; and walrus may eat seals if alternative foods are lacking. Feeding strategies may also depend on the age and experience of an animal, and may differ from one year to the next.

Figure 4·1. Biogeographical zones within the AMAP assessment area, a) High Arctic, b) Low Arctic, c) subarctic, and d) boreal forest.

4.4. Terrestrial ecosystems

4.4.1. Biogeographical zones

Throughout this section on terrestrial ecosystems, reference will be made to the High Arctic, Low Arctic, and subarctic (see chapter 2, Figure 2·2). These zones are distinguished on the basis of climate and the presence of certain vegetation types and animals (Bliss 1981b, Bliss and Matveyeva 1992). The High and Low Arctic regions roughly correspond to the polar desert and tundra geobotanical areas, respectively, described by Andreev and Aleksandrova (1981) (Muc *et al.* 1988). Some mention will also be made of boreal forests. While this forested zone is south of the Arctic, some studies of relevance to the Arctic Monitoring and Assessment Programme (AMAP) are carried out here.

4.4.1.1. High Arctic

The High Arctic, the most northern region of the Arctic, has a growing season which lasts only 1-2.5 months and mean July temperatures ranging from 4-8°C. Fewer flora and fauna are supported under these extreme conditions than in the Low Arctic (approximately 360 vascular plants and only 8 terrestrial mammals). Vascular plant cover ranges from 0-20%, with mosses and lichens increasing this to between 50 and 80% in some areas (Figure 4·1a) (Bliss 1981b). The High Arctic zone is often divided into the sparsely vegetated polar desert and the more productive polar semi-desert.

4.4.1.2. Low Arctic

The Low Arctic or tundra growing season ranges from 3-4 months, with mean July temperatures of 4-11°C. This region supports more than 600 vascular plant species and has 80-100% plant cover (Figure 4·1b) (Bliss 1981b).

4.4.1.3. Subarctic

The subarctic, or forest tundra, is the transition zone between the boreal forest and the treeless tundra (Figure 4·1c). The growing season here lasts from 3.5 months to a year and plant cover is 100% (Wielgolaski *et al.* 1981).

4.4.1.4. Boreal forest

Boreal forests are located in northern regions of Europe, Asia (Siberia), and North America, roughly between 50° and 70°N. They are bordered to the north by the subarctic and to the south by deciduous forests. The identifying life forms here are the coniferous trees (Figure 4·1d).

4.4.2. Primary production

Primary production in the Arctic terrestrial environment is limited by a combination of short growing season, low temperatures, and low nutrient availability (Warren-Wilson 1966, Haag 1974, McCown 1978, Bliss 1986). In some regions, especially at high elevations and in High Arctic polar desert areas, low soil water is also a limiting factor for production (Bliss 1986, Svoboda and Henry 1987, Oberauer and Dawson 1992). In general, however, water is not limiting in tundra ecosystems (Matthes-Sears *et al.* 1988). Table 4·1 shows primary production values for the Arctic and subarctic.

Table 4·1. Plant production in the Arctic (modified from Wielgolaski *et al.* 1981).

	Net production, g/m^2/y	Production, % Vascular plants	Production, % Cryptogams	Growing season, d	Productivity, g/m^2/d
High Arctic					
Polar desert	1-10	30-90	10-70	30-45	0.03-0.2
Polar semi-desert	10-50	20-95	5-80	45-60	0.2-0.8
Low Arctic					
Herbaceous	100-300	60-90	10-40	45-100	2.2-3.0
Dwarf shrub	150-700	65-85	15-35	50-150	3.0-4.7
Low shrub	500-1200	70-85	15-30	50-150	8.0-10.0
Subarctic	150-800	50-90	5-50	110-365	1.4-6.5

Low ambient temperatures result in low soil temperatures and permafrost (Stonehouse 1989). These low temperatures decrease the rate at which plant roots can absorb nutrients, and lead to very slow decomposition rates. In cold, continental regions it has been estimated that it takes over 300 years for 95% turnover of organic matter to be achieved. Thus, carbon accumulates in the soils, and nutrients such as nitrogen and phosphorus remain bound up in decaying plant material and are not readily available for new plant growth (Haag 1974, Chapin 1978, Bliss 1986). Arctic plants have adapted to their nutrient-limited environment by conserving essential nutrients from one season to the next. Compared to the numerous annual species of southern ecosystems, Arctic vegetation is predominantly comprised of perennial plants which are able to store nutrients over the winter (Haag 1974, Berendse and Jonasson 1992).

In response to nutrient limitation, Arctic plants have inherently slow growth rates (Bryant *et al.* 1983). Thus, northern plant communities are very slow to recover after being disturbed and are sensitive to changes in natural conditions (Haag 1974, Oechel 1989). With the characteristic few species and simple food chains of Arctic ecosystems, animals that depend on disturbed plant communities for forage will often have no alternative food options. This can result in population declines, both of herbivores and their predators. Due to this sensitivity, various anthropogenic activities in the Arctic, including energy development and exploitation of biotic and mineral resources, can greatly disrupt Arctic ecosystems (Oechel 1989).

4.4.3. Plants

Vegetation in the High Arctic consists of cushion plants (e.g., *Dryas integrifolia*, *Saxifraga oppositifolia*), prostrate shrubs of *Salix arctica*, and rosette species of *Saxifraga*, *Draba* and *Minuartia* (Bliss and Matveyeva 1992). Higher species diversity and greater productivity are found in 'Arctic oases', areas with more favorable environmental conditions, which are scattered throughout about 2% of the High Arctic region (Freedman *et al.* 1994).

Typical Low Arctic plants include low shrubs (e.g., *Alnus*, *Salix*, *Betula*), dwarf shrubs of heath species (e.g., *Ledum*, *Vaccinium*, *Cassiope*, *Empetrum*), sedges (e.g., *Carex*, *Eriophorum*), grasses (e.g., *Luzula*, *Poa*, *Arctagrostis*), cushion plants (e.g., *Dryas*), lichens, and mosses (Bliss 1981b, Bliss and Matveyeva 1992).

The subarctic contains many of the same plant species as are found in the Low Arctic, and some boreal species (e.g., *Deschampsia flexuosa*, *Epilobium angustifolium*, *Vaccinium myrtillus*) (Andreev and Aleksandrova 1981). Stands of trees are characteristic of this region. White and black spruce (*Picea glauca*, *P. mariana*) are common in North America, while Scots and stone pine (*Pinus sylvestris*, *P. pumila*) are typical in Eurasia (Stonehouse 1989). In subarctic Scandinavia, there are birch (*Betula* spp.) forests between the shrub belt and boreal forest.

Boreal forests consist largely of coniferous trees, especially spruces (*Picea* spp.), pines (*Pinus* spp.), and firs (*Abies* spp.). Deciduous trees (e.g., birch, *Betula* spp.; cottonwoods, *Populus* spp.; alder, *Alnus* spp.) are present in the early developmental stages of the boreal forest; in fully developed forests, they are restricted to areas with more favorable conditions, e.g., along brooks. A listing of the typical tree species and their circumpolar distribution is given in Table 4·2.

Table 4·2. Main regions within the boreal coniferous forests, and their dominant tree species.

Fennoscandian forests	
	Scots pine (*Pinus sylvestris*)
	Norway spruce (*Picea abies*)
	Birch (*Betula pubescens* and *B. pendula*)
West Siberian forests	
	Siberian fir (*Abies sibirica*)
	Siberian larch (*Larix sibirica*)
	Scots pine (*Pinus sylvestris*)
	Siberian pines (*Pinus cembra* var. *sibirica* and *P. pumila*)
	Norway spruce (*Picea abies* var. *obovata*)
East Siberian forests	
	Siberian fir (*Abies sibirica*)
	Dahurian larch (*Larix gmelini*)
	Scots pine (*Pinus sylvestris*)
	Siberian pines (*Pinus cembra* var. *sibirica* and *P. pumila*)
North American subarctic and boreal forests	
	Balsam fir (*Abies balsamea*)
	American larch (*Larix laricina*)
	Lodgepole pine (*Pinis contorta*)
	Jack pine (*Pinus banksiana*)
	White spruce (*Picea glauca*)
	Black spruce (*Picea mariana*)
	Poplars (*Populus balsamifera* and *P. tremuloides*)
	Birch (*Betula papyrifera*)
Northeast American coniferous forests	
	Jack pine (*Pinus banksiana*)
	Eastern white pine (*Pinus strobus*)
	Red pine (*Pinus resinosa*)
	American larch (*Larix laricina*)

4.4.4. Terrestrial animals

The Arctic, with its characteristic cold, long winters, permafrost, and low primary productivity, is home to relatively few species of land animals compared to the more favorable temperate and tropical ecosystems. However, those species that do live in the harsh northern ecosystems are very well adapted to their environment. A listing of Arctic terrestrial mammals, indicating regional distribution, is given in Table 4·3.

4.4.4.1. Invertebrates

A wide variety of microfauna inhabit Arctic soils. For example, at Truelove Lowland on Devon Island in the Canadian High Arctic, Ryan (1977) reported finding species of protozoa, rotifers, tardigrades, turbellarians, nematodes, enchy-

Table 4·3. Terrestrial mammals of the Arctic. After Sage (1985 as in Stonehouse 1989). (Species marked with asterisk are year-round residents).

	High Arctic	Marginal Arctic	Greenland	Eurasia	Alaska	Canada
INSECTIVORA						
Common shrew *Sorex araneus*				×		
Arctic shrew *S. arcticus*				×	×	×
Laxmann's shrew *S. caecutiens*				×		
Masked shrew *S. cinereus*			×	×	×	
Large-toothed shrew *S. daphaenodon*				×		
Pigmy shrew *S. minutus*				×		
Dusky shrew *S. obscurus*					×	×
Flat-skulled shrew *S. vir*				×		
RODENTIA						
Alaska marmot *Marmota broweri*					×	?
Black-capped marmot *M. camtschatica*				×		
Arctic ground squirrel *Spermophilus undulatus*				×	×	×
*Insular vole *Microtus abreviatus*	×				×	×
Narrow-skulled vole *M. gregalis*				×		
*Middendorff's vole *M. middendorffi*	×			×		
Tundra vole *M. oeconomus*				×	×	×
Meadow vole *M. pennsylvanicus*						×
*Arctic (collared) lemming *Dicrostonyx groenlandicus*	×		×	×	×	×
Hudson Bay lemming *D. hudsonius*	×					×
*Brown (Siberian) lemming *Lemmus sibiricus*	×		×	×		
Grey red-backed vole *Clethrionomys rufocanus*				×		
Northern red-backed vole *C. rutilus*				×	×	×
Eastern vole *Eothenomys lemminus*				×		
European water vole *Arvicola terrestris*		×		×		
Muskrat *Ondatra zibethicus*						×
Porcupine *Erithizon dorsatum*		×			×	×
LAGOMORPHA						
Snowshoe hare *Lepus americanus*	×				×	×
*Arctic hare *L. arcticus*	×		×			×
*Alaskan hare *L. othus*	×					
*Varying hare *L. timidus*	×					
Northern pika *Ochotona hyperborea*		×		×		
CARNIVORA						
Coyote *Canis latrans*	×				×	×
*Gray wolf *C. lupus*	×		×	×	×	×
Red fox *Vulpes vulpes*				×	×	×
*Arctic fox *Alopex lagopus*		×	×	×	×	×
Grizzly bear *Ursus arctos*				×	×	×
*Polar bear *U. maritimus*			×	×	×	×
*Stoat (ermine) *Mustela erminea*	×		×	×	×	×
*Least weasel *M. nivalis*	×			×	×	×
European mink *M. lutreola*		×		×		
American mink *M. vison*		×			×	×
*Wolverine *Gulo gulo*	×		×	×	×	×
Otter *Lutra canadensis*		×			×	×
Lynx *Lynx canadensis*		×			×	×
ARTIODACTYLA						
Moose/elk *Alces alces*				×	×	×
*Caribou/reindeer *Rangifer tarandus*	×		×	×	×	×
*Muskox *Ovibos moschatus*	×		×	×	×	×
Dall sheep *Ovis dalli*					×	×
Snow sheep *O. nivicola*			×			

traeid worms, copepods, ostracods, and cladocerans. Mites and spiders are widespread in the Arctic. During the summer, warmer tundra areas support beetles, moths, butterflies, ichneumon flies, bumblebees, craneflies, and blowflies. Warble flies parasitize the caribou and reindeer, laying their eggs under the skin. Visitors to the Arctic are all too familiar with the sometimes dense populations of biting simuliid flies and mosquitoes (Stonehouse 1989).

