

# Introduction to the limnology of high-latitude lake and river ecosystems

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## Outline

Polar lakes and rivers encompass a diverse range of aquatic habitats, and many of these environments have broad global significance. In this introduction to polar aquatic ecosystems, we first present a brief summary of the history of lake research in the Arctic and Antarctica. We provide an overview of the limnological diversity within the polar regions, and descriptions of high-latitude rivers, lakes, and lake districts where there have been ecological studies. The comparative limnology of such regions, as well as detailed long-term investigations on one or more lakes or rivers within them, have yielded new perspectives on the structure, functioning, and environmental responses of aquatic ecosystems at polar latitudes and elsewhere. We then examine the controls on biological production in high-latitude waters, the structure and organization of their food webs including microbial components, and their responses to global climate change, with emphasis on threshold effects.

## 1.1 Introduction

Lakes, ponds, rivers, and streams are prominent features of the Arctic landscape and are also common in many parts of Antarctica (see Appendix 1.1 for examples). These environments provide diverse aquatic habitats for biological communities, but often with a simplified food-web structure relative to temperate latitudes. The reduced complexity of these living systems, combined with their distinct physical and chemical features, has attracted researchers from many scientific disciplines, and high-latitude aquatic environments and their biota are proving to be excellent models for wider understanding in many fields including ecology, microbiology, paleoclimatology, astrobiology, and biogeochemistry. In northern lands, these waters are important hunting and fishing grounds for

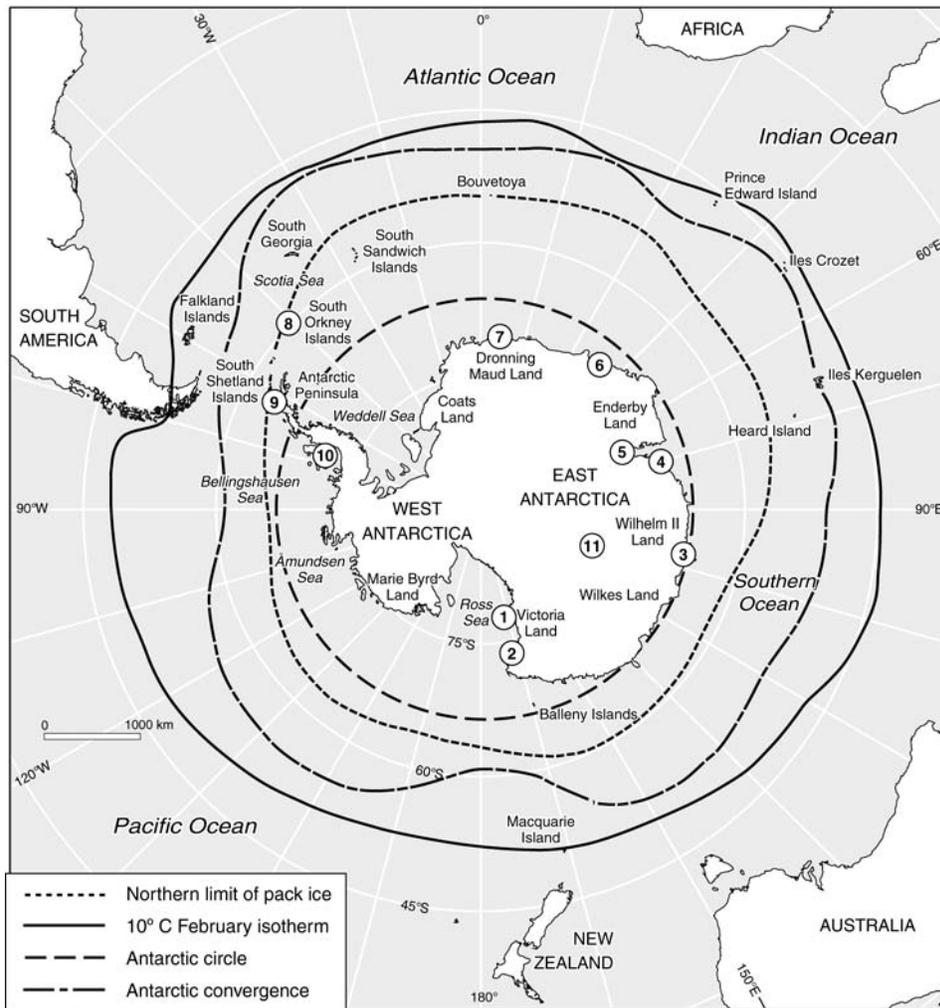
indigenous communities. They also provide drinking water supplies to Arctic communities and are a key resource for certain industries such as hydroelectricity, transport, and mining.

In addition to their striking limnological features, high-latitude aquatic environments have broad global significance; for example, as sentinels of climate change, as refugia for unique species and communities, as sources of greenhouse gases and, in the case of the large Arctic rivers, as major inputs of freshwater and organic materials to the World Ocean. There is compelling evidence that high-latitude regions of the world are experiencing more rapid climate change than elsewhere, and this has focused yet greater attention on many aspects of the polar regions, including their remarkable inland waters.

