UNIVERSITY OF THE ARCTIC

# Module 7

# Life on Land

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## Key Terms and Concepts

- climatic variation
- topography
- adaptation and survival strategies
- ecosystems
- nutrient status
- feeding and food webs

## Learning Objectives

This module you should help you to

1. explain, through selected examples, how life manages to survive and thrive in an apparently severe environment.

2. describe the climate that is experienced by plants and animals above and below the ground (micro-scale) and over landscapes (macro-scale).

3. identify the main climatic factors that influence aquatic environments on land.

4. describe the intimate relationship between land and water for individual species, ecosystems, and landscapes.

5. illustrate how different animals and plants have evolved strategies that enable them to thrive with the extreme climate on land.

6. illustrate how general ecological principles (see Module 6) can be applied to consideration of life on land.

## Reading Assignments

AMAP (1997), *Arctic Pollution Issues: A State of the Environment Report*.

CAFF (2001), *Arctic Flora and Fauna: Status and Conservation*.

# Overview

Life on land is a continuum that includes the wetlands, rivers, and lakes. In the Arctic, life is certainly dominated by climate, but climate is not simply temperature. $H_2O$ in all its forms, as well as radiation and wind, each plays a part in defining climate. Location—where you are in the landscape—also has significance.

This module explores three aspects of life on land:

- **Climate variation and its ecological effects.** In this section you will examine the ways climate influences plants and animals at a large scale, over landscape and continental scales. You will then consider climate at a micro-scale, particularly the effect of small changes in topography. In aquatic systems, variations in temperature are much less extreme than on land, but they are still critical to life.
- **Survival strategies of Arctic flora and fauna.** How do organisms adapt to the climate, and which characteristics have been selected over time? Adaptations may be physical, physiological, reproductive, or behavioural. They vary in combination and from place to place. Examples are taken from different taxonomic groups: mammals, birds, invertebrates, microflora, and plants.
- **Ecoystems, food webs, and nutrients.** In Module 6 you reviewed various general ecological principles. In this module, you will be asked to consider how these ecological principles are applied to two major ecosystems on land. The two examples are Lake Myvatn in Iceland, and Toolik Lake in Alaska. Their names suggest that they are freshwater ecosystems. The lakes are certainly the focus of attention, but it is soon apparent that what happens in the lakes is strongly influenced by what happens in the surrounding land—the catchment area—and vice versa. Where do these systems begin and end? Is it a question of scales of space and time and of gradients?

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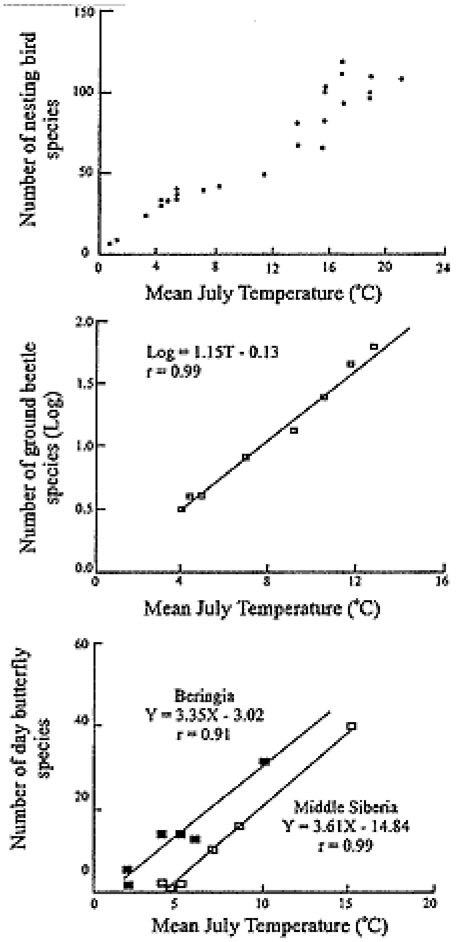
# Lecture

## Climate Variation and Its Ecological Effects

The Arctic is certainly distinguished by its cold climate. But we must not consider the climate that is experienced by the flora and fauna by what we, as humans, perceive and experience. We must explore the microclimate on and in the vegetation and soil, or in the burrows or lairs of the mammals, or in the habitats of the birds. Most of the Arctic biota live near the ground, or in it, or in the water where the temperature is very different; and they have developed many and varied methods of reducing the influence of the water's temperature. Water, in its many and varied forms and characteristics—such as snow depth and composition, ice cover, and liquids with varying salt concentration—is very important, often limiting, for life on land. The power of ice in freeze-thaw cycles is a major factor in the stability of habitats. Where water is available during the winter, life can go on. Drought seriously limits biological activity in polar semi-deserts and deserts. Light, or its low intensity, may limit plant growth for much of the year, especially in water darkened by dissolved organic matter. The reduction in terrestrial activity with increasing latitudes is also related to the length of time since the last ice cover as well as to temperature: time is a factor influencing the biota. So, in considering the physical environment that influences terrestrial and freshwater life, it is essential to identify the wide range of factors in which the organism lives and how these factors interact.

## Ecological Effects of Macroclimatic Variation on Land

Where other environmental factors such as topography and geology are almost constant, it is the length of the summer, or summer heat, or growing season that determines the diversity and productivity of the flora and fauna. This is most simply expressed by the July mean temperature to which many other climatic factors are correlated, including the length and intensity of the winter. The vast continental land mass of the Taimyr Peninsula in Siberia, where there is little change in topography and geology, provides a complete summer temperature gradient from 12°C at the timberline to 2°C in the polar desert. Here, many ecological features correlate directly to the mean July temperature (see fig. 7.1). This general relationship holds for other areas but is less clear because other factors are superimposed on the climatic gradient. Thus, in North America, the Brooks Range in Alaska and the Richardson Mountains in the Yukon Territory break the climate and vegetation patterns. In the Northwest Territories of Canada, extensive glaciation has limited soil and vegetation development, and the Canadian Arctic Archipelago creates a boundary between the mainland and islands, generating a steep gradient between continental and more oceanic climates (Matveyeva and Chernov 2000; Bliss and Matveyeva 1992).

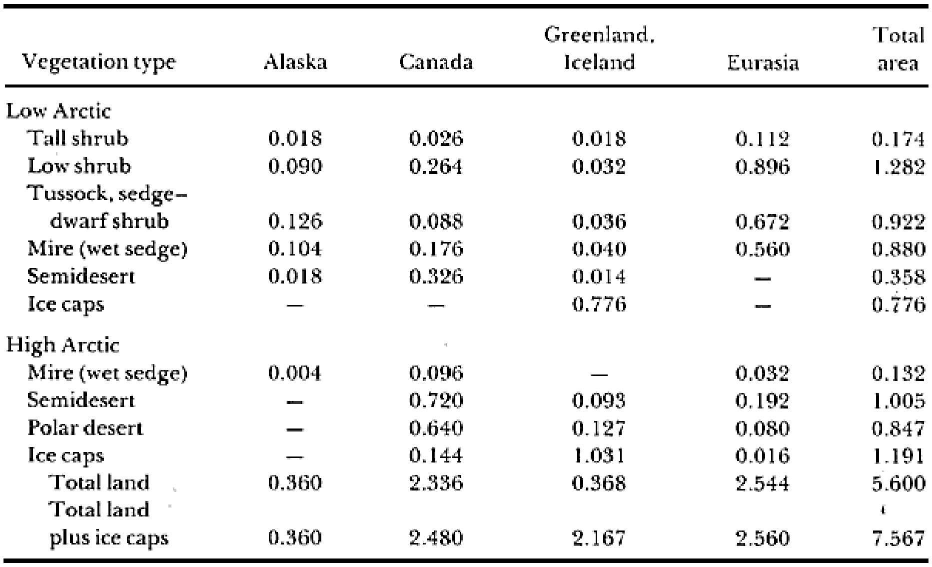


**Source:** Matveyeva and Chernov (2000)

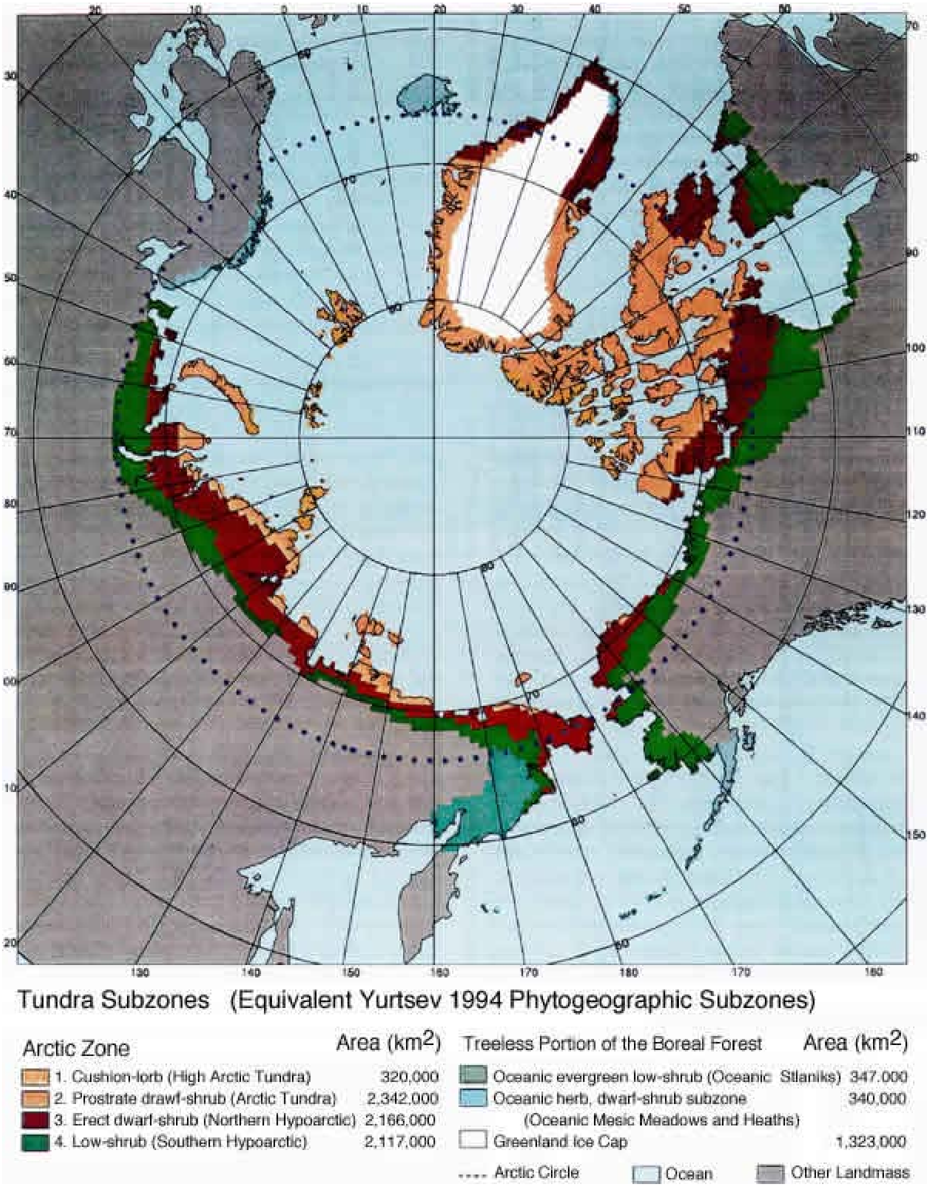
**Fig. 7.1** Relationship between number of species and mean July temperature. Top: Numbers of species of nesting bird species in western and middle Siberia. Middle: Number of species of ground beetles in local faunas of the Taimyr Peninsula. Bottom: Number of day butterfly species in the middle Siberia and Beringian sectors of the Arctic.