4.4.4.2. **Vertebrates**

4.4.4.2.1. **Birds**

Migratory birds

Each summer over 120 bird species migrate from temperate and tropical regions to the Arctic where they breed. Flying over land and oceans, some travel thousands of kilometers to reach their northern nesting grounds. The most common migrant species in the north are waders or shorebirds (e.g., Baird's sandpiper, *Erolius bairdii*), loons (e.g., red-throated loon, *Gavia stellata*), geese (e.g., snow goose, *Chen caerulescens*), ducks (e.g., common eider, *Somateria mollissima*), and birds of prey (e.g., long-tailed jaeger, *Stercorarius longicaudus*, peregrine falcon, *Falco peregrinus*) (Stonehouse 1989). Migrant songbirds which breed in the Arctic include the Lapland bunting (*Calcarius lapponicus*), snow bunting (*Plectrophenax nivalis*), common redpoll (*Carduelis flammea*), and Arctic redpoll (*C. hornemanni*) (Godfrey 1986).

The advantage of the Arctic as a summer nesting ground is that it is not densely populated, so there is more than enough forage to sustain the birds that reach this distant region. However, the actual numbers of forage species are few and food chains are short. Thus, if one or two foods are lacking in a given summer, alternatives are not readily available and the feeding birds may be unable to successfully reproduce that year. For example, when lemming numbers are low, breeding success of owls and jaegers is limited (Stonehouse 1989).

Many of the migratory birds are first- or second-level carnivores in terrestrial or freshwater food webs in both Arctic and southern habitats. They in turn are preyed on by birds of prey in the Arctic, including owls, accipiters, and falcons. The Arctic peregrine falcon feeds mostly on migratory waterfowl, which can accumulate contaminants in their overwintering areas, and is therefore more exposed to persistent contaminants than resident gyrfalcons (*Falco rusticolus*) which prey largely on non-migratory birds and Arctic hare (Jarman *et al.* 1994).

Resident birds

Of the many bird species that inhabit and nest in the Arctic terrestrial environment during the summer months, very few remain in the far north year-round. Two species of ptarmigan, rock ptarmigan (*Lagopus mutus*) and willow ptarmigan (*L. lagopus*), are well adapted to their year-round stay on the tundra. During winter, their plumage is white allowing the birds to blend in with their surroundings. This white plumage is replaced by a thinner brown plumage in the summer. Raven (*Corvus corax*) and snowy owl (*Nyctea scandiaca*), with their thick plumage and subcutaneous fat are also year-round residents. Ptarmigan are herbivorous, while raven and snowy owl feed on other birds and small mammals (Batzli *et al.* 1981, Stonehouse 1989).

Some species, including snow buntings, redpolls, and larger birds of prey, may overwinter in the Arctic (e.g., in Iceland) if necessary, or may migrate only as far as the subarctic or northern temperate regions.

4.4.4.2.2. **Mammals**

Approximately 50 species of land mammal are found in the Arctic. Of these, only 15 are widely distributed over the tundra throughout the year.

Small, herbivorous mammals, such as lemmings (e.g., *Lemmus sibiricus*, *Dicrostonyx groenlandicus*) and voles (e.g., *Microtus oeconomus*, *Clethrionomys rufocanus*), seek shelter under the snow during the Arctic winter. This not only protects them from the cold, but also gives them access to vegetative forage at the ground surface (Stonehouse 1989). Microtine rodent populations follow a cyclic pattern. Lemming numbers, for example, reach a peak approximately every 3-4 years (Fuller *et al.* 1977, Bliss 1977).

Other Arctic herbivores include the ground squirrel (*Spermophilius parryii*), Arctic hare (*Lepus arcticus*), black bear (*Ursus americanus*), caribou/reindeer (*Rangifer tarandus*), and muskox (*Ovibos moschatus*). Caribou and reindeer are North American and Eurasian representatives of the same species. Smaller subspecies roam the High Arctic, namely the Peary caribou (*Rangifer tarandus pearyi*) in the Canadian Arctic islands, and a subspecies of reindeer (*Rangifer tarandus platyrhynchus*) on Svalbard. Muskoxen extend into the Low Arctic, but are more abundant in the High Arctic, where they rely, along with Peary caribou, on the more lush meadow communities which extend over as much as 40% of the land area in the southern parts of the High Arctic to as little as 2% in Arctic oases scattered throughout the polar desert (Bliss 1981b, Wielgolaski *et al.* 1981, Freedman *et al.* 1994). Caribou and muskox graze intensively during the brief summer period, storing up fat reserves for the long winter when only poor-quality forage is available, and is found only on windswept slopes or by digging under snow (Bliss 1986, Klein and Bay 1990, Collins and Smith 1991).

Caribou herds have distinct migratory ranges which may cover hundreds of miles. In Canadian mainland tundra subspecies, the tundra summer ranges and forested winter ranges may be as much as 800 miles apart (Banfield 1974). However, most populations of caribou and reindeer move over considerably smaller distances. In Norway, Sweden, and Finland, reindeer are semi-domesticated and their traditional ranges often depend on which Saami village the herd belongs to.

Well-known among the Arctic predators is the polar bear (*Ursus maritimus*). Primarily a maritime dweller, this large animal feeds on ringed seals and is considered to be a top predator in the marine ecosystem (discussed further in section 4.6.7.3.4). The brown bear (*Ursus arctos*) is truly terrestrial, feeding mainly on plants, fish, and occasionally on small mammals and birds. The carnivorous gray or timber wolf (*Canis lupus*) preys on small mammals, birds, caribou and reindeer (Stonehouse 1989). The Arctic fox (*Alopex lagopus*) primarily hunts small mammals and birds, and scavenges on the remains of prey left behind by wolves and bears (Fitzgerald 1981). Foxes living near the sea, hunt ringed seal pups and are therefore part of the marine food chain (Walker *et al.* 1964). Other terrestrial predators include the least weasel (*Mustela nivalis*), stoat (or ermine) (*M. erminea*), European and American mink (*M. lutreola* and *M. vison*, respectively), wolverine (*Gulo gulo*), and red fox (*Vulpes vulpes*). These carnivores have a varied diet of small mammals and birds (Fitzgerald 1981, Stonehouse 1989). Mink feed both on small terrestrial mammals and on freshwater fish (Poole *et al.* 1995).

Predators, such as foxes, weasels, and raptors, that rely heavily on rodents as a food source are affected by the population fluctuations typical of these prey. When rodent numbers are high, predator populations rise rapidly. When availability of these prey is low, a corresponding drop in predator numbers occurs, resulting from decreased reproduction in the predator populations (Fitzgerald 1981).

4.4.5. Terrestrial food webs

Arctic terrestrial food webs are generally short, often consisting of plants or lichens at the primary producer level, a few herbivores, and one or two main predators (Figure 4·2a). The diversity and complexity of the food webs increases in subarctic habitats south of the treeline.

The air→plant→animal contaminant pathway is the major route of contamination into the terrestrial food chain (Thomas *et al.* 1992), e.g., the lichen→caribou→wolf food chain. Contaminants associated with atmospheric particulates deposited on plant and soil surfaces may be washed off and enter aquatic habitats. Some may then be cycled into the

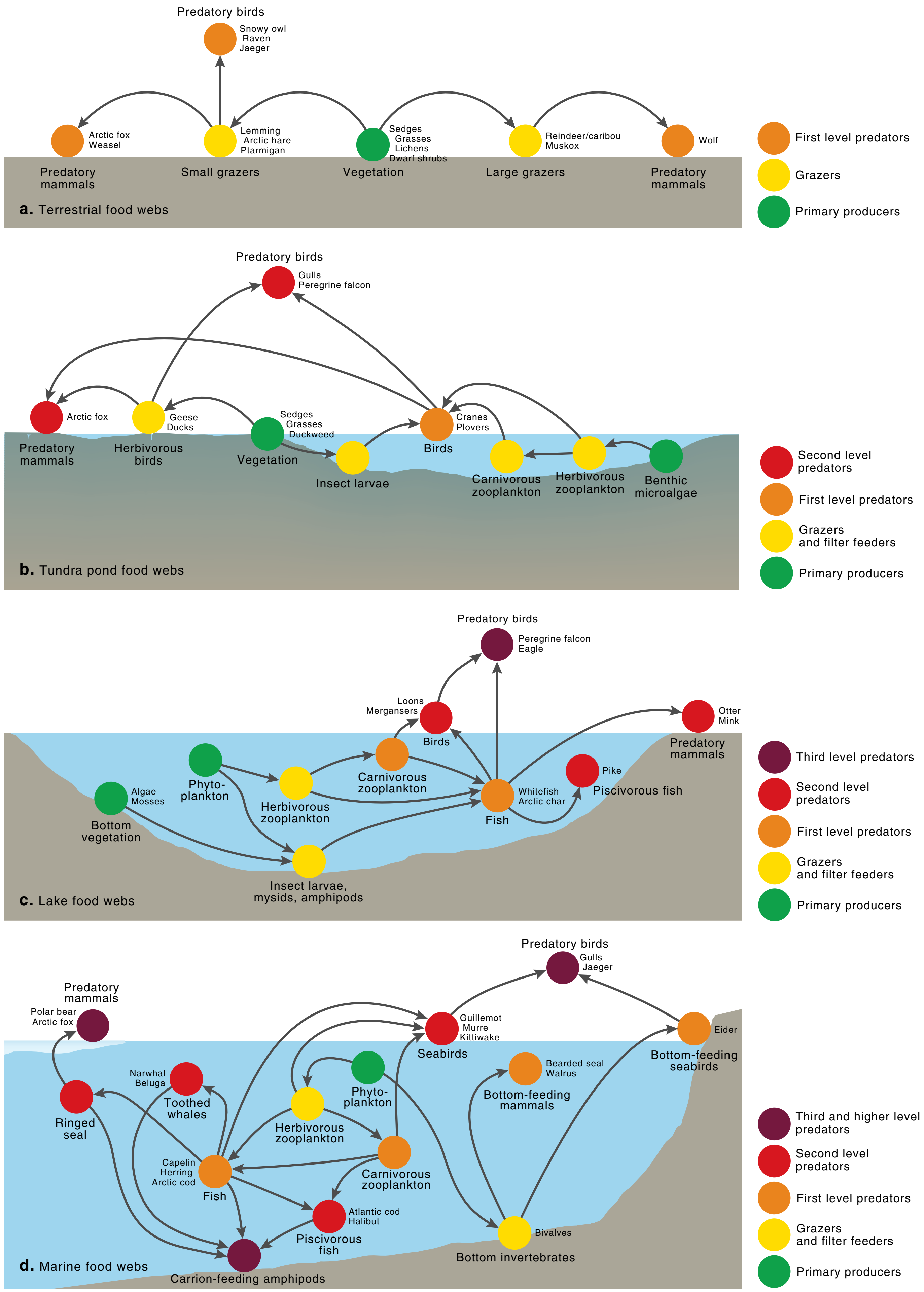

Figure 4·2. Examples of Arctic food webs, a) terrestrial, b) tundra pond, c) lake, and d) marine.

soil, where they are not readily taken up by plants. Others remain on plant surfaces where they can be eaten by foraging animals. For this reason, animals that eat perennial vegetation will be exposed to more contaminants than those eating annual herbs.

4.5. Freshwater ecosystems

4.5.1. Wetlands

4.5.1.1. Types of wetland

The different types and distribution of wetlands in the Arctic are described in chapter 2, section 2.5.3. The most important freshwater wetlands in the Arctic are bogs, fens, and shallow open waters such as tundra ponds. Swamps and marshes are also present, but are less common. These wetlands are primarily classified according to their vegetation composition.