Whereas Antarctica and the Arctic have much in common, their aquatic ecosystems are in many

ways dissimilar. Both southern and northern high-latitude regions experience cold temperatures, the pervasive effects of snow and ice, low annual inputs of solar radiation, and extreme seasonality in their light and temperature regimes. However, Antarctica is an isolated continent (Figure 1.1) whereas the Arctic is largely the northern extension of continental land masses (Figure 1.2) and this has major implications for climate, colonization,

and biodiversity. Arctic catchments often contain large stocks of terrestrial vegetation, whereas Antarctic catchments are usually devoid of higher plants. This results in a much greater importance of allochthonous (external) sources of organic carbon to lakes in the Arctic relative to Antarctica, where autochthonous (within-lake) processes likely dominate. Given their proximity to the north-temperate zone, Arctic waters tend to have



**Figure 1.1** The Antarctic, defined as that region south of the Antarctic Convergence, and the location of limnological sites referred to in this volume. 1, Southern Victoria Land (McMurdo Dry Valleys, Ross Island ponds, McMurdo Ice Shelf ecosystem); 2, northern Victoria Land (Terra Nova Bay, Cape Hallett); 3, Bunger Hills; 4, Vestfold Hills and Larsemann Hills; 5, Radok Lake area (Beaver Lake); 6, Syowa Oasis; 7, Schirmacher Oasis; 8, Signy Island; 9, Livingstone Island; 10, George VI Sound (Ablation Lake, Moutonnée Lake); 11, subglacial Lake Vostok (see Plate 1). Base map from Pienitz *et al.* (2004).



**Figure 1.2** The Arctic, which can be demarcated in various ways such as the treeline or by the 10°C July isotherm, and the location of limnological sites referred to in this volume. 1, Barrow Ponds, Alaska; 2, Toolik Lake Long-Term Ecological Research (LTER) site, Alaska; 3, Mackenzie River and floodplain lakes, Canada; 4, Great Bear Lake; 5, Great Slave Lake; 6, Northern Québec thaw lakes and Lac à l'Eau Claire (Clearwater Lake); 7, Pingualuk Crater Lake (see Chapter 2); 8, Amadjuak Lake and Nettiing Lake; 9, Cornwallis Island (Char Lake, Meretta Lake, Amituk Lake); 10, Ellesmere Island (Lake Romulus, Cape Herschel ponds); 11, Ward Hunt Lake and northern Ellesmere Island meromictic lakes; 12, Peary Land, northern Greenland; 13, Disko Island, Greenland; 14, Zackenberg, Greenland; 15, Iceland lakes (e.g. Thingvallavatn, Thorisvatn, Grænalón); 16, Svalbard lakes; 17, Kuokkel lakes, northern Sweden; 18, Lapland lakes, Finland; 19, Pechora River, Russia; 20, Ob River; 21, Yenisei River; 22, Lake Tamy; 23, Lena River; 24, Kolyma River; 25, Lake El'gygytyn. Base map from Pienitz *et al.* (2004).

more diverse animal, plant, and microbial compositions, and more complex food webs, than in Antarctica. Fish are absent from Antarctic lakes and streams, and many south polar lakes are even devoid of zooplankton. Insects (especially chironomids) occur right up to the northern limit of Arctic lakes and rivers, but are restricted to only two species in Antarctica, and then only to specific sites in the Antarctic Peninsula region. The benthic environments of waters in both regions have some similarities in that microbial mats dominated by cyanobacteria are common throughout the Arctic and Antarctica. Aquatic mosses also occur in lakes and streams of both regions, but higher plants are absent from Antarctic waters. These similarities and differences make the comparative limnology of the polar regions particularly attractive for addressing general questions such as the factors controlling the global biogeography of aquatic plants, animals, and microbes, the limiting factors for biological production, the causes and consequences of food-web complexity, and the responses of aquatic ecosystems to environmental change.

## 1.2 History of polar limnology

From the earliest stages of development of limnology as a science, it was realized that high-latitude lakes would have some distinctive properties. The pioneer limnologist, François-Alfonse Forel, surmised that water temperatures in polar lakes would never rise above 4°C as a result of the short summer and low solar angle at high latitudes, and thus the lakes would circulate only once each year (Forel 1895, p.30). In G. Evelyn Hutchinson's classification of polar lakes, he pointed out that these 'cold monomictic' lakes occur at both high latitudes and high altitudes (Hutchinson and Löffler 1956). Some low Arctic lakes are also dimictic (circulating twice) and some polar lakes with salinity gradients never circulate entirely (meromictic; see Chapter 4 in this volume). During the 1950s and 1960s, actual measurements of the thermal regimes of polar lakes began in Alaska, USA (Brewer 1958; Hobbie 1961), Greenland (Barnes 1960), and Antarctica (Shirtcliffe and Benseman 1964).

The earliest work on polar aquatic ecosystems was descriptive and came from short expeditions

to specific sites. For example, Juday (1920) described a zooplankton collection from the Canadian Arctic expedition 1913–1918 as well as a cladoceran collected in 1882 at Pt. Barrow, presumably during the First International Polar Year. From the 1950s onwards there were many observations made in lakes in the Arctic and Antarctic; almost all of these were summer-only studies. A notable exception was the work by Ulrik Røen at Disko Island, Greenland, on Arctic freshwater biology (e.g. Røen 1962). Process studies increased during the 1960s and 1970s but the most valuable insights came from intensive studies where many processes were measured simultaneously or successively, and for long periods of time.