These broad climatic gradients determine the main tundra habitats or vegetation types extending from the boreal forest at lower latitudes and altitudes to the polar deserts of the north and high mountains. The total land area of tundra is about 5.6 x $10^6$ km$^2$, mainly in Canada (2.3 x $10^6$ km$^2$) and Eurasia (2.5 x $10^6$ km$^2$), but excluding the ice caps of 7.6 x $10^6$ km$^2$. The classification of the land into main types of vegetation (see table 7.1) reflects the main patterns of climate and follows the broad distinction between Low Arctic and High Arctic. These calculations are not definitive. Other authors have generated slightly different estimates using different criteria, but the general pattern is consistent for the land north of the boreal forest and is mapped in figure 7.2.

**Table 7.1** Area of major Arctic vegetation types in 106 km$^2$ (Bliss and Matveyeva 1992)



| Vegetation type | Alaska | Canada | Greenland, Iceland | Eurasia | Total area |
|---|---|---|---|---|---|
| Low Arctic | | | | | |
| Tall shrub | 0.018 | 0.026 | 0.018 | 0.112 | 0.174 |
| Low shrub | 0.090 | 0.264 | 0.032 | 0.896 | 1.282 |
| Tussock, sedge–dwarf shrub | 0.126 | 0.088 | 0.036 | 0.672 | 0.922 |
| Mire (wet sedge) | 0.104 | 0.176 | 0.040 | 0.560 | 0.880 |
| Semidesert | 0.018 | 0.326 | 0.014 | — | 0.358 |
| Ice caps | — | — | 0.776 | — | 0.776 |
| High Arctic | | | | | |
| Mire (wet sedge) | 0.004 | 0.096 | — | 0.032 | 0.132 |
| Semidesert | — | 0.720 | 0.093 | 0.192 | 1.005 |
| Polar desert | — | 0.640 | 0.127 | 0.080 | 0.847 |
| Ice caps | — | 0.144 | 1.031 | 0.016 | 1.191 |
| Total land | 0.360 | 2.336 | 0.368 | 2.544 | 5.600 |
| Total land plus ice caps | 0.360 | 2.480 | 2.167 | 2.560 | 7.567 |

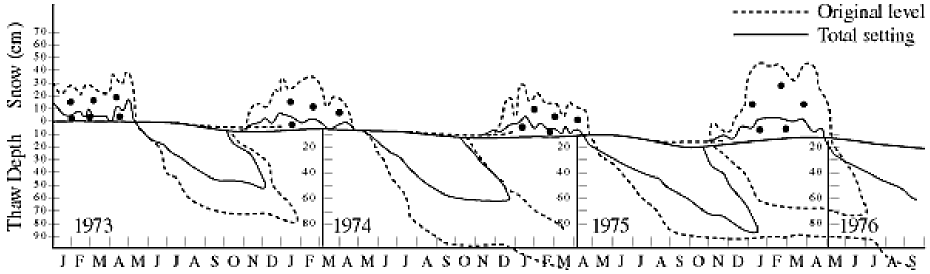


**Source:** Walker (2000)

**Fig. 7.2** Subzones of the Arctic Tundra Zone. The subzone boundaries are modified slightly from Yurtsev's (1994) phytogeographic boundaries. This map portrays Arctic tundra and treeless boreal subzones using 0.5° x 0.5° grid-cell size, the same as that used in numerous global modelling efforts.

## Ecological Effects of Microclimatic Variation on Land

It is within these broad habitats that small-scale variation in environmental conditions have direct effects on species and system ecology. In particular, the interlinked factors of snow and ice cover, soil type, and moisture content, and permafrost condition can significantly modify the microclimate in which the flora and fauna live. An example is shown by the Stordalen mire adjacent to Lake Tornatrask near Abisko in northern Sweden, where the peat surface shows distinct hummocks and depressions underlain by permafrost, typical of many tundra sites. The hummocks with a vegetation of *Empetrum hermaphroditum–Vaccinium microcarpon* association containing *Rubus chameamorus, Betula nana*, and crustose lichens has low moisture content compared to the hollows with a *Carex rotundata–Drepanocladus schulzei* association, including *Eriophorum vaginatum* and *Sphagnum balticum*. The snow is thin (5–15 cm) on the more exposed hummocks compared with the sheltered depressions (25–50 cm). Over four years of observations, snowmelt was completed and soil thaw began on the hummocks 4–10 days before the depressions, with their later snow blanket. Yet, when it began, the thaw was 2–3 times faster and continued for longer in the wet, more peaty depressions, and extended to twice the depth (80–120 cm) of the hummocks (see fig. 7.3). At the end of summer, the surface of the mire refroze and the frost front moved down until the soil was completely frozen under the hummocks by early January; but under the depressions, in three of the four years, freezing of the peat was incomplete and a layer of unfrozen peat remained throughout the winter—a so-called “talik” layer.

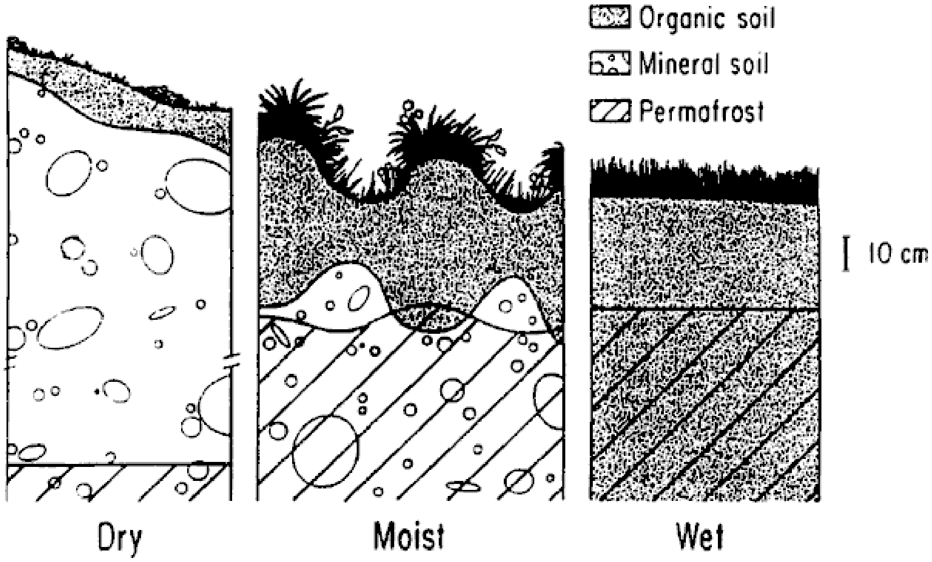


**Source:** Ryden and Kostov (1980)

**Fig. 7.3** Duration and depth of thaw and refreezing in a well-drained hummock (solid line) and wet depression (dotted line) on a peat mire in northern Sweden.

The example in figure 7.3 from northern Sweden shows how small differences in topography affected the snow cover, radiation, and wind exposure. These factors, combined with the soil moisture content and the soil thermal conductivity, determine the soil temperature and length of the active seasons. This has direct effects on plant root growth and activity, and selects for different plant species. The soil conditions also influence the soil microflora and fauna and, hence, the rates of decomposition and nutrient mineralization. Figure 7.4

gives a more general illustration of conditions in dry, moist, and wet tundra systems. The relatively deep active layer and thin organic layer often occurs in dry soils; while wet soils—in which organic matter tends to accumulate because the cold, anaerobic conditions retard the rate of decomposition—have a shallow active layer. Both organic matter and moisture content are important determinants of soil temperature, thaw depth, cation exchange capacity, aeration, redox potential, and other properties that affect biological processes in tundra soils (Nadelhoffer et al. 1992).



**Source:** Nadelhoffer et al. (1992)

**Fig. 7.4** Generalized views of dry, moist, and wet tundra ecosystems

These small-scale variations, the spatial and temporal patterns in the landscape (see fig. 7.5.a–b), provide opportunities for the animals and plants to extend their very short summer season or to assist in their winter survival. The Stordalen mire, with its hummocks and depressions, is just one example of how small changes in the microclimate can provide herbivores, such as lemmings or reindeer, with access to different plant species, at different times, as a result of changes in snow cover or timing of growth. Similarly, differential rates of thawing of the surface soil allows lemming nests to be established before the spring thaw is widespread—but with the risk of flooding by adjacent later snowmelt; small areas of early thaw provide migratory insectivorous birds with the opportunity to feed on soil invertebrates. General effects of variations in snow cover are shown in table 7.2.