1. Bogs commonly have a surface carpet of mosses, mainly *Sphagnum*, but may also support sedges, shrubs, and trees. These wetlands have an appreciable accumulation of peat.
2. Fen vegetation is similar to that of tundra meadows, with sedges and possibly grasses and reeds growing on peaty soils. *Sphagnum* is of minor importance. Shrubs are often present, occasionally together with sparse trees.
3. Swamps are dominated by woody plants, with some herbs and mosses. These wetlands have no surface accumulation of peat.
4. Marshes consist mainly of emergent non-woody plants such as rushes, reeds, reedgrasses, and sedges. The soils are wet, but not peaty. Open water areas may contain submerged and floating aquatic plants, while trees and shrubs may grow along the border of the marsh.
5. Shallow open waters, such as small ponds and channels within bogs, fens, and marshes, contain no emergent vegetation (Moore 1981).

The term mire is used to describe areas with considerable accumulation of peat. Bogs and fens fall into this category. Where the peat is acid (pH 3.0-5.0), the area is called a bog. Fens, on the other hand, are closer to neutral pH, as they are commonly flooded by basic waters. Peat accumulates in mires due to reduced decomposition of organic material and consists largely of decomposing plant parts and animal wastes. Slow decomposition in wetlands is largely due to waterlogged and therefore anaerobic conditions in the soil. Low soil temperatures also play a part in inhibiting breakdown of organic matter (Moore 1981).

The high content of dissolved and particulate organic matter in the water and soil of Arctic wetlands influences the fate and effects of contaminants. Organic matter affects transformation processes and bioavailability of contaminants to biota. Hydrophobic pollutants tend to bind to organic matter, and this interaction plays a major role in the determination of their fate and behavior.

4.5.1.2. Plants

The diversity of higher plants in Arctic wetlands is low. A few species of mosses (e.g., *Sphagnum* spp., *Drepanocladus revolvens*, *Bryum cryophilum*) and sedges (e.g., *Carex* spp., *Eriophorum* spp.) usually dominate the surface cover. Additional vegetation types that may be present include lichens (e.g., *Cladonia* spp., *Cetraria*), shrubs (e.g., *Ledum palustre*, *Betula grandulosa*) and, sporadically in the Low Arctic, trees (e.g., *Larix laricina*). Shallow ponds support aquatic vegetation such as horsetail (*Equisetum limosum*), water smartweed (*Polygonum amphibum*), duck weeds, and pond weeds (Zhadin and Gerd 1961).

Benthic microalgae (diatoms and blue-green algae) are also important primary producers in tundra ponds. Algae in the water column (i.e., phytoplankton) have low biomass, and annual productivity is among the lowest known (1.1 g C/m^2/y). Algal growth is limited by the scarcity of nutrients and reduced photosynthesis in the water column. Phytoplankton is comprised of very small flagellated nanoplankton, especially green algae, cryptophytes, and chrysophytes (Hobbie 1980).

More detailed descriptions of the vegetation of the different types of wetland have been given for Canada by Zoltai and Pollett (1983), and for Russia by Botch and Masing (1983).

4.5.1.3. Invertebrates

In the absence of fish predators, zooplankton thrive in wetland ponds; *Daphnia middendorffiana* may reach lengths of 3 mm, and fairy shrimp 20 mm. Strong grazing by zooplankton is likely to be responsible for much of the rapid algal turnover in the ponds. Herbivorous zooplankton are preyed on by predaceous zooplankton, including the copepods *Cyclops* and *Heterocope* (Hobbie 1980).

4.5.1.4. Vertebrates

Little has been published about the diversity of animals in Arctic wetland ecosystems. Among the higher vertebrates, only migratory birds are abundant and play an important role (Botch and Masing 1983). Waterfowl arrive in huge numbers after the ice melts to feed and breed. Common summer residents include geese (e.g., brant goose, *Branta bernicla*; bean goose, *Anser fabialis*; snow goose, *Chen caerulescens*), ducks (e.g., long-tailed duck, *Clangula hyemalis*; greater scaup, *Aythya marila*; red-breasted mergansers, *Mergus serrator*), swans (e.g., tundra swan, *Cygnus columbianus*; trumpeter swan, *Cygnus buccinator*), and gulls (e.g., herring gull, *Larus argentatus*; Sabine's gull, *Xema sabini*; Bonaparte's gull, *Larus philadelphia*) (Zhadin and Gerd 1961, Bellrose 1980, Godfrey 1986). These birds feed on plants, phytoplankton, zooplankton, and benthic animals (Hobbie 1980).

Fish cannot inhabit lakes that freeze to the bottom during the winter, and therefore are not found in the shallow wetland waters of the Arctic.

In general, higher animal life is richest both on wooded mire margins and on the wettest parts of wetlands, but rather poor in treeless areas without open water (Sjörs 1983). Small wetland areas, e.g., bogs, adjacent to or within northern boreal forests support a relatively rich fauna, including rodents, hare, marten (*Martes americana*), fox, mink, muskrat (*Ondatra zibethicus*), moose/elk (*Alces alces*), bears, and occasionally wolves.

4.5.1.5. Tundra ponds

With the exception of tundra ponds, very few ecological studies have been carried out on Arctic wetlands. Tundra ponds are small (about 30 × 40 m) and shallow (up to 0.5 m), with an average water temperature in summer of approximately 6°C. From late September until mid-June, the ponds and their sediments become solidly frozen (Hobbie 1980).

The annual primary productivity of tundra ponds is low (Table 4·4), as a result of the short ice-free season. The daily production during the growing season, however, is similar to that of ponds in more southern ecosystems. Plants, dominated by the sedge *Carex aquatilis* and the grass *Arctophila*

Table 4·4. Production of tundra pond communities (from Hobbie 1980).

Type of Community	Production, g C/m²/y
Phytoplankton	1.1
Benthic algae	8.4
Macrophytes	16.4
Zooplankton	0.2
Macrobenthos	1.65
Planktonic bacteria	0.01
Benthic bacteria	4-20
Protozoa	0.3
Microbenthos	0.2

fulva, cover about 30% of the bottom surface and are the dominant primary producers (Hobbie 1980).

In pond ecosystems, the grazing food chains are of lesser importance relative to detritus food chains. Since grazers of live plants are absent, large amounts of roots and leaves enter the detritus food chain, becoming either mineralized by bacteria and fungi or consumed by chironomid larvae. Despite the abundance of food, chironomids grow very slowly because the upper centimeters of sediment have an average summer temperature of only 3°C. It takes, for example, seven years for one species of *Chironomus* to metamorphose through four instar stages. Similarly, decomposition may take many years, owing to the cold temperatures, nine months of frost, and lack of shredders (e.g., chironomids) in the pond ecosystem (Hobbie 1980). Figure 4·2b illustrates a tundra pond food web.

4.5.2. Lakes

Within Arctic and subarctic regions, lakes range from typical temperate freshwater lakes to ultra-oligotrophic lakes in the High Arctic that are almost permanently covered with ice. The typical temperate lowland or coastal lake is often highly productive, and is characterized by transient ice cover, high summer temperatures, large species diversity, and complex food web structures. In contrast, a High Arctic lake ecosystem often has a low species diversity, short nutrient pathways, and simple food webs (Rigler 1975, Hobson and Welch 1995) (Figure 4·2c).

Availability of light, which is needed for photosynthesis, is an important factor in the productivity of Arctic lakes. During the polar night, the Arctic receives very little or no incoming radiation. When light levels rise in late winter and early spring, Arctic lakes are often covered with snow or ice which reflect the light. The albedo or reflectance of snow is approximately 80% and decreases progressively for white ice, candled ice, black ice, and water (Welch *et al.* 1987). Less light reaches the lake ecosystem the longer it takes for the snow and ice to melt off lakes in the spring. Some High Arctic lakes are covered with ice year-round and are very oligotrophic (Welch 1991).

Nutrients, particularly phosphorus, nitrogen, and silicon, are low in Arctic lakes. These chemicals are needed for photosynthesis, and thus their low concentrations limit productivity. Oxygen may also be low in Arctic lakes during winter when there is no photosynthesis (which produces oxygen). If oxygen drops below critical levels, fish in the lake will die. Winterkill generally occurs in lakes that are less than 4.5 m in maximum depth and 1.8 m in mean depth. In these shallow lakes, the oxygen supply is depleted before spring (Welch and Bergmann 1985).

4.5.2.1. Phytoplankton and primary production

Phytoplankton communities in High Arctic lakes have a lower number of species compared to temperate lakes, but still the number is relatively high. Small single-cell algae dominate in low-nutrient lakes. Chrysophytes and cryptophytes (many motile forms) are dominant groups, but diatoms and dinoflagellates (also many motile forms) can be important groups in deeper lakes.

Lakes within the Arctic region show great differences in primary production, depending on temperature regimes, nutrient input, light regime, and lake morphology. In the lakes Myvatn and Thingvallavatn, on Iceland, phytoplankton production may reach values >100 g C/m²/y (Jónasson and Adalsteinsson 1979, Jónasson *et al.* 1992), but in High Arctic lakes, production is very low (<10 g C/m²/y) (Hobbie 1984). Lake ice in Arctic areas is often clear (without air bubbles). Thus, even before the melting and breaking of the ice, periods of high irradiation lead to increased photosynthetic activity and phytoplanktonic population growth in the stable water layer beneath the ice. Increased vertical circulation of the water in summer gives rise to poor conditions for phytoplankton production.

Much of the primary production (photosynthesis) in Arctic lakes occurs on the lake bottom in the form of algae covering the rocks and sediment, and, in some lakes, beds of underwater moss. In the 27.5 m deep Char Lake, on Cornwallis Island, Canada (75°N), one fourth of the bottom is covered by mosses (Kalff and Wetzel 1971) and 80% of the primary production (22 g C/m²/y total) is by benthic moss and algae (Welch and Kalff 1974, Rigler 1975). Even at 64°N, primary production in lakes on the barrens is 50% benthic (Welch unpubl.), although phytoplankton production is higher (10-15 g C/m²/y) than in the High Arctic (Welch *et al.* 1989). Presumably in large lakes, the proportion of benthic primary production is less, although this is dependent upon the relative amount of shallow water in a particular lake.

4.5.2.2. Zooplankton

One characteristic of Arctic freshwater communities is the paucity, or even absence of species, or groups of species, in each trophic level of the food web. The recent evolutionary age of these communities, together with the low temperatures and poor feeding conditions, strongly limit the abundance and occurrence of zooplankton in High Arctic lakes. Low water temperature results in lower individual growth rates and lower numbers of generations per year (copepods 0.5-1 generations; cladocerans 1-2 generations). Further, several species have a nutrient threshold level that is too high for survival and reproduction under these extreme conditions. In general, the zooplankton biomasses measured in these lakes are comparable to those found in winter situations in temperate lakes, and in some Arctic lakes zooplankton are not present at all. The number of groups, the number of species within the groups, and abundance increase with increasing trophic level, and Hobbie (1984) has proposed the following general relationship between primary production (presence of phytoplankton) and zooplankton in Arctic lakes:

1. Extremely oligotrophic:
   few phytoplankton; no zooplankton.
2. Very oligotrophic:
   more phytoplankton; rotifers.
3. Quite oligotrophic:
   increasing number of phytoplankton; rotifers and calanoid copepods.
4. Oligotrophic:
   rotifers, calanoid copepods, and cyclopoids.
5. Oligotrophic-eutrophic:
   rotifers, calanoid and cyclopoid copepods, and Cladocera.

The general rule for Arctic ecosystems is that they are characterized by low species diversity, and the freshwater systems of Svalbard, a High Arctic archipelago, are typical examples of this. Despite the generally low number and density of species on Svalbard, there is a marked variation among lakes in species composition and abundance. In general, zooplankton communities have less than six species of rotatoria (common species are *Polyartra dolichoptera*, *Keratella hiemalis*, and *Kelicottia longispina*) and two to five species of Cladocera and Copepoda (common species are *Chydorus sphaericus* and *Cyclops abyssorum*) (Halvorsen and Gullestad 1976, Husmann *et al*. 1978, Jørgensen and Eie 1993). In fishless shallow lakes and ponds, predatory pressure is weak and the branchiopod (crustacea) *Lepidurus arcticus* and the cladocerans *Daphnia pulex* and *D. middendorffiana* are common species. In glacial-silted lakes, daphnids are excluded and the copepod *C. abyssorum* is often the only crustacean plankton.