The projects of the International Biological Programme (IBP) were funded by individual countries, beginning in 1970, to investigate the biological basis of productivity and human welfare. The many aquatic sites included two Arctic lake sites, ponds and lakes at Barrow, Alaska, and Char Lake, northern Canada (for details see Appendix 1.1). At both sites, all aspects of limnology were investigated from microbes to fish for 3–4 years. It was focused, question-based research at a scale of support and facilities that enabled scientists to go far beyond descriptive limnology and investigate the processes and controls of carbon and nutrient flux in entire aquatic systems. The Barrow project included both terrestrial and aquatic sections (Hobbie 1980) whereas the Char Lake project focused on the lake, with comparative studies on nearby Lake Meretta that had become eutrophic as a result of sewage inputs (Schindler *et al.* 1974a, 1974b). While the nine principal investigators on the Barrow aquatic project worked on many ponds, they all came together to make integrated measurements on one pond; when 29 scientists began sampling in this pond, the investigator effect was so large that an aerial tramway had to be constructed.

The success of the IBP led to a US program of integrated ecological studies at 26 sites, mostly in the USA. This Long-Term Ecological Research (LTER) program includes sites at Toolik Lake, Alaska, and the McMurdo Dry Valleys, Antarctica (see further details in Appendix 1.1). The observations at Toolik began in 1975 and in the McMurdo Dry Valley lakes in the late 1950s. Each LTER

project is reviewed every 6 years but is expected to continue for decades; each is expected to publish papers, support graduate students and collect data which are accessible to all on the Internet. The long-term goal of the Arctic LTER is to predict the effects of environmental change on lakes, streams, and tundra. The overall objectives of the McMurdo LTER are to understand the influence of physical and biological constraints on the structure and function of dry valley ecosystems, and to understand the modifying effects of material transport on these ecosystems.

The IBP and LTER projects illustrate the whole-system and synthetic approaches to limnology. The long-term view leads to detailed climate data, data-sets spanning decades, whole-system experiments, and a series of integrated studies of aspects of the physical, chemical, and biological processes important at the particular sites. Whereas there is a need for ongoing studies of this type, there is also a need for extended spatial sampling; that is, repeated sampling of many polar sites, to understand the effects of different geological and climatic settings throughout the polar regions. Other lake districts with important limnological records for Antarctica (Figure 1.1) include Signy Island and Livingston Island (Byers Peninsula; Toro *et al.* 2007) in the maritime Antarctic region, the Vestfold Hills, and the Schirmacher Oasis. Lake studies have now been conducted in many parts of the circumpolar Arctic (Figure 1.2), including Alaska, Canada, northern Finland, several parts of Greenland, Svalbard, Siberia, and the Kuokkel lakes in northern Sweden. Flowing waters have also received increasing attention from polar limnologists; for example, the ephemeral streams of the McMurdo Dry Valleys and the large Arctic rivers and their lake-rich floodplains.

Several special journal issues have been published on polar lake and river themes including high-latitude limnology (Vincent and Ellis-Evans 1989), the paleolimnology of northern Ellesmere Island (Bradley 1996), the limnology of the Vestfold Hills (Ferris *et al.* 1988), and the responses of northern freshwaters to climate change (Wrona *et al.* 2006). Books on regional aspects of polar limnology include volumes on the Schirmacher Oasis (Bormann and Fritsche 1995), McMurdo Dry Valleys

(Green and Friedmann 1993; Prisco 1998), Alaskan freshwaters (Milner and Oswood 1997), Siberian rivers (Zhulidov *et al.* 2008), and Siberian wetlands (Zhulidov *et al.* 1997). The rapidly developing literature on subglacial aquatic environments beneath the Antarctic ice sheet has been reviewed in a volume by the National Academy of Sciences of the USA (National Research Council 2007). Pienitz *et al.* (2004) present multiple facets of Antarctic and Arctic paleolimnology, with emphasis on environmental change, and current changes in Antarctic lake and terrestrial environments are summarized in Bergstrom *et al.* (2006).