**Source:** CAFF (2001)

**Fig. 7.5.a** Patterned ground: Polygon tundra at Bylot Island, Canada

**Source:** CAFF (2001)

**Fig. 7.5.b** Patterned ground: Tundra peatland mosaic in east-European Russia near Naryan-Mar

**Table 7.2** Effects of variations in snow cover (CAFF 2001)

| **Typical Ecological Factors** | | | | |
|---|---|---|---|---|
| | | Wind-Exposed Ridge | Sheltered Slope | Depression |
| Snow Cover | Depth (cm) | 0–20 | 20–80 | 80+ |
| | Length of snow-free period (typical values in months) | 4–5 | 3–4 | <3 |
| Soil | Moisture | Dry | Dryish-mesic | Mesic-moist |
| | Freeze-thaw processes | Intense | Low-Moderate | Low-Moderate |
| | Depth of soil active layer | Deep | Moderate | Moderate–Thin |
| | Nutrient status | Low | Moderate | Low–Moderate |
| Temperature | Variability | High | Moderate | Moderate |
| | Winter minima near soil surface | Very low | Moderate | Moderate–Near zero |
| Desiccative Stress in Spring | | High | Moderate | Low |
| Herbivore Activity in Winter | Reindeer | Moderate–High | Moderate | Low |
| | Microtines (e.g., lemmings, voles) | Low | Moderate–High | Moderate–High |
| | Rock ptarmigan, mountain hare | High | Low | Low |
| **Typical Plant Forms** | | Wind-Exposed Ridge | Sheltered Slope | Depression |
| | | | | |
| Plant Group | Vascular plants | Trailing dwarf shrubs, cushion plants | Dwarf shrubs | Low herbs, dwarf willows |
| | Mosses *Bryophytes* | Small, compact, drought-tolerant species | Mesophytic mosses | Meso-hygrophytic bryophytes |
| | Lichens | Wind-hardy fruticose species | Fruticose reindeer lichens | |
| **Typical Species** | | | | |
| | | Wind-Exposed Ridge | Sheltered Slope | Depression |
| Plant Group | Vascular plants | Alpine bearberry *Arctocstaphylus alpina*, Alpine azalea *Loiseleuria procumbens* | Dwarf birch Betula nana, Bog blueberry Vaccinium uliginosum | Polar willow |
| | Mosses *Bryophytes* | Wooly fringe-moss *Racomitrium lanuginosum* | Stairstep moss *Hylocomium splendens* | Kiaeria starkei |
| | Lichens | *Alectoria nigricans* | *Cladina mitis* | |

## Ecological Effects of Climate in Aquatic Systems

Wetlands cover vast areas of northern Canada and Siberia: 1.5 million km$^3$ north of lat $60^o$ N. Are they terrestrial or freshwater environments? The question is purely academic. What is much more important is to understand how the water content varies with space and time; how the climate influences the expansion of small pools into seasonal streams; how the water flows into, through, or around the lakes and rivers depending on ice, snow, and temperature; and, in all of these situations, how these changes in the physical environment influence the aquatic flora and fauna and the biological processes.

In general, the aquatic systems have much less severe climatic environments than do terrestrial systems in the Arctic. However, the biology of aquatic environments is still strongly influenced by four main characteristics (Vincent and Hobbie 2000): (1) persistent cold water temperatures; (2) seasonal freeze-thaw cycles; (3) prolonged ice cover; and (4) extreme seasonality of radiation. These climate-induced factors are interactive and are also influenced by responses on adjacent land.

The **cold water regime** is persistent throughout the year, and even in the summer, warming is minimal. The density of the water declines with increasing temperature, but the change is small at low temperatures. As a result, lakes do not become stratified as much as do lakes at low latitudes, where warm water at the surface is separated (by the thermocline) from the colder, more dense, deep water. This results in the mixing of the water by the Arctic winds to a greater extent than at lower latitudes, thus maintaining a supply of oxygen and nutrients throughout the lake. The **seasonal freeze-thaw cycle** causes changes in water depth within rivers where the flow is mainly from south to north. In spring, the melting of ice and snow occurs first in the northern headwaters before ice melt downstream. This causes an upstream rise in water levels with flooding of adjacent land and, on release, scouring of the riverbed and bank habitats. The spring flush also brings pollutants that have accumulated in winter precipitation, which can cause flushes of acid water affecting fish and invertebrates in the rivers or those migratory Arctic char (*Salvalinus alpinus*) waiting to run the river from the sea. At the end of the summer, the rivers freeze from the colder north, which again causes a rise in water level upriver. The **period of cover and depth of ice** on large rivers and lakes influences the penetration of photosynthetically active radiation (PAR) through to the water and to algae and other photosynthesizing organisms. This is particularly important given the **extreme seasonality of radiation**. A small increase or decrease in ice cover can have important consequences for primary productivity and consequently for secondary production. The penetration of ultraviolet radiation is also affected, but with the reverse effect: harmful exposure of micro-organisms to UV-B is reduced by thicker ice.

Radiation penetration is also inhibited by dissolved organic matter (DOM) that is leached from the soils in the catchment. High Arctic areas with a young, thin soil cover generate clear waters, but the peaty catchments of the extensive mires provide high DOM concentrations, waters that are often referred to as “black water systems,” such as the Lena River draining vast areas of central Siberia. The Lena discharges about 525 km$^3$ of water each year, carrying about 17.5 million tonnes of sediment and with DOC concentrations of 10 mg per litre. The slow flow allows much of the sediment to be deposited in the Lena Delta, covering an area of 30,000 km$^2$, with an estimated 6,500 channels and 30,000 lakes (see fig. 7.6). The organic matter and nutrient input provides a rich resource and diverse habitat that supports 368 vascular plants and many invertebrate and fish species and is a major feeding ground for migratory birds. Bird species recorded in the Lena Delta number 122, of which 67 breed there, including all 24 of the world’s sandpipers. The Lena then flows far out into the Laptev Sea, its dark plume providing clearly visible evidence of the nutrients that feed the rich faunas of the continental shelf.

**Source:** CAFF (2001)

**Fig. 7.6** The Lena Delta

Thus, the land feeds into the rivers, which build new land spreading into the sea and supporting the coastal marine system. The Arctic may be distinguished by its severe climate, with short summers, long dark winters, and extensive snow and ice cover. But those organisms that have adapted to these particular conditions have combined to form some highly productive and dynamic landscapes.

## Student Activity

1. What determines macroclimatic variation on land?
2. What is the climatic variation difference between Siberia and North America?
3. What determines microclimatic variation on land?
4. What effects does moisture have on soil and on the life forms in it?
5. What four main characteristics of aquatic environments influence their biology?
6. At what times of the year do Arctic river levels change?

# Survival Strategies of Arctic Flora and Fauna

The challenges and stresses for Arctic organisms are many. How to avoid death through cold or desiccation? How to find enough food to grow and reproduce in the short summer? How to disperse to new habitats? The individual adaptations that combine to form strategies are many and varied—physical, physiological, behavioural, reproductive—and they vary between species and between places (see Module 6). The diversity is explored here by brief examples from different main groups of organisms.

## Mammals

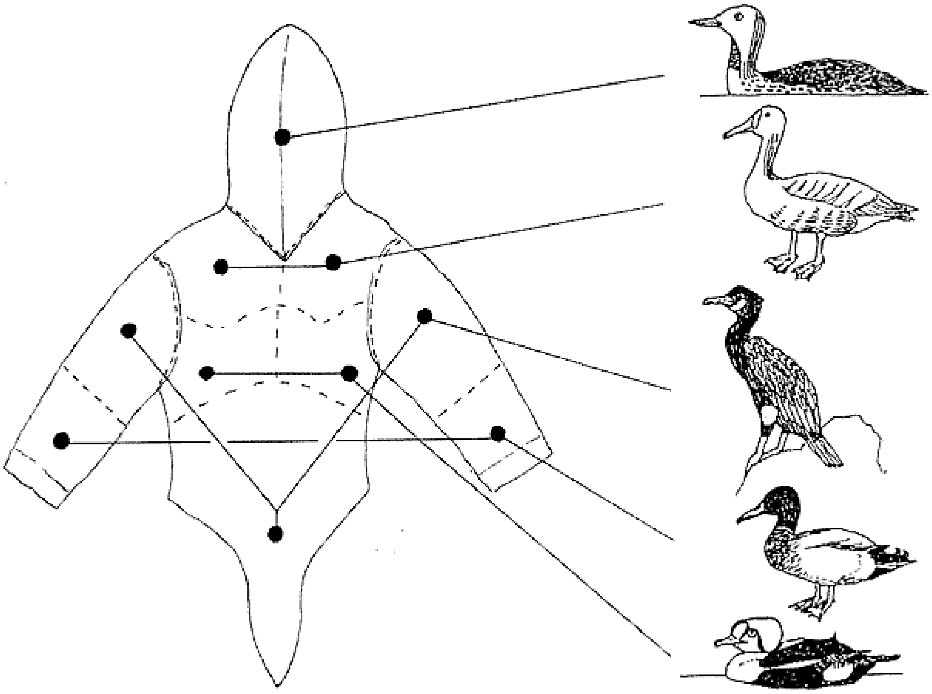
In the High Arctic, the extensive polar desert and semi-desert supports two large ungulates, muskox (*Ovibos moschatus*) and reindeer/caribou (*Rangifer tarandus*), despite the extremely sparse vegetation and the extreme cold and dry conditions. Their adaptations are contrasting but both are successful. Muskox are designed for a rather immobile existence. Their dense insulating underwool and subcutaneous fat layer extend over most of their body and limbs. They maximize heat retention and do not exert themselves, thus minimizing the problem of overheating. When challenged by predatory wolves or humans, they form an immobile defensive circle. In contrast, reindeer are highly mobile. They have a thick insulation of long hollow hairs over much of their body and a limited distribution of fat. The hairs can be erected to allow ventilation (thermoregulation) after strenuous activity. Their long legs, with their thin cover of hairs, are designed for rapid and prolonged running, combined with digging for forage, their large flat hooves helping to move over deep snow. The more active habit and wide range of the reindeer make greater physiological demands than do those of the more constrained muskox. As with many young Arctic mammals, reindeer calves are able to thermoregulate by activating their energy-rich brown fat, and they are provided with milk high in fat and protein. As adults, they have a high digestion efficiency based on a diet of good-quality lichens or forage high in carbohydrates. Muskox also have a high digestive efficiency (about 65%), which is maintained by long periods of ruminating in winter, despite the relatively low-quality food, such as willow twigs. The cold environment of the High Arctic has some benefits for the caribou: the mosquitoes (*Culex* spp.), black flies (*Simulium* spp.), and parasitic warble and bot flies that harass caribou in the warmer Low Arctic are absent or only in low numbers in the High Arctic (Klein 1999).