The calanoid copepod *Leptodiaptomus minutus* often appears in clear oligotrophic lakes of Greenland and Iceland. In Greenland, this copepod is common and often the dominant or only species in the most extreme environments (Mosegaard 1978). In Iceland and northern mainland Scandinavia and Russia, the species diversity and density strongly increase, and more than 50 species of rotifers and 15-20 planktonic crustacean species are found. However, lakes occurring in this region range from ultra-oligotrophic high-mountain lakes, where planktonic life is virtually absent, to mesotrophic or eutrophic lowland lakes with high species diversity and biomass. Crustaceans play a major role in fish production, particularly in the subarctic regions. For most fish species, crustacean plankton, mainly cladocerans, are the main food source in the first year after hatching. For some species, particularly among the whitefish (coregonids), zooplankton is the most important food throughout the life-cycle.

4.5.2.3. **Benthic animals**

Low numbers of species and low biomass characterize the zoobenthos of Arctic lakes and ponds. However, a high variation in species diversity is found between localities. This is, in part, a result of abiotic variation, e.g., differences in glacier influence, depth, climate, elevation, postglacial time, chemistry, etc. However, biological factors such as postglacial immigration history, isolation and evolution, keystone species, and ecological interactions must also have been critical.

The zoobenthos communities in the Arctic lack many taxa that occur farther south. For example, there is a gradual decline in coleopteran species and an increase in dipterans toward the north (Chernov cited in Chapin and Körner 1994). The Svalbard archipelago provides a general picture of the situation found elsewhere in the Arctic (Planas 1994). The macro-zoobenthos is dominated by Chironomidae, usually about 10 species (Styczynski and Rakusa-Susczczewski 1963, Hirvenoja 1967) (north Norway: >49 species), and in many lakes, chironomid larvae make up more than 95% of total number and biomass. Benthic cladocerans, the phyllopod *Lepidurus arcticus* and the trichopteran *Apatania zonella* are also common, and some very few species within the groups *Trichoptera*, *Ephemeroptera*, *Notostraca*, *Oligochaeta*, *Ostracoda*, *Hydracarina*, and *Nematoda* have also been registered (Jørgensen and Eie 1993).

Most chironomids in Arctic lakes and ponds are detritivorous and feed on benthic algae, decaying organic material, and bacteria. Therefore, the abundance of these organisms in a lake strongly depends upon the depth profile and organic content of the bottom sediments. Density of benthic animals shows great between-lake variation, with the highest number in shallow lakes and ponds (Spitsbergen lakes: 50-400/m^2 (5 m), 90-4000/m^2 (<5 m)) (Hansen 1983).

In several High Arctic lakes, chironomids are the most important, and sometimes the only food item preyed on by Arctic char. In these waters, chironomids play a key role in the transference of nutrients (and pollutants) to higher trophic levels and, therefore, in fish productivity. In subarctic areas, more invertebrate groups are included in the fish diet.

4.5.2.4. **Fish**

In coastal and high mountain lakes of Iceland (Jónasson 1992), the Faeroe Islands, northwest Scandinavia, and the Kola Peninsula, fish communities are normally composed of only 3-5 species, as a consequence of postglacial immigration barriers. Atlantic salmon (*Salmo salar*), sticklebacks, brown trout (*Salmo trutta*), and anadromous (sea-run) and landlocked Arctic char (*Salvelinus alpinus*) are common fish. The low diversity of these fish communities reflects the relatively simple food web structures as compared to temperate high-diversity systems.

In Greenland, three-spined stickleback (*Gasterosteus aculeatus*) occur in many lakes (Riget *et al*. 1986). Open lake-river systems often have mixtures of anadromous and resident char, and all grades of mixtures from complete anadromy to complete residency have been observed. This circumpolar salmonid is one of the most variable and polytypic fish species known, and this variability has also been well demonstrated on Svalbard (see Gullestad 1975, Klemetsen *et al*. 1985, Hammar 1991, Svenning 1993, Svenning and Borgstrøm 1995). Landlocked lakes may have sympatric char morphs with very different life histories. In these lakes, Arctic char feed predominantly on chironomid larvae and pupae, and body growth is slow (Svenning 1993, Bergersen 1993). However, individuals in landlocked populations may reach large sizes, probably as a result of cannibalism (Hammar 1982, Svenning 1993, Svenning and Borgstrøm 1995).

From northern Norway and central Kola Peninsula, through northern Sweden and Finland, the landscape flattens out toward northern Russia, giving rise to the lowland tundra, forest, and swamp areas. This landscape has provided easy post-glacial access to a range of freshwater fish species from southern latitudes through river and lake systems. The result is an increased piscine diversity with increasing degree of longitude (east). This has resulted in more complex intra- and inter-specific competitive interactions within the food webs. As few as 8-10 different species occur in the western region, and up to 18-20 species are found farther east in the region of the Pechora River in Russia. Salmonid species within the genus *Coregonus* (5-10 different species and forms are found) often dominate the fish communities, but perch (*Perca fluviatilis*), northern pike (*Esox lucius*), and burbot (*Lota lota*) are also important species. Benthic invertebrates and surface insects are the main food sources of fish, and only 4-5 species, primarily within the genus *Coregonus*, feed mainly on crustacean plankton. Of the 3-4 species that consume fish, only adult pike may be considered as strictly piscivorous.

The distribution of fish species in the Canadian Arctic varies. Arctic char are common in High Arctic lakes north of Parry Channel. Anadromous species in the High Arctic are rare, but do occur in areas where outflows are substantial enough to allow return migration in August. In these areas, the typically marine four-horned sculpin (*Myoxocephalus quadricornis*) is also present (Welch unpubl.).

South of Parry Channel in the Canadian Arctic, lake trout (*Salvelinus namaycush*) becomes abundant. Fish species present on Melville Peninsula include lake trout, char, ninespine stickleback (*Pungitius pungitius*), and Arctic grayling (*Thymallus arcticus*). Farther south and west in the western and Low Arctic, species diversity increases. As in the Russian Arctic, several species of coregonids are present, including cisco (*Coregonus artedii*), Arctic cisco (*C. autumnalis*), least cisco (*C. sardinella*), lake whitefish (*C. clupeaformis*), and broad whitefish (*C. nasus*). Additional species include round whitefish (*Prosopium cylindraceum*), northern pike, lake chub (*Couesius plumbeus*), longnose sucker (*Catostomus catostomus*), burbot, threespine stickleback (*Gasterosteus aculeatus*), and slimy sculpin (*Cottus cognatus*) (Scott and Crossman 1973).

Fish species found in Alaska include Arctic char, broad whitefish, burbot, Alaska blackfish (*Dallia pectoralis*), chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), Arctic grayling, dolly varden (*Salvelinus malma*), humpback whitefish (*Coregonus pidschian*), lake trout, least cisco, longnose sucker, northern pike, round whitefish, and sheefish (*Stenodus leucichthys*) (Schroeder *et al*. 1987).

4.5.3. Rivers

Rivers in Arctic regions are fed by snowmelt runoff, precipitation, groundwater, and glacial meltwater. In low precipitation areas, such as the High Arctic, the runoff in nonglacier-fed watercourses is low after the vernal snowmelt.

4.5.3.1. Primary producers and invertebrates

In glacial rivers, the peak discharge usually occurs during the spring and summer melt, and there may be significant physical changes to the riverbed and transport of suspended sediment. Thus, algae and some invertebrates have reduced abilities for attachment to the substratum. Chironomids of the genus *Diamesa* are the dominant and often the only invertebrates found in these streams (Milner and Petts 1994). Diatom films on the bottom substrate, together with allochthonous organic material serve as energy sources for these chironomids. In northern Scandinavian glacial streams, species within the groups Tricoptera, Ephemeroptera, and Plecoptera are also common (Steffan 1971).

Spring-fed streams and rivers have relatively stable discharges, clear water, stable substrata, as well as warm winter and cold summer temperatures (Ward 1994). Mosses and diatoms are abundant, and the insect fauna is rich, relative to waters fed by glaciers and runoff (Hobbie 1984). Chironomids (Diptera), which may occur in high densities, constitute a major faunal component in these streams and rivers (Jørgensen and Eie 1993), but other insects within the groups Plecoptera, Trichoptera, Ephemeroptera, Oligochaeta, and Nematoda may also be abundant.

Tundra streams, common along the west Siberian coastal tundra, are generally low in productivity. These streams freeze solid during winter, but reach relatively high temperatures in summer. Tundra streams drain pits and soils, and are therefore characterized by low pH values as well as high contents of humic material.

Rivers fed by glaciers and direct runoff, as well as valley rivers originating from larger lakes are common in Iceland. As a result of Iceland's relative isolation, the diversity of the benthic river fauna is low compared to Scandinavia (Gíslason 1995). In the highly productive river Laxá, the following insects have been recorded: Diptera (largely chironomid species), Trichoptera, Plecoptera, and Coleoptera. The Icelandic invertebrate fauna is, in general, dominated by grazers (Orthocladiinae, Diamesinae, Chironomidae) feeding on benthic algae. Filter-feeders (mainly *Simulium vittatum*), feeding on drifting organic material, are common in those rivers originating from larger lakes.

In northern Norway and on the Kola Peninsula, running water ranges from cold, nutrient-poor, high mountain, and glacier-fed streams to warm and highly productive streams and rivers. Large rivers, some extending more than 200 km inland, are abundant. All rivers in the region have many rapids and waterfalls with stony bottoms, sometimes superseded by long, low-current, lake-like widenings, where sand and organic material accumulate. Some rivers flow through several lakes, while others are only connected to the drainage area of lakes through their tributaries. In some cases, lakes may play a very negligible role in the river flow. In the connected lakes and the lake-like widenings of the rivers, the macrophyte community is often well developed. High summer temperatures, nutrient loading, heterogeneous river channels, and immigration from the east give rise to a high diversity of both invertebrates and fish. In the Alta and Reisa Rivers in northern Norway, the benthic macroinvertebrate fauna is dominated by Ephemerotera (mayflies), Chironomidae, Simulidae, and Plecoptera (stoneflies) (Huru 1980, Bergersen 1987).

In the flat landscape of the northwestern part of Siberia, the large North Dvina, Mezen, and Pechora Rivers drain into the Barents Sea. The lower Pechora is characterized by a vast floodplain covered by waterbodies of different origins, constant erosion, and alluviation of the river terrace, sand islands, shoals and spits (Zhadin and Gerd 1961). Due to erosion and transport of vast amounts of suspended matter, the riverbed is almost devoid of vegetation and the benthic fauna, which includes a few Oligocheta, Chironomid larvae, and Mollusca, is extremely sparse. The waterbodies on the floodplains are also poor in fauna, and among the zooplankton, rotifers are the dominant animals. However, in the upper reaches of these rivers, and on driftwood in the lower reaches, the fauna is much more diverse and abundant.

The dominant river in the Canadian Arctic is the Mackenzie in the Northwest Territories. It is the largest north-flowing river in North America and the fourth largest in the circumpolar North after the Yenisey, Lena, and Ob Rivers in Russia. Suspended solids in fast-moving rivers limit the presence of macrophytes due to limited light penetration, however, 14 species have been detected in the Mackenzie River. In the Yellowknife River, NWT, phytoplankton are dominated by chrysophytes in summer, diatoms in winter and green algae in early spring. Important invertebrates found in the Mackenzie River include Simuliidae, Plecoptera, Chironomidae, and Trichoptera, with Ephemeroptera and Oligochaeta also present (Rosenberg and Barton 1986). Little is known about invertebrates in eastern Canadian Arctic rivers, where they range from chironomids in the High Arctic to chironomids, trichops, blackflies, and others in the Low Arctic.

4.5.3.2. Fish

Atlantic salmon is the most common fish species in Icelandic rivers, along with Arctic char and brown trout. These same three species are the most common and, for the most part, the only fish species occupying coastal rivers in northern Norway and the Kola Peninsula. In the central part of northern Scandinavia and the Kola Peninsula, the rivers are often inhabited by the same 8-10 species as are found in lakes of this region.