### 1.3 Limnological diversity

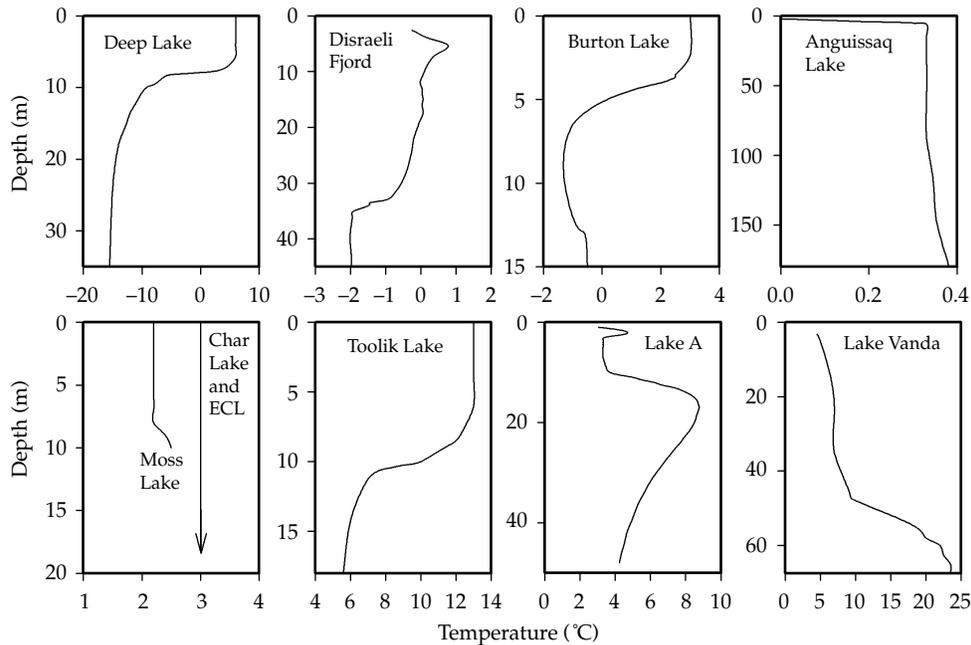
The Antarctic, defined as that region south of the Polar Frontal Zone or Antarctic Convergence (which also delimits the Southern Ocean) contains several coastal areas where lakes, ponds, and streams are especially abundant (Figure 1.1), as well as vast networks of subglacial aquatic environments. Lake and river ecosystems are common throughout the Arctic (Figure 1.2), which can be delimited in a variety of ways: by the northern treeline, the 10°C July isotherm, or the southern extent of discontinuous permafrost (for permafrost map definitions, see Heginbottom 2002), which in the eastern Canadian Arctic, for example, currently extends to the southern end of Hudson Bay (<http://atlas.nrcan.gc.ca/site/english/maps/environment/land/permafrost>). Of course, all of these classifications depend on climate, which is changing rapidly. These northern lands include the forest-tundra ecozone, sometimes referred to as the Sub-Arctic or Low Arctic, which grades into shrub tundra, true tundra, and ultimately high Arctic polar desert. Appendix 1.1 provides a brief limnological introduction to many of the polar rivers, lakes, or lake districts where there have been aquatic ecosystem studies.

Collectively, the polar regions harbour an extraordinary diversity of lake types (Plates 1–9) ranging from freshwater to hypersaline, from highly acidic to alkaline, and from perennially ice-covered waters to concentrated brines that never freeze. The diverse range of these habitats is illustrated by their many different thermal regimes in summer, from fully mixed to thermally stratified

over a 40°C span of temperatures (Figure 1.3). This physical diversity is accompanied by large variations in their chemical environments, for example from oxygen supersaturation to anoxia, sometimes within the same lake over time or depth. Permafrost thaw lakes (thermokarst lakes and ponds; Plate 8) are the most abundant aquatic ecosystem type in the Arctic, and often form a mosaic of waterbodies that are hot spots of biological activity in the tundra, with abundant microbes, benthic communities, aquatic plants, plankton, and birds. In the Mackenzie River delta for example, some 45000 waterbodies of this type have been mapped on the floodplain, with varying degrees of connection to the river (Emmerton *et al.* 2007; Figure 1.4), while

in the Yukon River delta the total number of thaw lakes and ponds has been estimated at 200000 (Maciolek 1989). Most thaw lakes are shallow, but lake depth in the permafrost increases as a square root of time, and the oldest lakes (>5000 years) can be up to 20 m deep (West and Plug 2008). Shallow rock-basin ponds are also common throughout the Arctic (e.g. Rautio and Vincent 2006; Smol and Douglas 2007a) and Antarctica (e.g. McKnight *et al.* 1994; Izaguirre *et al.* 2001).

Certain lake types are found exclusively in the polar regions, for example solar-heated perennially ice-capped lakes (e.g. northern Ellesmere Island lakes in the Arctic, McMurdo Dry Valley lakes in Antarctica; Figure 1.3), and the so-called epishelf



**Figure 1.3** From sub-zero cold to solar-heated warmth: the remarkable diversity of summer temperature and mixing regimes in high-latitude lakes. Deep Lake is a hypersaline lake in the Vestfold Hills (15 January 1978; Ferris *et al.* 1988); Disraeli Fjord, northern Ellesmere Island, at the time of study was an epishelf lake with a 30-m layer of freshwater dammed by thick ice floating on sea water (10 June 1999; Van Hove *et al.* 2006); Burton Lake is a coastal saline lake in the Vestfold Hills that receives occasional inputs of sea water (30 January 1983, Ferris *et al.* 1988); Anguissaq Lake lies at the edge of the ice cap in northwest Greenland and convectively mixes beneath its ice cover in summer (19 August 1957; Barnes 1960); Moss Lake on Signy Island (9 February 2000; Pearce 2003), Char Lake in the Canadian Arctic (isothermal at 3°C to the bottom, 27.5 m, on 30 August 1970; Schindler *et al.* 1974a), and El'gygytyn Crater Lake (ECL) in Siberia (isothermal at 3°C to 170 m on 1 August 2002; Nolan and Brigham-Grette 2007) are examples of cold monomictic lakes that mix fully during open water in summer; Toolik Lake, northern Alaska, is dimictic, with strong summer stratification (8 August 2005; see Figure 4.6 in this volume); Lake A is a perennially ice-covered, meromictic lake on northern Ellesmere Island (1 August 2001, note the lens of warmer sub-ice water; Van Hove *et al.* 2006); and Lake Vanda is an analogous ice-capped, meromictic system in the McMurdo Dry Valleys with more transparent ice and water, and extreme solar heating in its turbid, hypersaline bottom waters (27 December 1980; Vincent *et al.* 1981).