True lemmings (*Lemmus* spp.) and collared lemmings (*Dicrostonyx* spp.), the latter more resistant to low temperatures, are widespread throughout the Arctic and forage within the vegetation canopy. They avoid the extreme low winter temperatures by living below the snow, at the interface with the ground, many species building well-insulated winter nests. These are replaced in the summer by nests below the ground surface. They show rapid growth and breeding when conditions are good, an important attribute in a highly variable environment. Lemming predators tend to show a similar attribute, with suppressed reproduction when lemming populations are low but high reproductive rate when lemmings are abundant. An exceptionally high reproduction is recorded in the sibling, or Svalbard, vole (*Microtus rossiaemeridionalis*), which can produce four litters during the three-month summer season, with females giving birth when barely more than a month old. Average summer survival is 80–90%, but winter survival, although highly variable, is only 10% on average. This high variability associated with strong seasonality is not necessarily an evolved trait; the Svalbard vole was introduced from Russia in the mid-1900s.

People have long recognized the value of efficient insulation against the cold, combined with the different structures adjusted to suit different functions. This is beautifully shown in the parkas and other clothing of the fifteenth century Inuit preserved through natural mummification in Quilakitsoq in mid-west Greenland. Skins from five different birds are systematically used to construct the parkas. Skins with short, dense plumage are used where warmth is most important (eider and cormorant). More open-feathered skins are placed at the wrist and neck openings to let heat out (mallard and white-fronted goose). The hood uses the dense, short feathers of the red-throated diver, which can fit the head closely. (See fig. 7.7.a–b.) This pattern is repeated in a number of parkas. Caribou and sealskin are used elsewhere in the clothing to perform different functions.

**Source:** Hart Hansen and Gullov (1989)

**Fig. 7.7.a** Parka from fifteenth-century Inuit, constructed with different bird skins



**Source:** Hart Hansen and Gullov (1989)

**Fig. 7.7.b** Drawing of the front of the inner parka, showing how the skins from five different birds are placed. Hood: red throated diver; shoulder/yoke: white-fronted goose; chest: eider; upper sleeve and lower front panel: cormorant; and lower sleeve: mallard.

## Birds

The Arctic is rich in bird life during the summer, especially on the Russian and North American coastal tundra and wetlands. Waders are particularly widespread and account for 30–40% of tundra bird species. The key challenge for most Arctic birds is their migration to and from their overwintering grounds in southern latitudes. This is their strategy to avoid the winter climate and lack of access to food while making maximum use of the superabundance of invertebrate food concentrated in the summer months. The migration of the sandpipers (*Calidris* spp.) and other waders is an extremely demanding event. These birds overwinter in all of the continents of the globe (see fig. 7.8) and must build up their energy reserves to supply their high metabolic activity over the vast distances of the spring migration. They have the capacity to build or rebuild large fuel stores at high rates in order to service the long and energetically costly flights during migration. Along well-established flyways, the large flocks rest and feed in estuaries, lakes, and wetlands.

[Figure temporarily not available.]

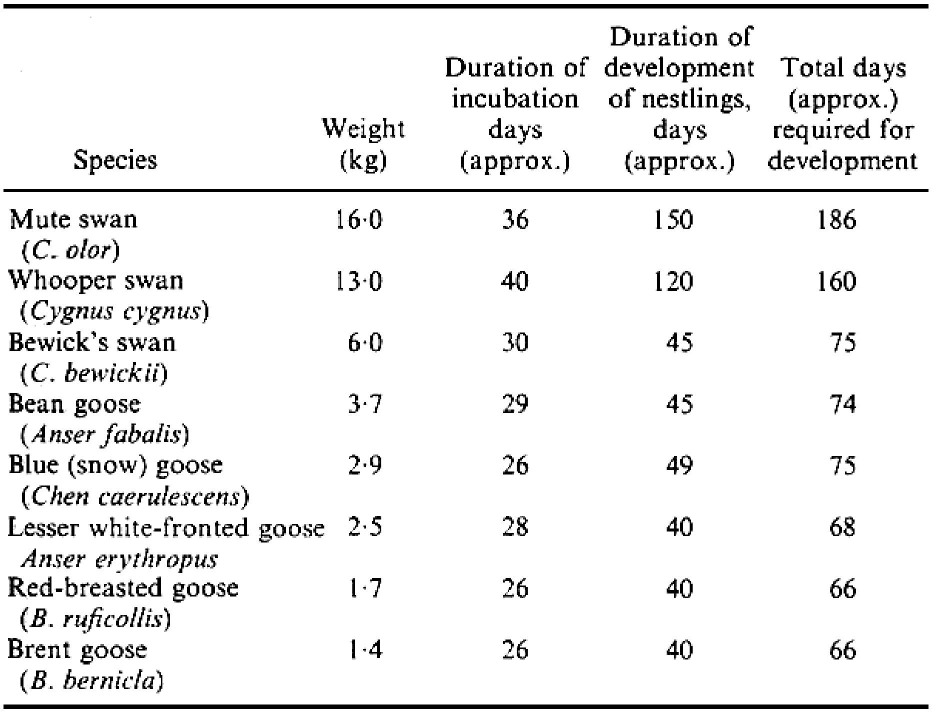
**Source:** CAFF (2001)

**Fig. 7.8** Breeding areas, migration routes, and staging/overwintering areas of different subspecies of knot (*Calidris canutus*)

The last leg of the migration north is critical because the birds must not only cover the last few thousand kilometres, but they must also immediately find and court mates and breed. The birds have the physiological capability to rapidly replace their reserves; but it is a time of mortality, and those birds with the largest remaining reserves tend to be most successful in breeding. Feeding on the emerging tundra insects and other invertebrates, plus some plants, supplies the high costs of breeding and thermoregulation for the adults. The chicks emerge fully fledged but have to find their own food supplies immediately, and they are vulnerable to low temperatures, precipitation, and predators. The adults feed vigorously to build their energy reserves before departing on the long autumn migration, leaving the young to follow later. The early departure of the adults may be a survival strategy to reduce competing with the young birds for food, or it may distribute risk of an early winter. The ability of the young to find the appropriate flyways and stopping points over vast distances must be genetically determined, and the independence of the young birds may also enhance the chances of finding alternative route options during periods of environmental change.

Bergman's Rule states that body size of warm-blooded animals tends to increase from equator to the poles. The reason is that the larger the body, the smaller is the relative surface and consequently the less heat it radiates and loses. This holds well for species of bear, with the polar bear (*Ursus maritimus*) being much larger than its southerly counterparts. But Bergman's Rule, proposed in the nineteenth century, is not universal. For some taxonomic groups there is a reverse situation with decreasing body size in more northern regions of the Arctic. The reason for this decline is probably related to the need to complete the breeding cycle within the short summer; and the smaller the body size, the shorter is the time required for growth and development (see table 7.3).

**Table 7.3** Maximum weight and duration of development of some species of swans and geese (Chernov 1985)



| Species | Weight (kg) | Duration of incubation days (approx.) | Duration of development of nestlings, days (approx.) | Total days (approx.) required for development |
|---|---|---|---|---|
| Mute swan<br>(*C. olor*) | 16·0 | 36 | 150 | 186 |
| Whooper swan<br>(*Cygnus cygnus*) | 13·0 | 40 | 120 | 160 |
| Bewick's swan<br>(*C. bewickii*) | 6·0 | 30 | 45 | 75 |
| Bean goose<br>(*Anser fabalis*) | 3·7 | 29 | 45 | 74 |
| Blue (snow) goose<br>(*Chen caerulescens*) | 2·9 | 26 | 49 | 75 |
| Lesser white-fronted goose<br>*Anser erythropus* | 2·5 | 28 | 40 | 68 |
| Red-breasted goose<br>(*B. ruficollis*) | 1·7 | 26 | 40 | 66 |
| Brent goose<br>(*B. bernicla*) | 1·4 | 26 | 40 | 66 |

## Invertebrates

Cold-blooded invertebrates (poikilotherms) have to adopt different survival strategies compared to warm-blooded mammals and birds (homeotherms; also spelled “homoiotherms”), although there are some parallels. The long-lived and hairy bumblebee (*Bombus* spp.) can raise its internal temperature to more than $30^{o}$C by shivering its flight muscles; and its “fur” provides insulation. The woolly bear caterpillar (*Gynaephora groenlandica*), like the polar bear, has adopted the “large-size, long-life” strategy with winter tolerance. It has a larval stage that lasts 10–15 years. However, resistance to freezing is widespread in polar soil fauna and is achieved in two ways: organisms either tolerate freezing in extra-cellular spaces, or they avoid nucleation by extensive supercooling (maintaining their body fluids in the liquid phase below their normal freezing point). Supercooling is the most widespread adaptation and is particularly efficient energetically and metabolically in cold environments that have a high frequency of freeze-thaw cycles. The mechanism of supercooling is obtained largely by the absence or masking of potential ice-nucleation agents, for example, by emptying the gut, and by the action of low-molecular weight, anti-freeze compounds, such as sugar alcohols and sugars.

## Microflora

Bacteria and fungi are widespread in Arctic soils and often extend into desert habitats where higher organisms are absent, cyanobacteria providing the primary production base of a terrestrial microbial food web. In several studies, cyanobacteria have shown nitrogenase activity below 0°C, and they readily resume nitrogen fixation on thawing—both traits have obvious adaptive value in tundra regions. Soil temperatures are lower and fluctuate less than those at the surface and above ground during summer. Metabolic activity of bacteria and fungi tends to be maintained at low temperatures; soil enzyme studies indicate that below 10°C extra-cellular activity is limited by the quality of the substrate rather than by temperature. Laboratory microcosm and soil enzyme studies both suggest that microbial activity is relatively temperature-insensitive across much of the 2–10°C range of growing season temperatures typical of most Arctic soils.

Moisture has a considerable influence on microbial activity, limiting activity through desiccation in polar semi-deserts. Cyanobacteria are often associated with mosses, which are very effective at holding moisture. Similarly, the mucilaginous matrix that makes up the *Nostoc* thallus also retains moisture. Free-living cyanobacteria and lichens have the ability to recover rapidly from an extremely desiccated state and resume photosynthesis and nitrogen fixation. The ability to tolerate desiccation is probably one of the major reasons that *Nostoc* spp. are ubiquitous from high to low latitudes and play such an important role in nitrogen fixation in the Arctic. The accumulation of nitrogen in Arctic soils is very small because the soils are relatively young and have had little time to accumulate much nitrogen from the atmosphere through biological fixation (e.g., by *Nostoc*).