In the northwestern part of Siberia, the fish fauna are dominated by whitefish (*Coregonus lavaretus*, *Coregonus* *autumnalis*) and Atlantic salmon. Other species found in Siberia include Arctic lamprey (*Lampetra japonica*), inconnu (*Stenodus leucichthys nelma*), broad whitefish, least cisco, Arctic cisco, round whitefish, Arctic grayling, Arctic char, longnose sucker, burbot, ninespine stickleback, and slimy sculpin (McPhail and Lindsey 1970).

Fish species inhabiting rivers of the western Canadian Arctic include Arctic lamprey, inconnu, broad whitefish, least cisco, Arctic cisco, Arctic grayling, lake trout, Arctic char, chinook salmon, chum salmon, northern pike, flathead chub (*Platygobio gracilis*), burbot, ninespine stickleback, slimy sculpin, and yellow walleye (*Stizostedion vitreum vitreum*) (McPhail and Lindsey 1970). Fish species in rivers of the eastern Canadian Arctic are depauperate, ranging from Arctic char only to lake trout, char, grayling, and burbot.

Alaskan rivers provide habitat for Arctic lamprey, inconnu, broad whitefish, least cisco, Bering cisco (*Coregonus laurettae*), Arctic grayling, lake trout, Arctic char, burbot, slimy sculpin, and coho, chinook and chum salmon (McPhail and Lindsey 1970).

Many stocks of freshwater fish species in both North America and Eurasia, including whitefish, Arctic char, and trout, feed in the sea in summer after reaching a certain size, and return to rivers and lakes in winter to avoid low seawater temperatures. While at sea, they feed mainly on crustaceans and small fish species, for example Arctic cod (*Boreogadus saida*) or Pacific herring (*Clupea harengus*). In the most extreme conditions, for example the Canadian High Arctic, these species may feed sparsely or not at all during the winter. Female Arctic char may not migrate to sea in a year when they will spawn.

4.6. Marine ecosystems

4.6.1. Introduction

The Arctic Ocean and associated waters within the AMAP region (see chapter 2, Figure 2·1) comprise one of the most complex regions of the world's oceans. Environmental factors that influence Arctic marine ecosystems and make them unique from other oceanic regions include:

1. Marked seasonal distribution and low level of sunlight.
2. Low temperatures.
3. Presence of extensive ice cover.
4. Hydrographic interactions between seawater, ice, meltwater, and brine formation.
5. A high relative proportion of continental shelves and shallow water.
6. An influence of freshwater (incoming rivers and ice melt) and estuarine conditions that is significantly greater than in other oceans.

Apart from these physical factors which may limit the growth of organisms, Arctic marine fauna is younger and less diverse than that in the other oceans – a response to loss of fauna during recent glaciations. Recolonization has been slow due to extreme environmental conditions of low temperature and reduced food availability.

In subarctic marine waters (e.g., Greenland, Norwegian and Iceland Seas, and southern Barents Sea), temperatures are more moderate and there is relatively little ice cover.

4.6.2. Arctic Ocean Basin

The Arctic Ocean Basin supports marine biological communities which are comparable, though reduced in abundance and complexity, to those in northern temperate oceans. Examples of Arctic marine food webs are illustrated in Figure 4·2d. The idea that the central Arctic Basin is a biological desert has been challenged by recent observations. The amount of light that penetrates the ice into the water column below is highly seasonal, and even during the growing season, light penetration is affected by snow cover. Recent observations (Wheeler *et al.* 1996) indicate that previous measurements of low phytoplankton primary production in the water column in the central Arctic Basin (< 1 g $C/m^2/y$) (English 1961) underestimated the production. This underestimation is attributed to the fact that productivity by ice algae, and the release of dissolved organic carbon during the determinations of productivity were not taken into account. In some central Arctic Ocean regions, production by ice algae can exceed that in the water column. Assuming a growing season of 120 days, these authors estimate that total annual primary production (water column plus ice algae) is approximately 10 g $C/m^2/y$, with ice algae accounting for approximately 70% of the total. Studies in the Lancaster Sound/Barrow Strait area of the Canadian Arctic islands showed that total annual primary production (by phytoplankton, ice algae, and macrophytes) was 60 g $C/m^2/y$, with ice algae contributing about 10% of the total (Welch *et al.* 1992). Ice algae contributed a similar proportion of the annual total primary production in the Barents Sea (Sakshaug *et al.* 1994).

It is now evident that large regional differences in primary production occur in northern latitude oceans, determined by water column stratification and the availability of dissolved nutrients and light. For example, high rates of primary production have been measured over continental shelf areas such as the Chukchi Sea (325-360 g $C/m^2/y$) (Walsh 1989, Wheeler *et al.* 1996) and the Barents Sea (110-150 g $C/m^2/y$) (Walsh 1989, Sakshaug *et al.* 1994). The range of rates is similar to calculated values of phytoplankton production for the northern North Atlantic Ocean (200-400 g $C/m^2/y$) based on satellite-derived chlorophyll profiles (Sathyendranath *et al.* 1995).

Blue-green algae (cyanobacteria) may also have a role in energy transfer in the Arctic Ocean Basin, although their relative importance is not known. This group of microalgae occurs both in the water column and in sediments of the Lomonosov and Gakel Ridges of the Arctic Basin, presumably after sedimenting out (Marshall 1982, Lochte and Turley 1988, Pomeroy *et al.* 1990, Kröncke *et al.* 1994). Bacterial production is also thought to be reduced due to low temperatures, but not necessarily due to a lack of organic substrates (Pomeroy *et al.* 1990). The amount of dissolved organic carbon in the water column has been reported to be equivalent to, or higher than, that in other oceans, perhaps as a result of lower bacterial decomposition rates (Kinney *et al.* 1971, Gordon and Cranford 1985).

Herbivorous zooplankton are an important link between phytoplankton and higher trophic levels in the region of the Arctic pack ice. Copepods constitute most of the planktonic biomass and generally are the most numerous faunal group, with *Calanus* the most important single genus. Other groups include hydromedusans, decapods, chaetognaths, predaceous amphipods (including *Themisto* spp.), and larvaceans. Zooplankton apparently reproduce there, and nauplii have been found year-round (Hopkins 1969). In some areas, the large copepods *Calanus glacialis* and *Calanus hyperboreus* are associated with colder water masses; *Calanus finmarchicus* is associated chiefly with the warmer waters of Atlantic origin. The species rise in the water column to reproduce, with young stages feeding and storing lipids during the Arctic spring/summer, and then descending to several hundred meters to overwinter in an inactive stage in which they do not feed (Hopkins 1969, Dawson 1978, Hargrave *et al.* 1989).

The predatory amphipod *Themisto libellula* is an important predator of herbivorous copepods and other zooplankton in the area of the Arctic pack ice, as it is in other Arctic waters. It has been suggested that this species fills the same niche as euphausiids in other world oceans (Dunbar 1957) and which are not present in the central Arctic Ocean.

Benthic macrofauna biomass in the central Arctic Ocean is low, reflecting the small amounts of organic matter reaching the benthos (George 1977, Marshall 1982, Kröncke 1994). Faunal diversity is also low, probably as a result of the relatively youthful evolution of the fauna (Kröncke 1994). Benthic organisms include suspension and deposit feeders (Marshall 1982) as well as scavengers such as the amphipod *Eurythenes gryllus* which feeds on carcasses of fish and mammals (Hargrave *et al.* 1992). As in other areas of the world oceans, benthic standing crop decreases with increasing depth (Kröncke 1994), and ridges (e.g., the Lomonosov Ridge) have higher benthic standing crops than adjacent basins, evidently the result of an increased supply of organic carbon in water masses impinging on the bottom at these depths or the sedimentation/accumulation pattern associated with bottom topography. Suspension feeders predominate on coarse-grained sediments which occur on ridges, while deposit feeders are associated with fine-grained sediments of the deeper Arctic basins (Kröncke 1994).

Primary productivity in the Arctic Ocean Basin does not appear to be sufficient to support the energy demands of the planktonic and benthic populations (Hopkins 1969, Walsh 1989). It has been suggested that primary production on, or riverine inputs to, the Arctic shelves contributes to meeting energy requirements. The off-shelf flow of cold, dense water during the period of ice formation could transfer particulate organic material to deeper waters (Honjo 1990). Rivers bring a significant amount of organic matter to the Arctic Ocean, and for seas having significant river input (e.g., Beaufort, Laptev, and East Siberian), the contribution within 10 kilometers of the coast is significant – perhaps equal to the primary productivity in some coastal areas (Walsh 1989). However, it is not known how much organic material from rivers contributes to the organic matter over the shelf as a whole, or how much eventually reaches the deeper waters of the Arctic Basin. Sedimentation in an area of permanent ice cover off Ellef Ringnes Island was maximal in July and September, during the period of meltwater runoff and peak primary production (Hargrave *et al.* 1989, 1994)

4.6.3. Shelves and marginal seas

The complex of marginal seas surrounding the Central Arctic Ocean exhibits diverse physical and biological features. In general, they fall into two categories: 1) those which occur in areas of water exchange (portals) between the Atlantic and Pacific Oceans and the Arctic Basin, and 2) those on shelves on the northern margins of the Asian and North American continents which are bounded by the Arctic pack ice or ice-covered waters.

Marginal seas in areas where the influence of waters of the Atlantic and Pacific Oceans is significant include the Bering, Chukchi, Nordic and Barents Seas, and northern parts of the Labrador Sea (Baffin Bay and Davis Strait). Of these, the Chukchi, Bering and Barents Seas have among the most productive ecosystems in the world. Areas of elevated primary productivity tend to be spatially concentrated, associated with oceanic features such as ice edges, fronts, upwellings, or marginal ice zones (where ice cover grades into open water).

Ecosystems in ocean portal seas on the margins of the Arctic Ocean Basin are complex, in part the result of utilization of the elevated productivity of the waters by diverse groups of organisms. Species composition is varied, reflecting origins in both warmer oceanic areas and also more frigid areas. In these seas, phytoplankton blooms are generally dominated by large, chain-forming diatoms and the prymnesiophycean flagellate *Phaeocystis pouchetii* (Heimdal 1989). In the Norwegian Sea, influenced by Atlantic water masses, coccolithophorids are relatively more important, accounting for a considerable fraction of the transfer of biologically derived material to the deep waters in the Nordic Seas (Honjo 1990), but are a minor element in the Barents Sea (Heimdal 1983). The amount of organic carbon sedimenting into the deep parts of the Nordic Seas is large, almost equivalent to that found in temperate and tropical oceans, and appears to be fairly uniform throughout the year (see Honjo 1990 for a review, Bodungen *et al.* 1995, Noji *et al.* 1996).

The seas bordering northern Asia and North America (Kara, Laptev, East Siberian, and Beaufort) may be considered truly Arctic seas since they are influenced only to a minor extent by waters of Atlantic or Pacific origin. The seas are similar in character. All are influenced by freshwater runoff from large continental rivers (Golikov and Averincev 1977) and dominated by landfast ice which occurs during most of the year, and can extend to the edge of the continental shelf up to 400 kilometers from shore (Baird 1964).

Biological processes in these Arctic shelf seas are strongly influenced by ice, ice melt, and freshwater from river discharge. Water column productivity is limited either to coastal waters that are open in summer or to polynyas in the shear zone between landfast ice and the polar pack ice. In these open-water areas, processes and ecosystems associated with ice (e.g., ice edge productivity, under-ice communities) are important. The shear zone roughly coincides with the edge of the continental shelf, and thus productivity here may be an important component of the transfer of organic matter produced on the Arctic shelves and channeled into the deep water of the respective Eurasian and Canada Basins, as discussed in section 4.6.2 above. Freshwater discharge from rivers leads to an advance in the timing of open water in the nearshore zone – on average by 2.5 months for the Laptev and East Siberian Seas (Golikov and Averincev 1977) and by a similar time in the Beaufort (Percy *et al.* 1985).