lakes, tidal freshwater lakes that sit on top of colder denser seawater at the landward edges of ice shelves; for example Beaver Lake, Antarctica, and Milne Fjord in the Arctic. Networks of subglacial aquatic environments occur beneath the thick ice of the Antarctic ice cap (Plate 1), and include the vast, deep, enigmatic waters of Lake Vostok. Ephemeral rivers and streams are found around the margins of Antarctica with biota that are active for only a brief period each year (Plate 6). Flowing surface waters play a much greater role in the Arctic where there are extensive catchments and some of the world's largest rivers that discharge into Arctic seas (Plate 7). Many polar lakes are classed as ultra-oligotrophic or extremely unproductive, whereas some are highly enriched by animal or human activities.

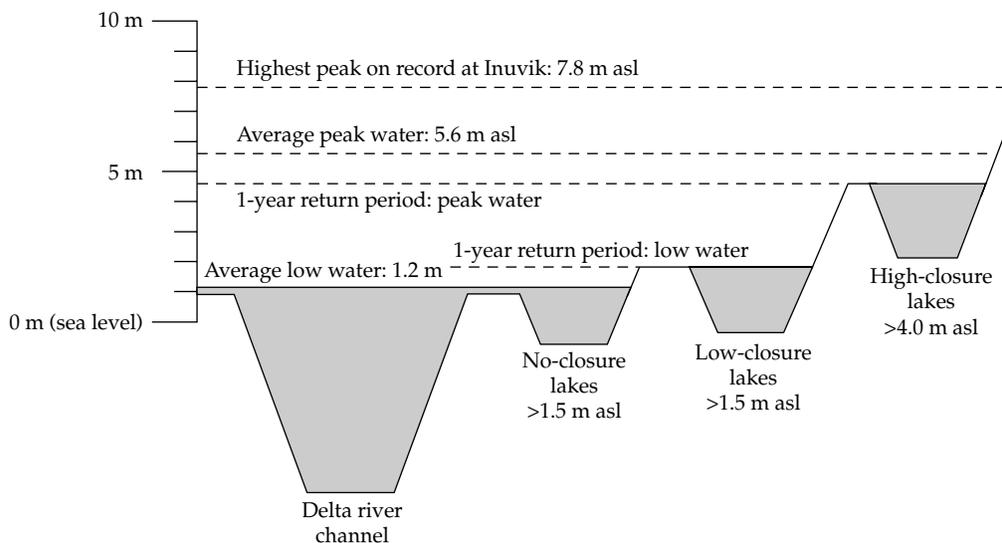
## 1.4 Controlling variables for biological production

What factor or combination of factors limits biological production in high-latitude freshwater

ecosystems? This question is not only of interest to polar limnologists, but it may also provide insights into the controlling variables for aquatic productivity at other latitudes. Such insights are especially needed to predict how inland water ecosystems will respond to the large physical, chemical, and biological perturbations that are likely to accompany future climate change (see Section 1.6 below).

### 1.4.1 Water supply

The availability of water in its liquid state is a fundamental prerequisite for aquatic life, and in the polar regions the supply of water is severely regulated by the seasonal freeze–thaw cycle. For a few ecosystem types, this limits biological activity to only a brief period of days to weeks each year, for example the ephemeral streams of Antarctica and meltwater lakes on polar ice shelves. For many high-latitude lakes, however, liquid water persists throughout the year under thick snow and ice cover, and even some shallow ponds can retain a



**Figure 1.4** Lake classification in the Mackenzie River delta according to the extent of isolation from the river. Large Arctic rivers carry 3300 km<sup>3</sup> of freshwater to the Arctic Ocean each year and during their spring period of peak flow they recharge vast areas of flood-plain lakes. The Mackenzie River delta in the Canadian western Arctic has some 45 000 lakes of more than 0.0014 km<sup>2</sup>, and its total open-water surface area (including the multiple channels of the river) in late summer is about 5250 km<sup>2</sup>. Climate change is modifying the amplitude and duration of seasonal flooding and therefore the connectivity of these lakes with the river (Lesack and Marsh 2007). Redrawn from Emmerton *et al.* 2007, by permission of the American Geophysical Union. asl, above sea level.

thin layer of water over their benthic communities in winter (e.g. Schmidt *et al.* 1991). The larger rivers of the Arctic are fed from their source waters at lower latitudes and they continue to flow under the ice during autumn and winter, albeit at much reduced discharge rates. Thus many polar aquatic ecosystems are likely to be microbiologically active throughout the year, but with strong seasonal variations that are dictated by factors other than or in addition to water supply. During summer, the availability of meltwater for aquatic habitats is favored by the continuous, 24-h-a-day exposure of snow and ice to solar radiation, combined with the slow rates of evaporative loss at low temperatures. Polar streams and rivers are fed by melting glaciers and snow pack, and for the large Arctic rivers the peak snowmelt in spring gives rise to extensive flooding of their abundant floodplain lakes and generates a vast interconnected freshwater habitat (Plate 8).