## Plants

Plants adapt in many ways to their physical environment, but as with mammals and birds, “dwarfism” has distinct advantages in the Arctic. Vascular plants in exposed habitats increase the temperature differentials between the tissue and the ambient air by dwarf or prostrate growth or by forming compact cushions. By these growth forms, they take advantage of the warmer air and low convection close to the soil surface and, when growing in cushions, they reduce the heat flux by increasing the ratio of volume to surface area, which conserves heat. Most Arctic vascular plants are perennial and capitalize on the ability to resorb and translocate nutrients within the plant. Forty to ninety per cent of peak leaf nutrients are translocated before leaf senescence. This attribute provides the opportunity to initiate early growth in the following year before conditions are suitable for photosynthesis (e.g., through snowbeds). Related to the prostrate habit, rhizomes and stolons spread across the heterogeneous environment and facilitate transfer from relatively nutrient-rich microhabitats to growing parts of the plant.

Many Arctic plants have “spread the risks” associated with sexual reproduction by combining it with the less-risky asexual or vegetative reproduction. Formation of bulbils, viviparous propagules, clones, daughter ramets from stolons or rhizomes occur with increasing frequency towards the poles. New shoots from rhizomes and stolons maintain connection with the mother shoots for a varying and extended time, during which resources are supplied by the mother to the daughter. The connection reduces the risk of juvenile mortality if the progeny happen to develop in a microsite with low nutrient levels. This strategy is typical for many of the dominant species and life forms in Arctic vegetation—for example, many grasses and sedges; dwarf shrubs; and vascular cryptogams, such as club moss (*Lycopodium* spp.) and horsetails (*Equisetum* spp.). Seed production by many species generates large numbers of seedlings in disturbed or open ground; seedling density is much lower on undisturbed tundra. Seedling mortality of 50% or more occurs in each of the first years after emergence. Summer mortality is attributed to many environmental factors, including drought and desiccation of the substrate; frost activity at thawing and freezing; and competition with the adults for space and light.

# Conclusion

Although low temperatures are obviously important to Arctic biology, there are many other factors potentially and actually limiting life on land and in fresh water. These factors act in isolation and in combination. In response, as illustrated above, particular attributes of the flora and fauna have evolved or been selected. The result is that although the total diversity of species in the Arctic is smaller than in more temperate latitudes, those species that can survive are able to exploit the highly variable environment and benefit from the relatively little competition. The populations tend to be large, a situation sometimes referred to as “super abundance,” and species tend to be generalists rather than specialists: they tend to have a wide niche breadth. These attributes of individual species result in ecosystems that also have distinctive characteristics, as considered in the next section of this module.

## Student Activity

1. What are some challenges or stresses related to survival for Arctic organisms?
2. What are two survival adaptation strategies for mammals, birds, invertebrates, microflora, and plants?
3. How have humans learned from these survival adaptation strategies?

# Ecosystems, Food Webs, and Nutrients

How do the individual factors and species combine to function as an ecosystem—that is, a system involving the interactions between a biological community and its non-living environment? Life on land, especially in the Arctic, includes the wetlands, lakes, and rivers. Consideration of two lakes and their surrounding catchments—Lake Myvatn in Iceland, and the Arctic tundra at Toolik Lake in Alaska—provide case studies that illustrate the structure and function of Arctic ecosystems.

## Lake Myvatn and Laxa River

Myvatn (see fig. 7.9) in northern Iceland illustrates dramatically the combined effect of the biological and non-living environment. Formed only 2,300 years ago in the volcanically active rift zone, it is 37 $km^2$ in area with an average depth of only 2 m. Cold springs (3.6–6.7°C) are a main source of phosphates, while warmer springs (7.2–26.2°C) from the southern basin supply nitrates and silica. The annual input loading rates have been 1.5 g P, 1.4 g N, and 340 g Si $m^{-2}yr^{1}$. The river Laxa drains Myvatn to the sea, 60 km to the north.

**Source:** CAFF (2001)

**Fig. 7.9** Lake Myvatn in northern Iceland

Primary production in this nutrient-rich (eutrophic) lake is dominated by benthic diatoms (400 g. $m^{-2}$. $yr^{-1}$) combined with the blue-green alga (*Anabaena flos-aquae)* in the phytoplankton, rooted macrophytes (*Potamogeton filiformis, Myriophyllum spicatum, Ranunculus trichophyllus*), and the green alga (*Cladophora aegagrophila)* in deeper water (< 4 m). The diatoms support vast numbers of chironomid midge larvae. Bivalve molluscs and water fleas (*chydorid cladocerans*) graze on and in the sediment and on vegetation surfaces, while the copepod *Cyclops abyssorum* and cladoceran *Daphnia longispina* are planktonic herbivores. The main predators are three invertebrates (the oligochaete *Chaetogaster diaphanus*; *Hydra* sp.; and chironomid larvae, *Tanytarsus* sp.) and three fish species (three-spined stickleback, *Gasterosteus aculeatus*; Arctic char, *Salvelinus alpinus*; and brown trout, *Salmo trutta*). The Laxa River supports vast numbers of filter-feeding black fly larvae (*Simulidae*), which are eaten by brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) and by many waterfowl.

The food web is clearly stratified between primary producers, herbivores, and primary and secondary carnivores. However, there is considerable flexibility, and most species will switch foods depending on availability. At Myvatn, the most spectacular feature is the large populations of waterfowl, especially diving ducks that migrate to the area in spring. Twenty-four species, including 15 species of duck, breed at Myvatn, with an average of about 10,000–15,000 pairs. The birds vary between species in their feeding preferences and will also change diet, but years with low chironomid populations are associated with poor breeding success among diving ducks (e.g., common scoter, *Melanitta nigra*; oldsquaw, *Clangula hyemalis*; greater scaup, *Aythya marila*; and tufted duck, *Aythya fuligula*).

Analyses of the remains of the flora and fauna in sediment cores from Lake Myvatn indicate long-term changes. The analyses show that although the general composition of the biota has changed little, the relative abundance of different groups have changed over the last two millennia. Three patterns have emerged: (1) a one-way succession in time with increasing benthic flora and fauna and decreasing planktonic forms, probably associated with sediment accumulation and a decreasing depth of the lake; (2) large oscillations in algae with a periodicity of about 500 years, correlated with volcanic ash in the sediment, suggesting enhanced productivity through direct input of nutrients or through increased soil erosion; (3) a 600-year anomaly from the first to seventh centuries AD with changes in algae, cladocerans, and rotifers, combined with low sedimentation rate, which may reflect reduced geothermal activity and low silica content of groundwater.

Historical information from the first half of the twentieth century has been obtained from records of harvested duck eggs and catches of salmonids, mainly char. The results indicate that in the first four decades of the twentieth century, a succession of population peaks passed through the Myvatn ecosystem: first the Barrow’s goldeneye peaked; then the common scoter and oldsquaw; then the Arctic char; followed by the red breasted merganser. This succession suggests that an era of large benthic organisms gradually gave way to one dominated by smaller Crustacea. Quantitative scientific monitoring of wildfowl and their food since the mid-1970s has shown that local food abundance largely determined changes in numbers of ducks. Reproductive performance determined subsequent changes in spring population density in the Eurasian wigeon (*Anas penelope*), tufted duck (*Aythya ferina*), greater scaup (*A. marila*), common scoter (*Melanitta nigra*), and harlequin duck (*Histrionicus histrionicus*). Thus, in the short term, the breeding density is determined by local food conditions as experienced by the adults one year previously; events in the overseas winter territories have relatively little influence on density in this breeding area.

To what extent have different local or regional factors influenced the structure and function of Myvatn? The evidence indicates that the eutrophic status of Myvatn was established early through its volcanic origins and that initial changes reflected the gradual physical development of the lake. Human colonization of Iceland in the ninth century was followed by forest clearance, the introduction of grazing, and the use of fish and wildfowl. There is no detectable evidence of any effect of these activities on the lake. Traditional subsistence farming, fishing, harvesting, and use of other natural resources were maintained through to the mid-twentieth century, still without marked ecological impact.

The subsequent intensification of farming, particularly the use of artificial fertilizers, was not influential because it occurred outside the catchment. There have been limited effects of modern developments, including changes in fishing techniques, industrial hydropower developments, and water regulation near Myvatn, plus increased human populations, including tourists. Feral American mink reached Myvatn about 1953, causing a major redistribution of waterfowl nesting sites, but having little effect on population levels. The only significant human impact at Myvatn has been the extraction of the natural biological product from the lake bottom. Diatomite extraction on an industrial scale began in 1967. Although only 3 $km^3$ of the lake are being excavated, this has resulted in a redistribution of sediment over a wider area. The first of a number of simultaneous crashes in nearly all duck populations occurred in 1970, followed in 1976, 1983–84, 1988–89, and 1997. The crashes are related to fluctuations in chironomid populations and, for diving ducks, to the influence of reduced populations of crustaceans. Mining of diatomite has now been restricted in area and will be terminated in 2010. (Full analysis of Myvatn is in Jonasson 1979 and is summarized in Gardarsson and Einarsson 1997.)

What conclusions can we draw from the case study of Lake Myvatn and Laxa River?