Rivers and their associated organic material support estuarine ecosystems, including both primary productivity and heterotrophic processes, and impact adjacent marine areas by increasing turbidity, raising temperature, and lowering salinity over large areas (Golikov and Averincev 1977, Parsons *et al.* 1989, Walsh 1989). Productivity of the estuarine systems may be of the same order as that found in seasonally open water (Parsons *et al.* 1989). A significant proportion of the terrigenous organic matter from rivers may be metabolized by bacteria (Griffiths and Morita 1981 in Andersen 1989). The portion of the organic matter which is not used by organisms and not advected into the central Arctic Basin is incorporated into sediments. Local pockets of relatively high organic carbon can be found in sediments at the mouths of major rivers entering the Arctic Basin (Walsh 1989).

4.6.4. Special cases

4.6.4.1. Ice edges

Ice edges and associated water column features are key areas of elevated productivity in all regions of the Arctic (Smith and Sakshaug 1990). Melting ice leads to an increase in the stability of the water column which allows phytoplankton to be retained in a defined active photosynthetic layer at the margin of the ice (Marshall 1957). In many areas, the ice edge phytoplankton bloom follows the retreat of the ice margin, and can extend to 50 km or more from the ice edge (Smith and Sakshaug 1990). The spawning of zooplankton takes place during the phytoplankton bloom, so the new generation can feed on the remnants of this bloom. Zooplankton are preyed on, in turn, by fish (Sakshaug *et al.* 1994). This process follows the ice edge as it moves northward during summer.

4.6.4.2. Fjords, channels, straits, and polynyas

Semi-enclosed water bodies in the Arctic Basin include fjords, bays, and straits and channels between islands. Each environment is unique and characterized by exposure to tidal current regimes and occasionally extreme tides, the occurrence of continuous fast ice cover in winter, and open water during part of the year. Some polynyas arise in semi-enclosed areas (e.g., North Water polynya at the mouth of Lancaster Sound in Baffin Bay). Fjords in some regions, for example in Norway, are ice-free year-round.

4.6.4.2.1. Fjords

The coasts of Greenland, Norway, Iceland, and many of the islands fringing the Arctic Ocean Basin are characterized by fjords. Unique biological features of these areas include, in some cases, two phytoplankton blooms interrupted by turbidity from meltwater, significant depth, and enhanced productivity in the vicinity of melting glaciers and icebergs (Andersen 1989). Some fjords may have low benthic biomass (Petersen and Curtis 1980). Norwegian fjords, such as the Balsfjord, may be influenced by warmer water than in other areas of the Arctic (Hopkins *et al.* 1989). Fjords and bays usually have higher rates of primary productivity than Arctic Ocean waters (Subba Rao and Platt 1984). Although productivity is low (e.g., 6-14 g C/m^2/y) in turbid, High Arctic fjords (Andersen 1989), one fjord on West Svalbard was found to have a relatively high rate of annual primary productivity of 150 g C/m^2/y (cited in Walsh 1989). Sedimentation in fjords can occur as intensive pulses related to phytoplankton production (Noji *et al.* 1993, Wassmann *et al.* 1996).

4.6.4.2.2. Channels and straits

Channels and straits in the midst of island groups (particularly the Canadian Arctic Islands) represent unique environments. They typically freeze with landfast ice in winter and can show variable ice conditions in the summer season, being exposed to annual and multi-year ice, as well as significant tidal currents. These areas are moderately productive, but less biologically diverse than highly productive seas.

4.6.4.2.3. Polynyas

Polynyas occupy a small proportion of the area of the Arctic Ocean Basin, but in general are highly productive relative to ice-covered Arctic seas. They provide conditions that support ice-edge and open-water communities that are a locally important source of habitat and food for a variety of animals, including human populations. The absence of ice cover means that light levels suitable for photosynthesis occur earlier in the year and there is a longer production season (Lara *et al.* 1994). Food web productivity associated with ice edges helps to support marine mammals and seabirds. Polynyas in shallow water areas can result in a close coupling between benthic systems and water column primary productivity. The North East Water off northeast Greenland, for example, has enhanced benthic populations which support large stocks of walrus and eiders (Hirche *et al.* 1994).

4.6.5. Pelagic food webs

Primary productivity in the central basin areas and continental shelf regions of the Arctic Ocean is discussed above (section 4.6.2). Highest productivity occurs in areas where polar fronts occur (e.g., Barents Sea, Bering Sea), intermediate values are found in Arctic currents (such as the East Greenland Current) and marginal ice zones, followed by Arctic shelf seas, and finally by the central Arctic Basin which has a very low rate of primary production (Table 4·5). Although phytoplankton productivity is low (< 10 g C/m^2/y) in the central ice-covered region relative to temperate areas where rates are more than an order of magnitude higher, some marginal seas (such as the Chukchi Sea) support primary productivity comparable to other highly productive oceans (Wheeler *et al.* 1996). Microalgal communities that develop at the ice edge and under the ice are responsible for creating regions of high productivity in Arctic marine regions which otherwise would not be considered productive (Smith and Sakshaug 1990, Horner *et al.* 1992).

As in the Antarctic, primary production in the Arctic Ocean is different from other world oceans in that permanent, or semi-permanent, ice cover allows the development of under-ice biotic communities. The irregular bottom surface of the ice and the opening of leads and fractures presents a highly variable environment for these communities in space and time. Ice-algal communities develop before maximum summer production by phytoplankton, and therefore they provide an early food source for ice fauna (Carey 1985). Since growth of ice algae and planktonic algal communities are highly seasonal, a significant proportion of annual production may be introduced into Arctic marine ecosystems in one or a few short pulses (Legendre *et al.* 1992). Year-to-year variability may occur as the areal extent of ice cover and of snow cover changes. Further, large regional differences in productivity mean that a large proportion of the transfer of organic carbon from surface to deeper water is localized in a few areas.

4.6.6. Benthic food webs

Water depth is particularly important in determining the transfer of energy between pelagic and benthic organisms in various ecosystems of the Arctic Ocean. In shallow water, more organic matter is available for benthic consumers. Consequently, coastal margins and shallow shelf areas of marginal seas and embayments have benthic communities characterized by a high benthic macrofauna biomass, often dominated by large bivalves and other suspension feeders (Petersen and Curtis 1980, Welch *et al.* 1992) (Table 4·6). In Disko Bight on the west coast of Greenland, the productivity of the shallow benthic community of largely suspension-feeding mollusks equals that of zooplankton (Petersen and Curtis 1980).

Sequestering of organic carbon from primary production by benthic macrofauna in shallow waters provides an important trophic link to sea mammals, such as walrus and seals, and to birds. Examples include the shallow (< 50 m) northeastern Chukchi Sea, where advected organic particle loads and shallow depth are combined with relatively high local primary productivity (50-100 g C/m^2/y), leading to

Table 4·5. Annual phytoplankton primary productivity (g C/m²/y) for selected regions of the Arctic Ocean Basin.

Region	Primary productivity	Source
Polar pack		
Central Basin	0.6	English 1961
Central Basin	10[a]	Wheeler *et al.* 1996
Shelf seas		
Eastern Beaufort	22[b]	Parsons *et al.* 1989
Western Beaufort	20-40	Walsh 1989
Open ocean seas		
Deep Bering Sea	50	Walsh 1989
Alaskan Shelf Coastal Water	60	Walsh 1989
Nordic Seas	40-80	Walsh 1989
Barents Sea	110	Sakshaug *et al.* 1994
South Bering Sea Shelf	165	Walsh 1989
Chukchi Sea	325-360	Walsh 1989
Fjords, channels, bays and straits		
Canadian Arctic Islands	35-70	Platt *et al.* 1987
Barrow Strait	54	Welch *et al.* 1992
Disko Bight	60-90	Petersen and Curtis 1980
Balsfjord	115	Hopkins *et al.* 1989
Barents Sea Fjord	150	Walsh 1989
Representative temperate seas		
Scotian Shelf	102	Mills and Fournier 1979
Scotian Slope	128	Mills and Fournier 1979
North Sea	80	Steele 1974
Georges Bank	450	Cohen *et al.* 1982

a. Includes ice algae production (ca. 70%).
b. Estimated from daily rate for a season of 90 days.

Table 4·6. Macrobenthic biomass (g wet weight/m²) for selected regions of the Arctic Ocean Basin.

Region	Standing crop	Source
Polar pack		
Nansen Basin	<2	Kröncke 1994[a]
Alpha Cordillera	0.01-0.02	George 1977
Shelf seas		
E. Beaufort Shelf (estuarine)	0.1-20	Wacasey 1975
E. Beaufort Shelf (marine)	1-72	
W. Beaufort Shelf (21-100m)	9-120	Carey and Ruff 1977
W. Beaufort Shelf and Slope (101-2600 m)	4-227	
Kara Sea (<100 m)	123	Filatova and Zenkevitch 1957[b]
Open ocean seas		
E. Bering Sea (20-103 m)	23-786	Stoker 1973[b]
Baffin Bay (28-440 m)	47-69	Ellis 1960
Barents Sea (0-100 m)	311	Idelson 1934[b]
Barents Sea (100-400 m)	48-168	
Barents Sea (80-240)	13-104	Piepenburg *et al.* 1995
Davis Strait (180-970 m)	21-113	Stewart 1983
Grand Banks/W. Labrador Sea (50-100 m)	312	Nesis 1965
Grand Banks/W. Labrador Sea (500-1000 m)	46	
Fjords, channels, bays and straits		
Lancaster Sound (5-105 m)	55-1 094	Thomson 1982
Lancaster Sound (106-750 m)	33-180	
Hudson Strait/Ungava Bay (106-179 m)	109-480	Stewart 1983
W. Greenland Fjords (3-107 m)	39-411	Petersen and Curtis 1980
Representative temperate seas		
Georges Bank (50-200 m)	313	Steimle 1986
US Middle Atlantic Bight (0-200 m)	79-266	Wigley *et al.* 1976
US Middle Atlantic Bight (200-500 m)	28	
NE. Pacific Abyssal Plain	<12	Carey 1981

a. 95% of samples.
b. From Carey and Ruff (1977).

high production of mollusks, which play an important role in the diet of walrus (*Odobenus rosmarus*) and bearded seal (*Erignathus barbatus*) (Feder *et al.* 1994). Particle-feeding benthic communities are also important in the Lancaster Sound Region in the Canadian Arctic Islands (Welch *et al.* 1992). In contrast, the deeper waters of fjords show limited energy transfer into benthic systems. In the Balsfjord in northern Norway, most of the primary production is consumed by pelagic or bentho-pelagic organisms (e.g., shrimp) (Hopkins *et al.* 1989), while other fjords in Arctic Canada and Greenland have benthic populations with a relatively low biomass (Curtis 1975).

As mentioned above, ice is both a major limiting and enabling factor in overall productivity in all Arctic marine ecosystems, since its presence limits light penetration and it controls productivity at ice edges. Ice also impacts the benthic community, comprising one of the factors (together with reduced salinity and reduced light) which limits the subtidal distribution of macroalgae, typically resulting in a barren zone above depths of about 30-50 meters in most areas. Subtidal areas of the Laptev Sea have virtually no macroalgae due to the prolonged coverage by landfast ice (Golikov and Averincev 1977). Consequently macroalgal communities tend to contribute less to total primary productivity than in more southerly waters. Benthic microalgae are more widespread and limited to shallow Arctic waters, where productivity (although seldom measured) can be significant and comparable if not greater than water column primary productivity (Andersen 1989).

4.6.7. Arctic marine animals

4.6.7.1. Seabirds

The Arctic supports some of the largest seabird populations in the world. For example, several million little auks (or dovekies) (*Alle alle*) nest along the coast of northwest Greenland in summer (Boertmann *et al.* 1996). Numbers of seabirds are in fact greater in Arctic marine waters than in the tropics (Gaston 1995). Key nesting areas include the islands of the Bering and Chukchi Seas and the Sea of Okhotsk, the Beaufort Sea coast, the islands in the eastern Canadian Arctic archipelago, Hudson Strait, the northwestern coast of Greenland, the coasts of Iceland and Svalbard, Franz Josef Land, the north coast of Norway, and the west coast of Novaya Zemlya (Noble and Elliott 1986, Gabrielsen 1994, Bernes 1996, Boertmann *et al.* 1996, Hansen *et al.* 1996, Gaston pers. comm.). Many seabirds remain in the Arctic during the winter at areas of open water, such as polynyas and leads. Wintering seabirds in Greenland, for example, include common eiders (*Somateria mollissima*), black guillemots (*Cepphus grylle*), thick-billed murres (*Uria lomvia*), and little auks.