#### 1.4.2 Irradiance

The polar regions receive reduced amounts of incident solar radiation relative to lower latitudes (annual solar irradiance drops by about 50% over the 50° of latitude from 30° to 80°), and this effect is compounded by the attenuating effects of snow and ice on underwater irradiance. This limits the total annual production in Arctic and Antarctic aquatic ecosystems, and it has a strong influence on the seasonality of photosynthesis, which ceases during the onset of winter darkness and resumes with the first return of sunlight. Underwater irradiance does not, however, appear to be the primary variable controlling the large variation among lakes in daily primary production by the phytoplankton during summer. Polar lakes may show an early spring maximum in phytoplankton biomass and photosynthesis immediately beneath the ice, with pronounced decreases over summer despite increased irradiance conditions in the upper water column (Tanabe *et al.* 2008, and references therein), but likely decreased nutrient availability (Vincent 1981). Nearby lakes such as Meretta and Char in the Canadian High Arctic, and Fryxell and Vanda in the McMurdo Dry Valleys, show contrasting phytoplankton biomass concentrations and photosynthetic rates despite

similar incident irradiances but large differences in nutrient status (see Chapter 9).

#### 1.4.3 Low temperature

Contrary to expectation, some polar aquatic habitats have warm temperatures in summer, and some even remain warm during winter. Shallow thaw lakes can heat to 10°C or above, and the surface waters of northern lakes with high concentrations of light-absorbing dissolved organic matter and particles may undergo diurnal heating, with temperatures rising to >15°C. The large Arctic rivers begin more than 1000 km further south of their discharge point to the Arctic Ocean, and these waters can warm during summer over their long transit to the sea; for example, the Mackenzie River can be up to 17°C at its mouth, despite its far northerly latitude of 69°N. Stratified, perennially ice-covered lakes can heat up over decades to millennia via the solar radiation that penetrates the ice (Vincent *et al.* 2008, and references therein; see also Chapter 4). Examples of these solar-heated, meromictic lakes are known from both polar regions, and in these waters the deep temperature maxima lie well above summer air temperatures and up to 70°C above winter temperatures. 'Warm' of course is a relative term, and even liquid water temperatures of 0°C beneath the ice of most polar lakes, or -2°C in the subglacial Antarctic lakes capped by ice many kilometers thick, provide hospitable thermal conditions for biological processes relative to the extreme cold of the overlying atmosphere (down to -89°C at Vostok station in winter).

Most polar aquatic habitats experience water temperatures close to 0°C for much of the year. Many of the organisms found in these environments appear to be cold-tolerant rather than cold-adapted, and the cool ambient conditions likely slow their rates of metabolism and growth. Although cold temperatures may exert an influence on photosynthesis and other physiological processes, it does not preclude the development of large standing stocks of aquatic biota in some high-latitude waters. Conversely, lakes with warmer temperatures do not necessarily have higher phytoplankton and production rates (e.g. compare Lake Vanda with Lake Fryxell in the McMurdo Dry Valleys; Vincent 1981).

#### 1.4.4 Nutrient supply

Several features of polar lakes and their surrounding catchments result in low rates of nutrient delivery for biological production, especially by their plankton communities. The combination of low temperature, low moisture, and freezing constrains the activity of soil microbes and slows all geochemical processes including soil-weathering reactions. This reduces the release of nutrients into the groundwater and surface runoff, which themselves are limited in flow under conditions of extreme cold. The severe polar climate also limits the development of vegetation, which in turn reduces the amount of root biomass, associated microbes (the rhizosphere community), and organic matter that are known to stimulate weathering processes (Schwartzman 1999). Nutrient recycling rates are also slowed by low temperatures within Arctic and Antarctic waters. Additionally, the presence of ice cover inhibits wind-induced mixing of polar waters throughout most of the year. This severely limits the vertical transport of nutrients from bottom waters to the zone immediately beneath the ice where solar energy is in greatest supply for primary production. It also results in quiescent, stratified conditions where inflowing streams can be short-circuited directly to the outflow without their nutrients mixing with the main body of the lake (see Chapter 4), and where nutrient loss by particle sedimentation is favored.