- In its 2,500 years of existence, the biological community has shown gradual changes in composition related to the physical development of the lake. These are the long-term trends.
- The exceptional eutrophic conditions have generated a highly productive and structured ecosystem, with large populations of few species and considerable flexibility in heterotrophic feeding habits.
- Short-term fluctuations in primary and secondary populations and production result from climatic variation, causing marked population changes in “top” predators—wildfowl and fish—despite some flexibility in feeding habits.
- Spring populations of adult migratory wildfowl are determined by climate-related breeding success in the previous year. This is an example of “bottom-up” regulation within the food web.
- Human impacts on the lake ecosystem have been limited, possibly because of the overriding highly productive eutrophic condition and the

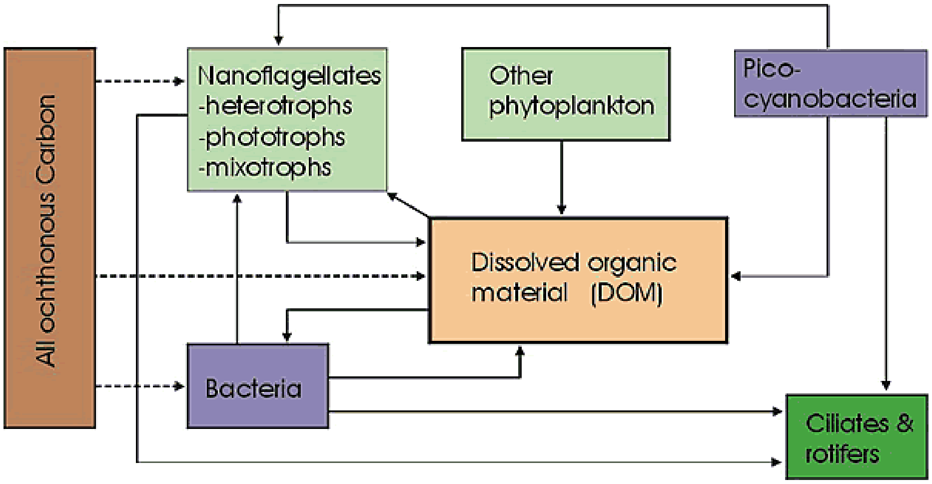
> relatively low intensity of human use—at least, that is, until the introduction of diatomite extraction.

And what about the effects of future climate change? The eutrophic basis and long-term stability of the Myvatn ecosystem have minimized the effect of climatic changes during the last 2,500 years. The evidence argues that current and future climate change will have little effect. But the thermohaline circulation and the North Atlantic Oscillation (NAO) help to maintain a relatively warm climate in the seas and on land in northern Iceland. Given the melting of massive Arctic sea ice and terrestrial glaciers, significant cooling of the northern Icelandic waters may occur. Such regional cooling could be contrary to the general anthropogenic warming. Similar cooling events have occurred in the North Atlantic in the past, but the boundary between northern cool and southern warm waters is close to the northern coastline of Iceland. Thus, local climatic changes may be more rapid than previously experienced at Myvatn, and they may occur sooner than generally expected. There is nothing in the current climatic records to indicate that such changes are in progress, but one cannot say that they will not happen.

## Arctic Tundra at Toolik Lake, Alaska

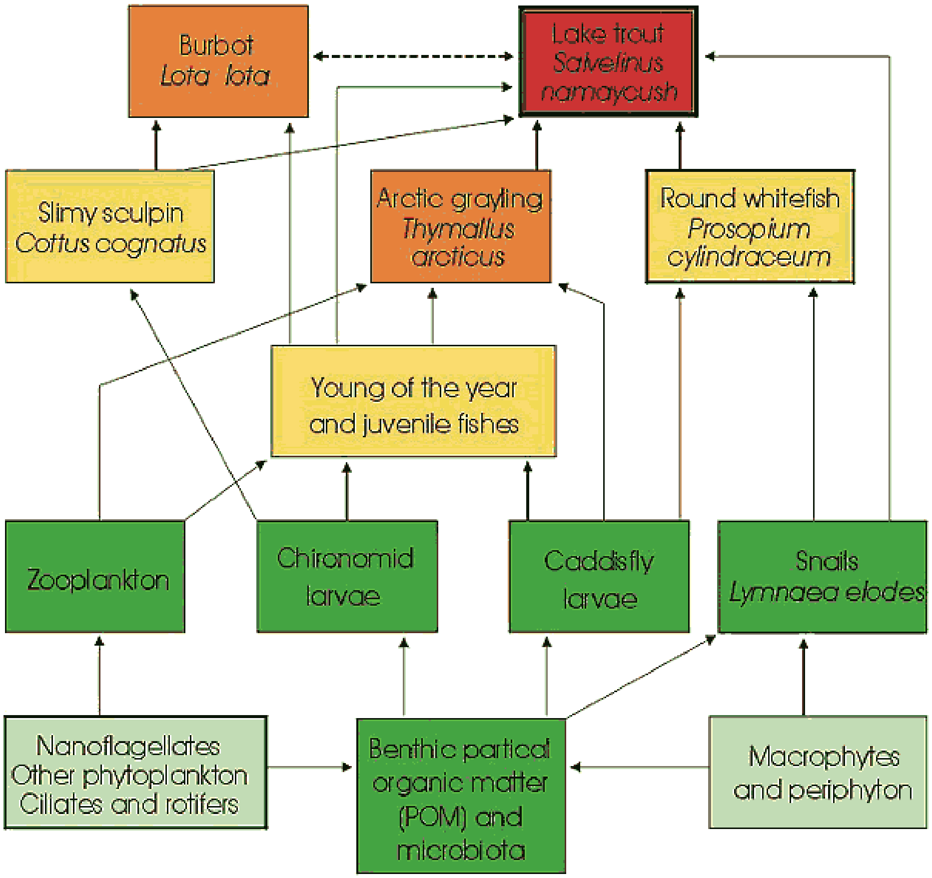
On the northern foothills of the Brooks Range, tussock tundra dominates, but there are extensive areas of drier heath tundra on the ridgetops as well as river-bottom willow communities. Toolik Lake is one of many large and small nutrient-poor (oligotrophic) lakes, with a surface area of 150 ha and maximum depth of 25 m, and with streams and rivers, including the Kuparuk and Sagavanirktok rivers. The area has been the focus of a major US program within the Long-Term Ecological Research (LTER) network of sites initiated in 1980. The land and water are intimately connected into large catchment units, but it is convenient to first consider the lake, river, and land elements separately.

Of the many lakes in the area, Toolik Lake shows the clearest food web, including a newly recognized microbial food web that is important in both freshwater and marine systems. Toolik Lake receives particulate and dissolved organic matter from surrounding land, which helps to fuel the microbial food web in which carbon and nutrients are circulated through a diverse array of nutritional modes. Minute picocyanobacteria (blue-green algae) rely exclusively on photosynthesis, their tiny cell size giving them a large surface to volume ratio that probably helps in absorption of nutrients in this oligotrophic environment. Other micro-organisms are autotrophs depending on photosynthesis; others absorb dissolved organic matter or ingest organic particles as their energy sources (heterotrophs); some adopt a mixture of sources (mixotrophs). This community of cyanobacteria, algae, bacteria, and protozoa comprises a large fraction of the total community biomass, despite the extremely small size of individuals (see fig. 7.10). This microbial food web contributes to the community of larger, interacting benthic and planktonic organisms. The community is not stable, and abundance of species between years is variable. For example, in recent years, two large planktonic cladocerans (*Daphnia middendorffiana* and *Holopedium gibberum*) have nearly disappeared from the lake, probably because numbers of small grayling (*Thymallus arcticus*) have increased as numbers of predatory lake trout (*Salvelinus namaycush*) have been reduced by fishing (see fig. 7.11).



**Source:** CAFF (2001)

**Fig. 7.10** The microbial food web of Toolik Lake, Alaska

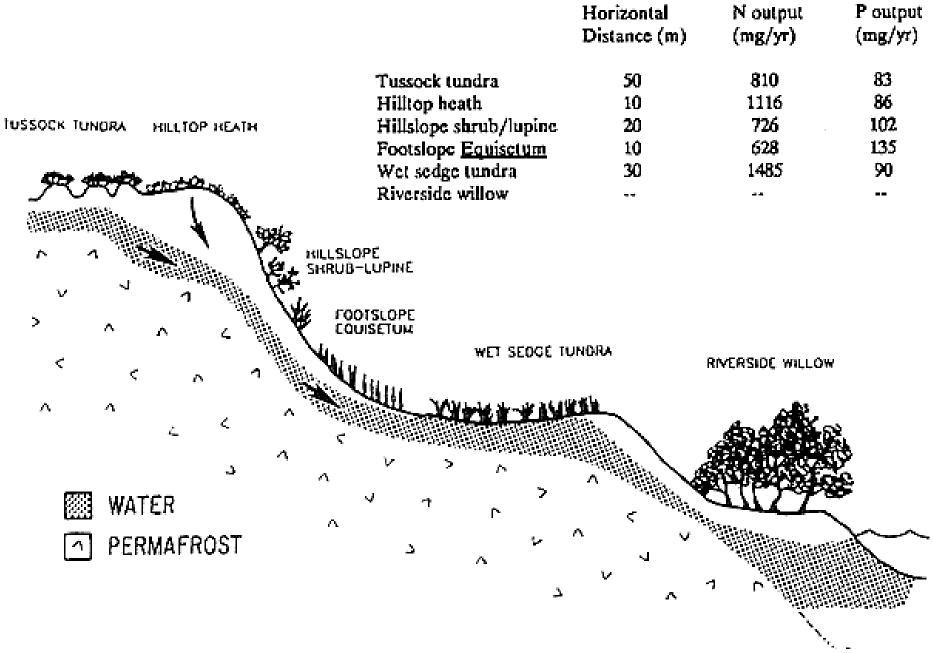


**Source:** CAFF (2001)

**Fig. 7.11** The higher trophic levels of the main food web of Toolik Lake, Alaska

Clearly, the food web is not static, but what determines change? Two experimental manipulations in the Toolik Lake area illustrate the importance of both top-down and bottom-up controls on the food web. Trout are the top predators in the lake and apparently control numbers of the slimy sculpin (*Cottus cognatus*), larger zooplankton, and snails. The slimy sculpin is also a predator and controls the numbers of chironomids. When all the trout were removed from a large lake, burbot (*Lota lota*) populations expanded rapidly—and unexpectedly—to replace the trout as top predator and to control sculpin numbers. This represents a strong top-down control of lower trophic levels by predators. In different experiments, phosphorus has been added to experimental lakes to examine its effect on the populations in these oligotrophic systems. Initially, some of the P is absorbed; but, after saturation capacity has been reached, P returns to the water. Populations of bacteria, protozoa, and rotifers tend to increase, as do some planktonic Crustacea. These changes represent a strong bottom-up control of the food web structure; but as the system becomes eutrophic, the top fish predators expand, controlling populations of their prey and resulting in a top-down control. Thus, the balance of power shifts as external limitations are removed and internal control predators take over.