Approximately 40 species of seabirds breed in Arctic marine waters. Large populations of several other species breeding outside the Arctic spend the summer in Arctic waters, and several species of birds associated with Arctic terrestrial and freshwater habitats are dependent on the marine environment for periods of their life cycle. Several auk species are among the most abundant of Arctic seabirds, including the thick-billed murre (or Brünnich's guillemot), common murre (or Atlantic guillemot) (*Uria aalge*), little auk, least auklet (*Aethia pusilla*), and Atlantic puffin (*Fratercula arctica*). Among the gull species in the Arctic, the black-legged kittiwake (*Rissa tridactyla*) is the most numerous, but the glaucous gull (*Larus hyperboreus*) is also important. One of the most specialized Arctic species is the ivory gull (*Pagophila eburnea*), which is associated with the pack ice throughout its life cycle. Also common on Arctic coasts during the summer are northern fulmar (*Fulmaris glacialis*), common eider, and parasitic jaeger (*Stercorarius parasiticus*) (Noble and Elliot 1986, Gaston and Elliott 1989, Pattie 1990, Gabrielsen 1994, Gaston 1995, Bernes 1996, Boertmann *et al.* 1996, Hansen *et al.* 1996).

The majority of Arctic seabirds nest in large colonies on cliffs or isolated offshore islands, including the northern fulmar and most of the auks and gulls. Steep cliffs are inaccessible to predators such as Arctic fox, and are therefore favorable nesting sites for birds such as murres. Eiders and Arctic terns (*Sterna paradisaea*) tend to nest on islands, which are free of predators, while jaegers are more common on the tundra near the coast (Gaston and Elliott 1989, Gabrielsen 1994, Hansen *et al.* 1996).

Seabirds tend to be inshore feeders (e.g., black guillemot, eider) or offshore feeders (e.g., thick-billed murre, fulmar, puffin, little auk). Ice edges, marginal ice zones, and upwelling areas in the Arctic are important foraging areas for seabirds (Hunt 1991 in Mehlum and Gabrielsen 1993). Some seabirds forage on the tundra as well as at sea, including gulls and jaegers (Gaston 1995).

Seabirds feed at different trophic levels of the Arctic marine food chain. The little auk, for example, feeds largely on plankton (such as copepods); eiders consume benthic invertebrates (mainly bivalves); murres and puffins take fish when feeding their chicks, but may switch to planktonic crustaceans outside the breeding season; northern fulmar and the large gull species are omnivorous, consuming fish, crustaceans, squid, carrion, etc. (Mehlum and Gabrielsen 1993, Gaston 1995, Gabrielsen *et al.* 1995). The glaucous gull acts as a top predator when feeding on seabird eggs, chicks and adult little auks and is thus more prone to accumulating persistent contaminants (Noble and Elliot 1986, Gabrielsen *et al.* 1995) than many other seabirds.

4.6.7.2. **Fish**

Over 150 species of fish inhabit Arctic and subarctic marine waters, however, most of these are present in low numbers. The species described below are the most abundant and the most important in the diets of fish, birds and marine mammals.

4.6.7.2.1. **Arctic cod**

Arctic cod or polar cod (*Boreogadus saida*) has a circumpolar distribution and remains within the cold water masses of the Arctic region. It ranges from nearshore regions along the coast to well out at sea, and from the surface, where it can occur in holes in the sea ice, to as deep as 450 m (Lowry and Frost 1981) and 900 m (Walters 1955). In the autumn, Arctic cod tend to move to coastal areas, a behavior believed to be associated with seeking favorable temperatures for spawning. Arctic cod show extensive migration patterns in the Russian Arctic, thought to be in response to feeding and spawning behavior (Monstad and Gjøsæter 1987).

Arctic cod is a key species in many Arctic food chains and is a major link in the transfer of energy from the zooplankton to the top level carnivores. This small-sized and short-lived species consumes plankton along the ice edge. Young fish feed on phytoplankton, while the diet of older fish consists of copepods and amphipods (Sameoto 1984, Ajiad and Gjøsæter 1990). It is consumed by fish, including Arctic char (Moore and Moore 1974) and plaice; birds such as murres, guillemots, and kittiwakes; harp and ringed seals; and narwhal and beluga whales (Bradstreet and Cross 1982).

4.6.7.2.2. **Atlantic cod**

Atlantic cod (*Gadus morhua*) inhabits cool-temperate to Arctic waters from offshore regions to the edge of the continental shelf (Scott and Scott 1988). It is found in most coastal areas in the North Atlantic Ocean and in the Baltic Sea (Bergstad *et al.* 1987), as well as in the North Sea and Barents Sea. There are several different stocks of cod within the North Atlantic. All of these stocks have a seasonal feeding migration and, in addition, the mature fish have a rather long spawning migration (Gulland and Williamson 1962, Bergstad *et al.* 1987).

Atlantic cod is an opportunistic feeder, and the diet may vary considerably from year to year based on availability of prey species. As fry, they feed on copepods, amphipods, crustaceans, and crabs, and as adults, on redfish, capelin, herring, shrimp, and their own larvae. The diet may vary for different areas (Pálsson 1981, Mehl 1991, Jónsson 1992). Cannibalism is prevalent within this species, with larger cod eating smaller cod. This fish is preyed on by seals and minke whales.

4.6.7.2.3. **Other cods**

Greenland cod (*Gadus ogac*) also inhabits cold-temperate to Arctic waters, usually within inshore regions in the northern part of its range. It occurs from Alaska, along the Canadian Arctic coast to Greenland, and southward into Hudson Bay. Little is known of its movements.

Pacific cod (*Gadus macrocephalus*) extends north to the Chukchi Sea in Pacific waters. Its life habits are similar to those of Atlantic cods.

4.6.7.2.4. **Greenland halibut**

Greenland halibut (*Reinhardtius hippoglossoides*), a deep-water flatfish, is a target of commercial fisheries in both the Atlantic and Pacific Oceans. Recently, Greenland halibut have also been caught in the Beaufort Sea (Chiperzak pers. comm.), where they were previously considered absent. Tagging studies of Greenland halibut have shown that at least some individuals migrate over 1000 km (Sigurdsson 1981, Bowering 1984). Bowering and Brodie (1991) suggest that Greenland halibut from off the coast of Labrador and eastern Newfoundland migrate to deep-water spawning areas, moving back to summer feeding areas after spawning (Chumakov 1969, Sigurdsson 1981). These fish primarily consume squid, shrimp, herring, blue whiting, and capelin, and are preyed on by narwhal and hooded seals.

4.6.7.2.5. **Capelin**

Capelin (*Mallotus villosus*) is a commercially important planktivorous fish in Arctic and subarctic areas. It has a circumpolar distribution, with large stocks in the Labrador Sea, in the Iceland-Greenland-Jan Mayen area, and in the Barents Sea. The largest capelin stocks, in the Barents Sea (Gjøsæter 1995) and in the Iceland-Greenland-Jan Mayen region (Vilhjalmsson 1994), have been subject to large stock fluctuations in recent years.

Capelin mainly eat copepods, however, adult individuals also consume large amounts of euphausiids and some amphipods. It is consumed by fish, including cod and other demersal fish (Mehl 1991), seals (mainly harp seal) (Nordøy *et al.* 1995a), toothed whales (Haug *et al.* 1995a, 1995b, Nordøy *et al.* 1995b), and birds (mainly common guillemot and Brünnich's guillemot) (Mehlum and Gabrielsen 1995).

4.6.7.2.6. **Redfish**

Redfish (*Sebastes* spp., e.g., *S. marinus* and *S. mentella*) are common in the northern North Atlantic. They are rare in the North Sea and are not found farther south along the European continent (Pethon 1985). Important spawning areas for redfish are off the northern coast of Norway and the Irminger Basin southeast of Greenland. Redfish are ovoviviparous, i.e., the eggs are hatched within the ovary of the female, and spawning areas refer to where offspring are released. Fertilization takes place in feeding areas.

Zooplankton, such as euphausiids and copepods, are the preferred diet of redfish (Pálsson 1981). Various other fish and fish larvae are also included in the diet of larger individuals (Pedersen and Riget 1992, Jónsson 1992). Redfish are eaten by other fish (Atlantic cod, Greenland halibut) and whales. Redfish grow very slowly and can reach an age of 60 years, however, specimens older than 25 years are rare. They mature at a fairly late age of 10-20 years (Pedersen and Riget 1992).

4.6.7.2.7. Long rough dab or American plaice

Long rough dab or American plaice (*Hippoglossoides platesoides*) can be found on both sides of the northern North Atlantic. It is the most abundant flatfish in the Barents Sea (Albert *et al.* 1994). There has been little commercial interest in long rough dab, which live near the bottom and prey mainly on various benthic organisms, such as Ophiuroidea and Polychaeta (Pálsson 1981). Small long rough dab also feed on planktonic prey groups. Their main predator is cod.

4.6.7.2.8. Herring

Herring (*Clupea harengus*) is a boreal species which can also be found in arcto-boreal regions. There are several stocks in the Atlantic area, around Newfoundland and Iceland, and in the Norwegian Sea. The latter is the largest herring stock in the world. It spawns off the western Norwegian coast, and the young stages (0-3 years old) are found in the Barents Sea. The adult stock migrates to the open Norwegian Sea to feed, and is found in most of the areas between Norway, the Faeroe Islands, Iceland, and Greenland during the feeding season (Gjøsæter 1995).

The herring stocks play a major role in the ecosystems where they are found, utilizing the plankton production in highly productive frontal areas in the open seas, and serving as food for numerous predators, amongst which sea mammals are probably the most important. Herring stocks are harvested and often play an important commercial role.

4.6.7.3. Marine mammals

Often the top predators in Arctic marine food webs (Figure 4·2d) and important in the diets of Arctic peoples, marine mammals are of special interest as monitors of spatial and temporal trends in the accumulation of contaminants.

4.6.7.3.1. Seals

Seals are very important predators in Arctic marine food chains. They are usually second or third level carnivores, and are in turn preyed on by killer whale, polar bear, and humans.

The ringed seal (*Phoca hispida*) is by far the most abundant and widely distributed resident Arctic pinniped, with a widespread circumpolar distribution. Ringed seals have a preference for annual, landfast ice, but are also found in multi-year ice (Kingsley *et al.* 1985). Although ringed seals are generally territorial and philopatric, some may leave their overwintering areas as ice cover decreases in the summer. Their diet consists of fish, mainly Arctic cod, and crustaceans (amphipods, mysids, and euphausiids). A summer diet of over 50% cod has been estimated for ringed seal in Barrow Strait (Hobson and Welch 1992).

Ringed seals inhabiting the Arctic Ocean and adjacent seas may be a single population. High rates of immigration and emigration have been reported. For example, ringed seals tagged at Point Parry, NWT (70°N, 125°W), were later found at Point Barrow in Alaska and East Cape in Siberia (66°N, 170°W) (Smith 1987). However, ringed seals are not generally considered to be a highly mobile species. During the period of landfast ice, ringed seals will remain in very small areas (Smith and Hammill 1981, S. Innes pers. comm.). Based on site tenacity and territoriality, Smith and Hammill (1981) estimated that male ringed seals may occupy the same small under-ice habitat for as much as nine months of the year.

Bearded seals (*Erignathus barbatus*) have a circumpolar distribution and are found all along the European, Asiatic and North American coasts of the Arctic Ocean. Two subspecies are generally recognized, one from the Laptev Sea in Siberian Russia and westward across the Atlantic into Hudson Bay, the other from the Laptev Sea and eastward through the Canadian Arctic (Lydersen and Wiig 1995). Bearded seals are normally associated with drifting ice floes, and their general benthic feeding habits (primarily epibenthos; crustaceans and mollusks in particular) restrict their range to relatively shallow waters (Burns 1981). Bearded seals do not form dense congregations during whelping, which normally takes place on loose pack ice between April and May. Regular seasonal migrations are not undertaken, but the animals may drift or move actively over long distances.

Harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) are important Atlantic species, inhabiting Arctic and subarctic waters. Both species feed primarily on small marine fish and secondarily on crustacean macroplankton. Pups feed on crustaceans, mainly krill and amphipods of the genus *Themisto* (Haug *et al.* 1996b). The diet of older harp seals also comprises krill and *Themisto*, but in addition, is characterized by substantial amounts of fish such as Arctic cod, Atlantic cod, capelin, and herring (Nilssen 1995, Anon. 1997). Hooded seals, which are deep divers, feed on demersal and benthic species including mussels, starfish, squid, octopus, shrimp, and fish such as Greenland halibut, redfish, Atlantic cod, wolffish, and blue whiting (Folkow and Blix 1995, Anon. 1997).

There are three separate harp seal populations in the Arctic, all of which migrate annually between southerly breeding sites and the northern feeding grounds, both at the edge of the pack ice (Lavigne and Kovacs 1988). Herds that breed in the Gulf of St. Lawrence migrate north to Hudson Bay, Davis Strait, and Baffin Bay. Animals that reach the maximum extent of the range may migrate as far as 5000 km. The breeding population that congregates in the White Sea off the coast of Russia, and the population that pups mainly between Jan Mayen and Svalbard, move to ice patches north of the breeding areas which include the northern Barents and Kara Seas north of Svalbard, Franz Josef Land, and Severnaya Zemlya.

Hooded seals share much of their range with harp seals, however, they remain farther offshore and feed in deeper water. The main breeding areas are the Gulf of St. Lawrence, Davis Strait, and near the 'West Ice' off Jan Mayen. All migrate north to feeding areas off the pack ice. Hooded seals wander more widely than harp seals.

The harbour seal (*Phoca vitulina*) is one of the most widespread pinnipeds in the Northern Hemisphere, where it mainly inhabits temperate and subarctic regions, but to some extent also Arctic regions (e.g., Svalbard, see Lydersen and Wiig 1995). Harbour seals are regarded as non-migratory and rather sedentary. Grey seals (*Halichoerus grypus*), like the harbour seals, are also confined mainly to coastal areas in temperate and subarctic regions, apparently preferring the outlying exposed islets and skerries. Three distinct populations are known: in the Baltic Sea, and in the eastern and western North Atlantic (Bonner 1981). Young grey seals may occasionally move widely, while adults are considered more localized. Both the harbour and grey seals are mostly coastal in their food habits, feeding opportunistically on a wide variety of fish, some cephalopods, and crustaceans (Bigg 1981, Bonner 1981).

The walrus (*Odobaenus rosmarus*), which is the largest of the Arctic seals, has a disjunct circumpolar distribution with two recognized subspecies. The Atlantic walrus (*O. r. rosmarus*) ranges from the eastern and central Canadian Arctic eastward to the Kara Sea (Reeves 1978, Born *et al.* 1995), while the Pacific walrus (*O. r. divergens*) is confined to the Bering and Chukchi Seas (Fay 1981). Born *et al.* (1995) suggested that the usually bivalve-eating walruses occupy a comparatively narrow ecological niche, their populations probably being dependent on: 1) the availability of large areas of shallow water (80 m) with suitable bottom substrate to support a productive bivalve community, 2) the presence of reliable open water over rich feeding areas, particularly in winter when access to many feeding areas is denied due to ice cover, and 3) the presence of haul-out areas (ice pans, beaches) in close proximity to feeding areas. Most walrus populations appear to be migratory, moving southward with the advancing ice in autumn and northward as the ice recedes in spring (Fay 1981).

Other seals inhabiting Arctic waters include the spotted (*Phoca largha*) and ribbon (*P. fasciata*) seals of the Bering, Chukchi and Beaufort Seas and the northern fur seals (*Callorhinus ursinus*) which breed in the Pribilof Islands of Arctic Alaska. The principal prey of these three seal species are fish.

4.6.7.3.2. **Whales**

The white whale or beluga (*Delphinapterus leucas*) has a disjunct circumpolar distribution. This toothed whale has a nearly continuous distribution across the Russian Arctic coast, limited in the Atlantic to the north coast of Norway, and in the Pacific to the Okhotsk Sea (Kleinenberg *et al.* 1964). They are also present along the east and west coasts of Greenland and in North America, extending from Alaska across the Canadian western Arctic to a large population in Hudson Bay and among the islands in the eastern Canadian Arctic (Banfield 1974, Boertmann *et al.* 1992, 1994). They feed in shallow estuaries on a variety of foods, which include capelin, herring, cisco, sculpin, Atlantic and Arctic cods, flounder, salmon, and char, as well as invertebrates such as octopuses, squids, shrimps, and paddleworms (Banfield 1974). Beluga commonly dive to 800 meters (P. Richard pers. comm.).

Movement of the beluga pods is seasonal and predictable, coming into the coastal waters and estuaries in mid-summer, and wintering offshore in loose pack ice and polynyas (Brodie 1989). These migrations are responses to offshore feeding opportunities, coastal ice formation, and the need for estuarine conditions during the summer calving period. Some general facts of the migration of major stocks are known. Tagging experiments of beluga in Hudson Bay suggest that the migratory range is 800 km, from southwest to northwest Hudson Bay (Sargeant and Brodie 1969). Another stock of beluga migrates from its summer domain in the Canadian High Arctic to Baffin Bay for the winter. A number of extralimital observations suggest that some individuals, probably males, will wander great distances (Boertmann *et al.* 1994, Norris 1994, Stewart and Burt 1994, P. Richard pers. comm.).

Narwhal (*Monodon monoceros*) is the northernmost cetacean, most commonly inhabiting the Arctic seas between 70 and 80°N. It frequents the waters within the eastern Canadian Arctic archipelago, along the west and east coasts of Greenland, and around Svalbard and Novaya Zemlya, moving north in spring and south in winter, and generally remaining in deep water near landfast ice and ice floes. This species is well known for its long, spiraled tusk, a modified tooth which protrudes through the upper lip in males and infrequently in females. The diet of narwhal includes Arctic cod, Greenland halibut, cephalopods, and crustaceans. Though sometimes preyed on by polar bear, the principle predator of the narwhal is humans (Banfield 1974, Reeves and Tracey 1980).

Other toothed whales, such as killer whale (*Orcinus orca*), white-beaked dolphin (*Lagenorhyncus albirostris*), and harbour porpoise (*Phocoena phocoena*) occur mainly in ice-free waters (Boertmann *et al.* 1992). The killer whale is at the top of the food web, feeding on everything from baleen whales to seals, birds, and different fish species.

The bowhead whale (*Balaena mysticetus*) is the only baleen whale which spends its entire life in and around Arctic waters. It has a nearly circumpolar distribution, seasonally determined by the localization and configuration of the drifting pack ice, but is today rather rare in many areas due to heavy exploitation (Braham 1984, Shelden and Rugh 1995). Five stocks are recognized, probably with geographic and reproductive isolation between the two in the North Pacific and the three in the North Atlantic (Shelden and Rugh 1995). Bowhead whales feed exclusively on planktonic crustaceans such as krill, copepods and, to some extent, hyperiid amphipods (Braham 1984).

Several other baleen whale species are known to occur in Arctic regions of the Northern Hemisphere at certain times of the year. In the North Atlantic, blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), minke whales (*Balaenoptera acutorostrata*), humpback whales (*Megaptera novaeangliae*), and occasionally sei whales (*Balaenoptera borealis*) are known to penetrate into polar waters (Jonsgård 1966, Christensen *et al.* 1992a), while fin and humpback whales occur seasonally in the Pacific Arctic (the Bering Sea, see Nishiwaki 1966). Distribution is connected with the feeding and breeding habits of the whales. Blue whales feed almost entirely on planktonic crustaceans, while fin, humpback, and minke whales eat planktonic crustaceans and shoaling fish such as herring, capelin, and pollack; minke whales consume even larger fish such as gadoids (Nemoto 1970, Christensen *et al.* 1992b, Haug *et al.* 1996a). Feeding by baleen whales in Arctic regions occurs during the summer months, while during autumn and winter most of these whales migrate southward to warmer waters where breeding takes place (Jonsgård 1966, Nishiwaki 1966).

4.6.7.3.3. **Polar bear**

The ecology of polar bears (*Ursus maritimus*) is closely tied to that of ringed seals (*Phoca hispida*). Densities of seal vary in response to the overall productivity of the ecosystem in different areas, and these changes also cause changes in the productivity of bears (Stirling and Øritsland 1995). Polar bears preferentially consume ringed seal blubber and skin. In addition to ringed seal, they may eat lesser amounts of bearded seal (Stirling and Archibald 1977), and occasionally prey on beluga and walrus (Lowry *et al.* 1987, Calvert and Stirling

1990). In late spring, polar bears become highly active in response to readily available young and molting seals. The bears acquire most of their annual nutrient reserves during this period (Ramsay and Stirling 1988). It has been shown that polar bears do not eat significant amounts of terrestrial food, even when forced onto land (Ramsay and Hobson 1991).

Polar bears mate in the spring (Wiig *et al.* 1992). Fertilized eggs do not implant before September-October, about the same time that the pregnant female enters the den (Ramsay and Stirling 1988). Cubs are born around Christmas and the female usually emerges from the den with two cubs in March or April after six months of fasting and three to four months of nursing. Polar bear milk has a high fat content (Arnoud and Ramsay 1994) and lactation seems to occur more or less until weaning at 2.5 years.

Polar bears occur in low densities throughout the Arctic Basin and are circumpolar in their distribution. Several general populations are recognized in the main Arctic Basin, these being: 1) Wrangel Island and western Alaska, 2) northern Alaska, 3) the Canadian Arctic archipelago, 4) Greenland, 5) Svalbard and Franz Josef Land (Wiig 1995), and 6) central Siberia (DeMaster and Stirling 1981). A more recent study recognizes 11 populations (Taylor 1994).

Two general patterns of polar bear movement are evident in these populations. Polar bears in the Canadian Arctic have an archipelagic migration pattern, with extensive use of offshore sea ice and ice-covered inter-island channels during fall, winter, and spring. During summer, the sea ice may melt completely and polar bears become stranded on land to await the return of the ice (Derocher and Stirling 1990), or retreat to ice-covered bays and later over-summer on land (Stirling *et al.* 1984). In this habitat, as well as on Wrangel Island, females are faithful to the same denning locations (Schweinsburg *et al.* 1984). In contrast, polar bears in the Beaufort, Barents, Bering, and Chukchi Seas, and presumably throughout much of the Arctic Basin, have a pelagic migration pattern and use offshore sea ice throughout the year with only limited use of land in summer months (Garner *et al.* in press, Wiig 1995). Females frequently den on sea ice (Amstrup and Gardner 1994). In Svalbard, a mixture of these two general patterns is seen (Wiig 1995). Some bears tend to stay in the same fjord all year round while others migrate far out to the Barents Sea and even into the Russian Arctic. In the ice-free period along the coast, bears may either stay on land or follow the sea ice when it retreats north. Each spring females tend to come back to the same area to breed (Wiig 1995).

Annual movements vary greatly from region to region. In the Beaufort Sea, movements have been estimated to range over 10 000-23 000 km^2 (Amstrup *et al.* 1986); in the archipelagic habitats of Arctic Canada, they range between 2500 and 23 000 km^2 (Schweinsburg and Lee 1982); in Svalbard, the movement is much more variable, in the range of 1000-325 000 km^2 (Wiig 1995); and in the Bering and Chukchi Seas, the movements are extensive, in the range of 150 000-350 000 km^2 (Garner *et al.* in press).

Polar bear distributions are affected by locations of polynyas or shear zones between shore-fast and multi-year ice pack floes. Polynyas in the Arctic are more temporally constant than is the case in open water, pelagic regions. Polar bears become habituated to polynya locations, and thus their migrations are limited (e.g., at the North Water polynya; Boertmann *et al.* 1994).

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