Several lines of evidence indicate that nutrient supply exerts a strong control on phytoplankton production in polar lakes, in combination with light and temperature. First, large variations in primary production occur among waters in the same region, despite similar irradiance and temperature regimes, but differences in nutrient status (see above). Second, in stratified waters, highest-standing stocks of phytoplankton and primary production rates are often observed deep within the ice-covered water column where light availability is reduced, but nutrient supply rates are greater (Plate 14; details in Chapter 9). Third, waterbodies in both polar regions that have received nutrient enrichment from natural or human sources show strikingly higher algal biomass stocks and production rates; for example, penguin-influenced

ponds on Ross Island (Vincent and Vincent 1982) and Cierva Point, Antarctica (Izaguirre *et al.* 2001), and high Arctic Meretta Lake, which was enriched by human sewage (Schindler *et al.* 1974b). Finally, nutrient bioassays show that high-latitude plankton assemblages respond strongly to nutrient addition; for example Toolik Lake, Alaska (O'Brien *et al.* 1997); lakes in northern Sweden (Holmgren 1984); Ward Hunt Lake in the Canadian Arctic (Bonilla *et al.* 2005); and McMurdo Dry Valley lakes (Priscu 1995). However, although nutrients may impose a primary limitation on productivity through Liebig-type effects on final yield and biomass standing stocks, there may be secondary Blackman-type effects on production rates per unit biomass, and thus specific growth rates (see Cullen 1991). Low temperatures reduce maximum, light-saturated photosynthetic rates, and to a lesser extent light-limited rates, and low irradiances beneath the ice may also reduce primary production. These effects may be further compounded by nutrient stress, which limits the synthesis of cellular components such as light-harvesting proteins and photosynthetic enzymes to compensate for low light or low temperature (Markager *et al.* 1999).

#### 1.4.5 Benthic communities

In many high-latitude aquatic ecosystems, total ecosystem biomass and productivity are dominated by photosynthetic communities living on the bottom where the physical environment is more stable, and where nutrient supply is enhanced by sedimentation of nitrogen- and phosphorus-containing particles from above, nutrient release from the sediments below and more active bacterial decomposition and nutrient recycling processes than in the overlying water column. Some of these communities achieve spectacular standing stocks in polar lakes, even under thick perennial ice cover (Plate 10); for example, cyanobacterial mats more than 10 cm in thickness, and algal-coated moss pillars up to 60 cm high in some Antarctic waterbodies (Imura *et al.* 1999). These communities fuel benthic food webs that lead to higher trophic levels, including fish and birds in Arctic lakes. The phytobenthos may be limited more by habitat and light availability than by nutrients. For

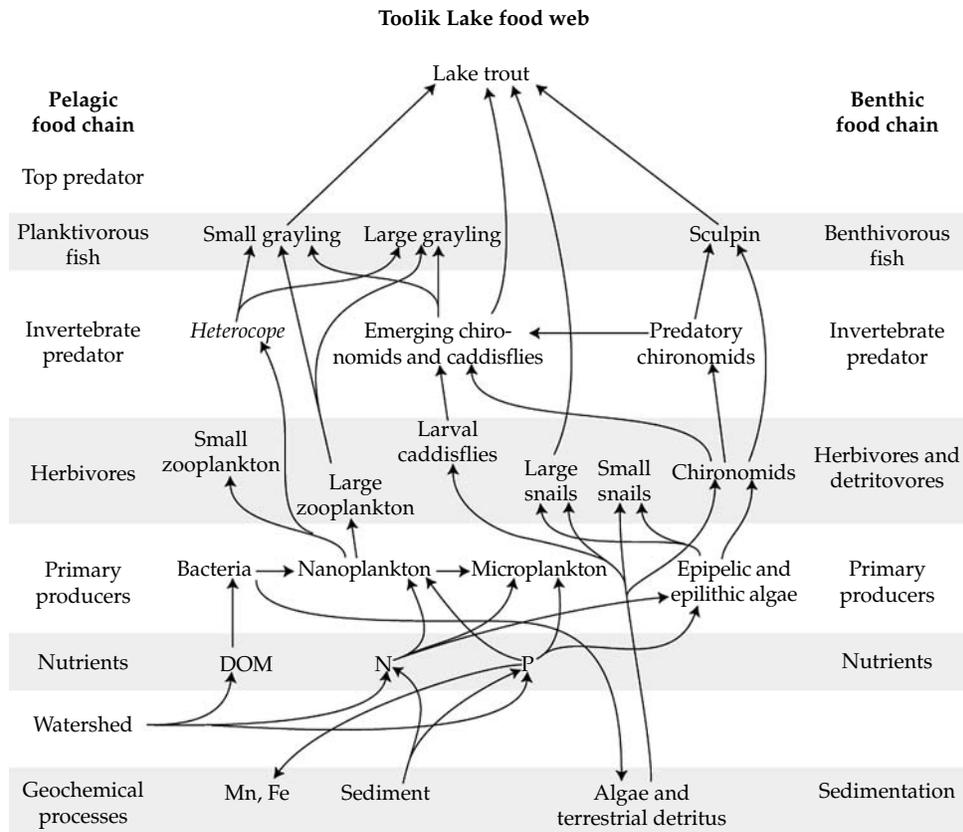
example, bioassays of microbial mats in an Arctic lake showed no effect of nutrient enrichment over 10 days, while the phytoplankton showed a strong growth response (Bonilla *et al.* 2005). On longer timescales, however, even the benthic communities may respond to nutrients, as shown by the shift of Arctic river phyto-benthos to luxuriant moss communities after several years of continuous nutrient addition (Plate 7; Bowden *et al.* 1994; for details see Chapter 5), and longer-term shifts in benthic diatom communities in a sewage-enriched Arctic lake (Michelutti *et al.* 2007).