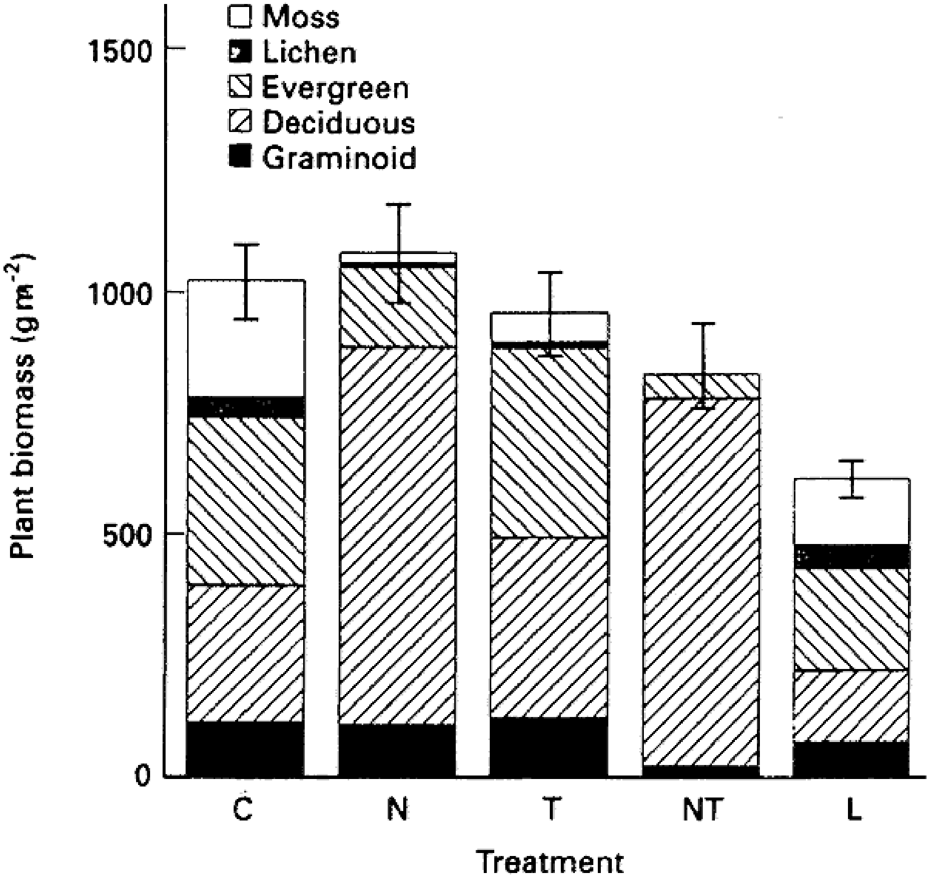
Nutrient input to the lakes and rivers comes mainly by runoff from the land. Amounts transported annually differ between different ecosystem types, influenced by the type of vegetation, the slope conditions that influence permafrost and runoff, and the moisture content of the soil (see fig. 7.12). The amounts of nitrogen (N, nitrate and ammonium) and phosphorus (P) released from the soil are small compared with the amounts cycled internally. This retention reflects the severe nutrient limitation on plant growth—a feature that also limits the plant and soil response to other environmental variables (e.g., climate and light). The relative importance of nutrients is shown by experimental manipulation of temperature, light, and nutrients (N and P) on tussock tundra at Toolik Lake (see fig. 7.13). Both the biomass of vegetation and the composition of the plant community were most strongly affected by nutrient addition. The experiments also showed that short-term responses were not good predictors of long-term change.



| | Horizontal Distance (m) | N output (mg/yr) | P output (mg/yr) |
|---|---|---|---|
| Tussock tundra | 50 | 810 | 83 |
| Hilltop heath | 10 | 1116 | 86 |
| Hillslope shrub/lupine | 20 | 726 | 102 |
| Footslope *Equisetum* | 10 | 628 | 135 |
| Wet sedge tundra | 30 | 1485 | 90 |
| Riverside willow | -- | -- | -- |

**Source:** Van Cleve and Martin (1991)

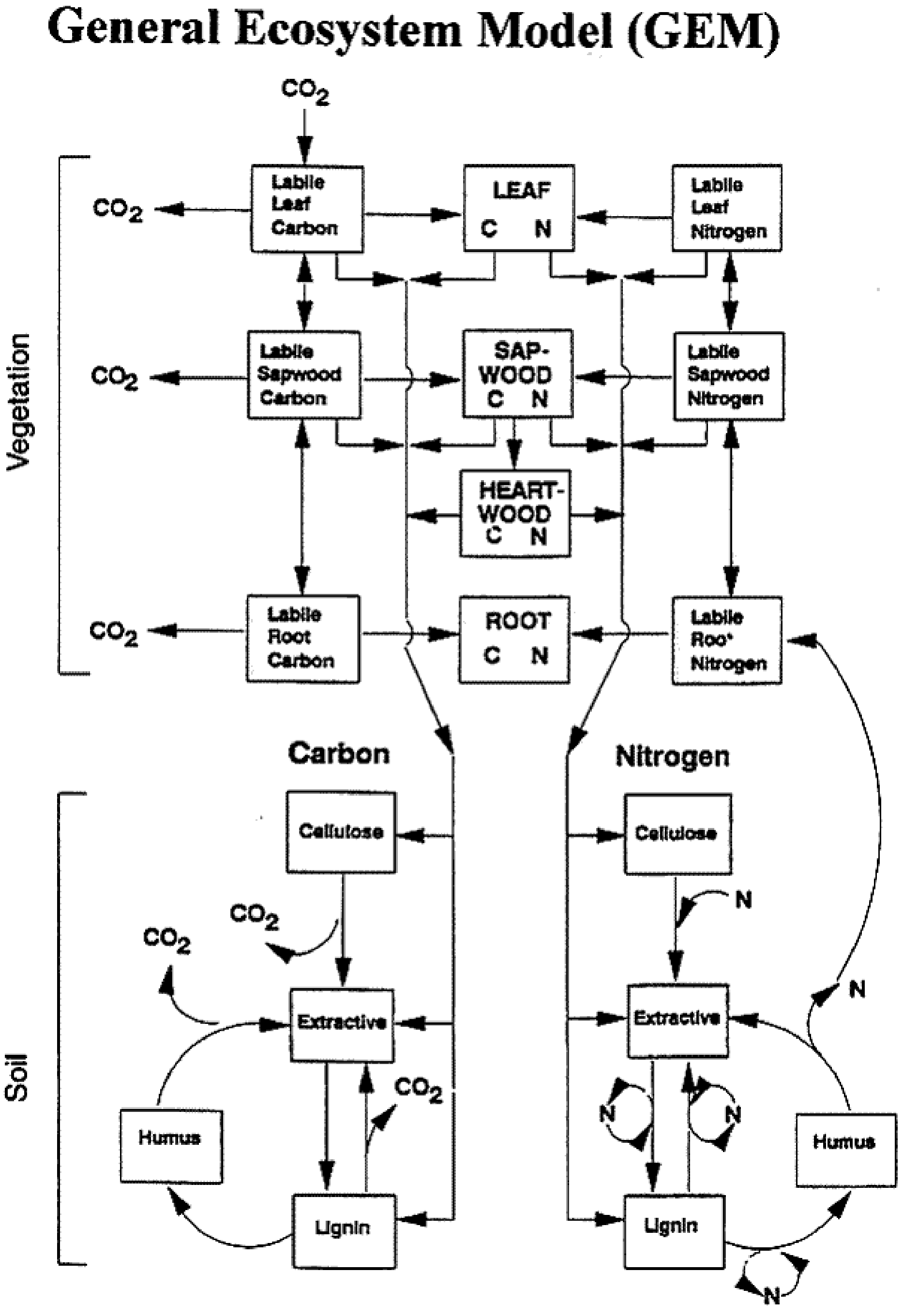
**Fig. 7.12** Terrestrial habitats along a topographic gradient showing the amounts of N and P that they contribute annually to streams and lakes



**Source:** Chapin et al. (1997)

**Fig. 7.13** Peak plant biomass and community composition after nine years of treatment. Legend: C: control; N: nutrient addition (10g N and 5g P $m^{-2}y^{1}$); T: summer temperature raised by 3°C; L: light attenuation by 50%; NT: a combination of nutrient and temperature treatments.

The low levels of nutrients derived from the rocks and soils at Toolik Lake influence the nutrient composition of the plants and the subsequent rate of decomposition by bacteria, fungi, and soil fauna. The slow rate of decomposition is reduced further by wet soil conditions that reduce oxygen availability. In contrast, the lack of moisture in soils on the well-drained slopes also limits the rate of decomposition. Thus, the nutrient quality of the litter, combined with the soil temperature and moisture conditions determine organic matter decomposition and, hence, its accumulation. At Toolik, the depth of information now available has enabled the research team to create a General Ecosystem Model (GEM), which describes the production and decomposition processes and quantifies the terrestrial carbon and nitrogen cycles (see fig. 7.14). The model has been useful in exploring changes that result from different conditions derived from the long-term experiments and from conditions in the historical past (1829–1990). The model indicates that historical increases in temperature and atmospheric $CO_2$ would have increased the loss of carbon to the atmosphere through soil and plant respiration. But these losses were smaller than the increased plant growth that was helped by increased mineralization of nitrogen. As a result, the amounts of total ecosystem carbon increased by about 2%; the tundra was a small sink for atmospheric carbon. In contrast, when soil moisture changes were taken into account, reduced waterlogging enhanced rates of soil decomposition more than rates of photosynthesis, causing a decrease in stored carbon by about 5%; the tundra was a slightly larger source of atmospheric carbon (McKane et al. 1997b).

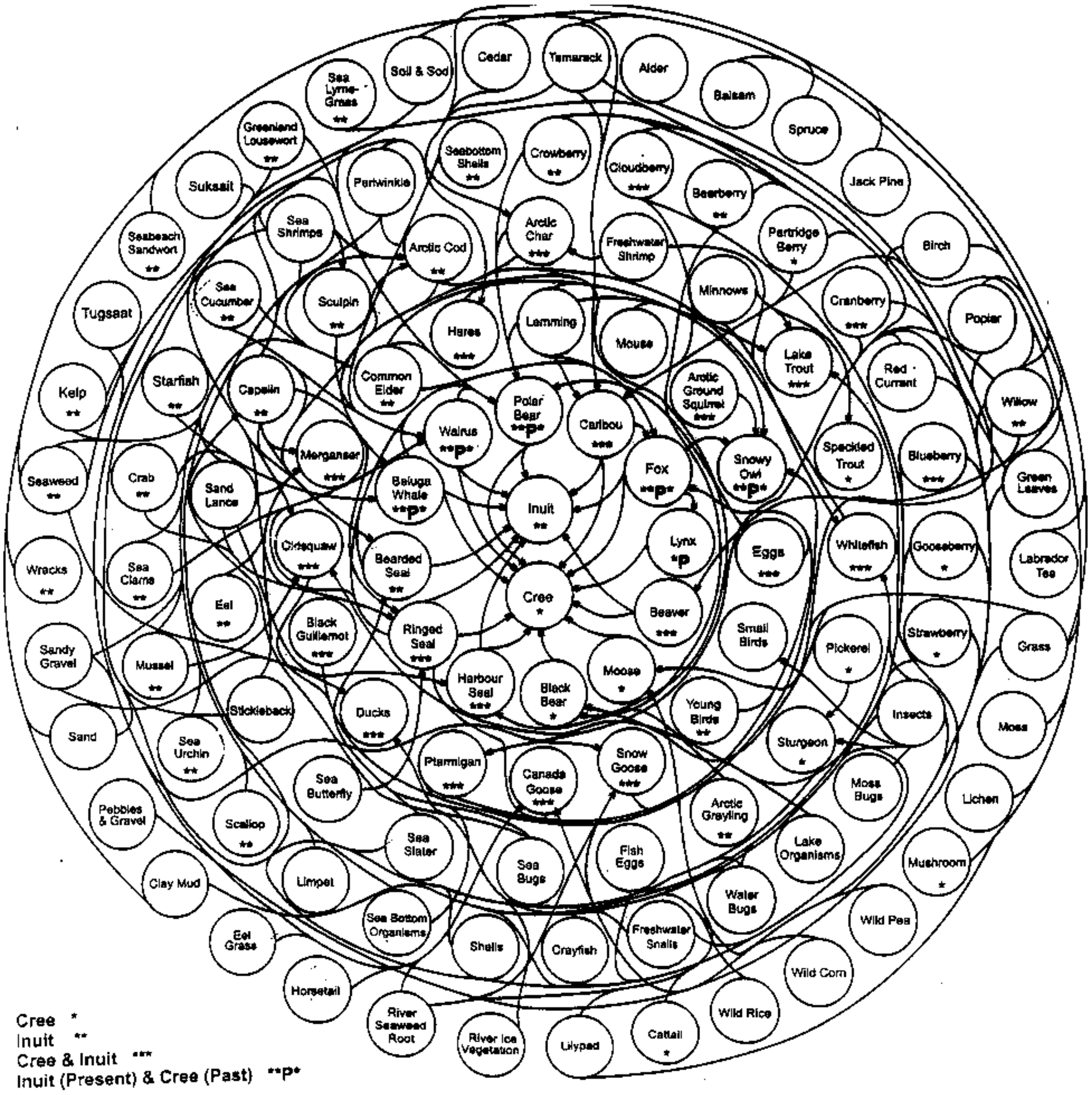


**Source:** McKane et al. (1997a)

**Fig. 7.14** Schematic diagram of the General ecosystem model of carbon (C) and nitrogen (N) cycles within terrestrial ecosystems

## Conclusion

Once again, the combination and interaction of different environmental factors result in changes in the composition of the organisms and the rates of ecosystem processes. The relative importance of different factors varies between different habitats. The food web of the eutrophic Myvatn responds strongly to temperature and biotic relationships. In contrast, the species composition and processes at the oligotrophic Toolik are very sensitive to changes in nutrients and moisture. In both Myvatn and Toolik, the terrestrial and freshwater habitats are intimately linked. They join together to form large catchments, as seen earlier in the case of the Lena Delta. The interactions extend even further as seen in the food webs of the Inuit and Cree of the Hudson Bay that extend across marine, terrestrial, and freshwater environments (see fig. 7.15), another example of increasing spatial scale.



**Source:** McDonald et al. (1997)

**Fig. 7.15** Hudson Bay food web, drawn from information on seasonal foods in Cree and Inuit diets and the foods eaten by the animals in these diets

## Student Activity

1. How many of the animal and plant named in figure 7.15 do you recognize?
2. What do you think is the value of knowing the Latin names for plants and animals?
3. Is the nearest body of water to you eutrophic or oligotrophic? What would suggest this?
4. What do you think would happen to the composition of the organisms and the rates of ecosystem processes if a top predator were removed? Vegetation destroyed?

# Summary

It is a hard life in the Arctic. Or is it? The 4,000 plant species, 5,000 fungi, 60 mammals, 200 birds, and 3,000 insects—not to mention the countless microscopic algae, protozoa, and bacteria—are proof that life thrives in this apparently inhospitable environment, and that is without counting the freshwater species. How do they do it?

This module has illustrated how each species has developed a set of adaptations—a strategy—to ensure survival and to thrive in this particular cold environment. The adaptations take many forms: physical, physiological, behavioural; and reproductive; singly, or in combination. The climate is obviously a dominant feature of the Arctic, in all its dimensions, but it is not always a threat to life. For example, snowbeds provide shelter for both plants and animals during extreme low temperatures or winds. The short summer is extended by continuous daylight, which, combined with nutrient-rich wetlands, such as Lake Myvatn, generate high primary and secondary productivity that attracts vast numbers of migrants from lower latitudes.

As always, the system can be analyzed at different spatial and temporal scales. The climate experienced by organisms living in soil or water has very different diurnal and seasonal patterns from those living on or above the surface. But what happens when climate changes, as it has done in the past and is doing now? We will explore some of the responses in Module 12: Arctic Biodiversity in a Global Context.

# Study Questions

1. How are humans locally adapted to the Arctic climate? Is this related to history?

2. Are there any adaptations, other than those mentioned, that you think animals or plants have adopted to overcome the climate in your area?

3. Can you measure some temperature profiles above and below the ground over 24-hour periods? How do these profiles vary with different snow cover, plant cover, or soil types? Can you design experiments to test the effects of different snow cover, plant cover, or soil type on temperature profiles?

4. How does the colour of the surface influence temperature of a body? Design an experiment to test the effect of colour on reflection or absorption of radiation.

5. Can you identify the main strategies adopted by animals or plants in your area to enable them to thrive in the climate conditions?

6. Draw the food web for a particular ecosystem with which you are familiar.

7. What do think are the main changes in climate in your area over your lifetime that will result from climate warming? What will be the main effects on a particular ecosystem or a species?

# Glossary of Terms

| | |
|---|---|
| adsorb | (usually of a solid) hold (molecules of a gas or liquid or solute) to its surface, causing a thin film to form. |
| bulbils | *Botany* **1** a small bulb that grows among the leaves or flowers of a plant. **2** a small bulb at the side of an ordinary bulb. |
| cation | a positively charged ion; an ion that is attracted to the cathode in electrolysis. |
| cation exchange capacity | the total amount of exchangeable cations that a soil can adsorb. It is sometimes called “total exchange capacity,” “base exchange capacity,” or “cation adsorption capacity.” It is expressed in milliequivalents per 100 g of soil or of other adsorbing materials such as clay. |
| copepod | any small aquatic crustacean of the class Copepoda, many of which form the minute components of plankton. |

| | |
|---|---|
| crustacean | any arthropod of the class Crustacea, having a hard shell and usually aquatic, e.g., the crab, lobster, and shrimp. |
| cyanobacteria | any prokaryotic organisms of the division Cyanobacteria, found in many environments and capable of photosynthesizing. |
| desiccate | **1** remove the moisture from, dry (esp. food for preservation). **2** deprive (land, plants, etc.) thoroughly of moisture. |
| diatom | a microscopic unicellular alga with a siliceous cell wall, found as plankton and forming fossil deposits. |
| eutrophic | rich in nutrients and therefore supporting a dense plant population, which can suppress animal life by depriving it of oxygen. |
| fledged | *adjective* **1** able to fly. **2** independent; mature. |
| geothermal | relating to, originating from, or produced by the internal heat of the Earth. |
| midge | **1** *informal* a gnatlike insect. **2 a** any small dipterous non-biting insect of the family Chironomidae, accumulating in swarms. **b** any similar insect of the family Ceratopogonidae with piercing mouthparts for sucking blood or eating smaller insects. |
| nitrogen fixation | a chemical process in which atmospheric nitrogen is assimilated into organic compounds in living organisms and hence into the nitrogen cycle. |
| nitrogenase activity | chemical reaction involving nitrogen. |
| *Nostoc* thallus | *Nostoc* is a common alga in the Arctic in the form of an undifferentiated mat, or thallus. |
| oligotrophic | *adjective* (of a lake etc.) relatively poor in plant nutrients. |
| primary productivity | the quantity of organic matter that is synthesized from inorganic materials by autotrophs. |
| resorb | absorb again. |
| rhizome | an underground rootlike stem bearing both roots and shoots. |
| rotifer | any minute aquatic animal of the phylum Rotifera, with rotatory organs used in swimming and feeding. |
| secondary productivity | the quantity of consumer and decomposer biomass created. |
| senescence | the process of growing old. |

| | |
|---|---|
| stolon | *Botany* a horizontal stem or branch that takes root at points along its length, forming new plants. |
| UV-B | ultraviolet radiation of relatively short wavelengths. |
| viviparous | *adjective* **1** *Zoology* bringing forth young alive, not hatching them by means of eggs (as compared to "oviparous"). **2** *Botany* producing bulbs or seeds that germinate while still attached to the parent plant. |
| wildfowl | a game bird, esp. an aquatic one. |

# Supplementary Readings/Materials

## Glossaries

- One of the best dictionaries for this area of study is the *Oxford Concise Dictionary of Ecology*, edited by Michael Allaby (Oxford University Press, 1996).
- See the *Glossary of Composting Terms* (September 1996) from the British Columbia Ministry of Agriculture, [online] http://www.google.ca/search?q=cache:h1THNPAcCckJ:www.agf.gov.bc.ca/resmgmt/publist/300series/382500-17.pdf+%22soil+or+of+other+adsorbing+materials%22&hl=en&start=1&ie=UTF-8.
- *Interactive Glossary. Invitation to Oceanography* (third edition), by Paul R. Pinet has an online home with an interactive glossary, OceanLink [online], http://www.jbpub.com/oceanlink/glossary.cfm. Jones and Bartlett Publishers.
- There is also a good short glossary at the back of Chapin, Matson, and Mooney (2002), Principles of Terrestrial Ecosystem Ecology (New York: Springer-Verlag), 375–392.

## Other Resources

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