### 1.5 Food webs in polar lakes

There is no typical food web for polar lakes (see Chapters 11–15). Instead there is a continuum of types of food web ranging from low Arctic lakes

with well-developed zooplankton and fish communities to high Arctic and Antarctic lakes with flagellates, ciliates, and rotifers at the top of the food web. The structure and diversity of the various food webs depend primarily on the trophic state of the lake and secondarily upon biogeography. Thus, some Antarctic lakes could likely support several types of crustacean zooplankton but few species have reached the continent (see Chapter 13), and many lakes are devoid of crustaceans.

Toolik Lake, Alaska (68°N, see Appendix 1.1), is an example of an oligotrophic low Arctic lake (Figure 1.5). The planktonic food web is based on small photosynthetic flagellates and on the bacteria that consume mainly dissolved organic matter from the watershed. Small flagellates (e.g. *Katablepharis*, Plate 11) consume bacteria and some of these (e.g. the colonial flagellate *Dinobryon*, Plate 11) are also



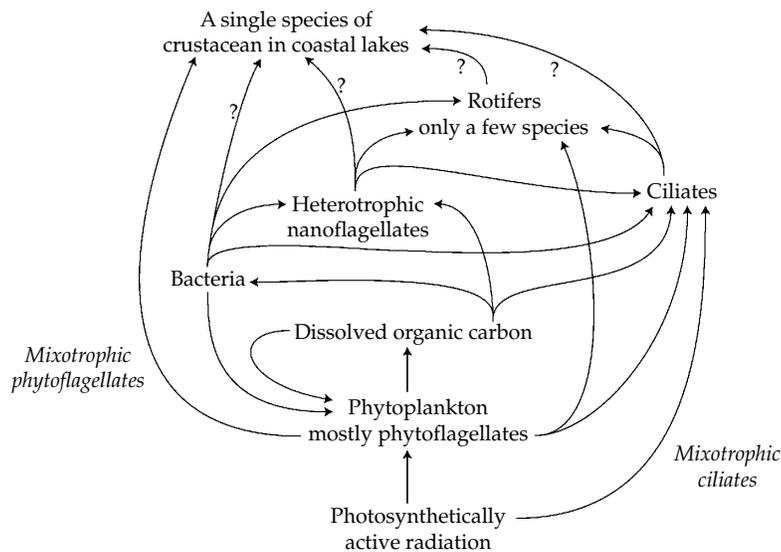
**Figure 1.5** The food web of a low Arctic lake: Toolik Lake, Alaska. Modified from O'Brien *et al.* (1997). DOM, dissolved organic matter.

photosynthetic (mixotrophic). These forms are consumed by seven species of crustacean zooplankton and eight species of rotifer. Zooplankton, in turn, are consumed by some of the five species of fish. Although this appears to be a conventional lake food web, it differs from the usual in several ways. First, almost all of the primary productivity is by nanoplankton. Second, the low primary productivity supports only a few zooplankton, not enough to control the algal abundance by grazing. Third, the sparse zooplankters are not abundant enough to support the fish growth. Therefore, the food web based on phytoplankton ends with zooplankton.

Stable-isotope analysis of the Toolik Lake food web reveals that the fish rely on the benthos as their main source of energy. In this benthic food web the energy passes from diatoms on rocks and sediments into snails and from detritus into chironomid larvae. Small fish eat the chironomids and are consumed in turn by the lake trout that also consume snails. A similar benthic-based food web supporting fish was also described by Rigler (1978) from Char Lake (75°N, see Appendix 1.1), where there was but one species of copepod and Arctic char (often spelled charr; *Salvelinus alpinus*; Plate 13) as the only fish species. Char occur in some of the

northernmost lakes in North America, for example Lake A at 83°N, where their diet may also depend on benthic invertebrates.

Antarctic lakes are species poor and possess simplified and truncated planktonic food webs dominated by small algae, bacteria, and colorless flagellates (Figure 1.6 and Chapter 11). There are few metazoans and no fish. The phytoplankton are often both photosynthetic and mixotrophic. The latter are species that can ingest bacteria as well as photosynthesize. One important pathway in both Antarctic and Arctic lakes is the microbial loop which may be defined as carbon and energy cycling via the nanoplankton (protists less than 20 μm in size). It includes primary production plus production of dissolved organic carbon (DOC) by planktonic organisms as well as uptake of DOC by bacteria, with transfer to higher trophic levels via nanoflagellates, ciliates, and rotifers (see Vincent and Hobbie 2000). In many Arctic and Antarctic lakes, picoplanktonic (<2 μm in diameter) and filamentous species of cyanobacteria are also components of the phytoplankton and microbial loop. Examples of cyanobacteria include *Synechococcus* sp. in Ace Lake in the Vestfold Hills (Powell *et al.* 2005) and Char Lake, Lake A and Lake Romulus in



**Figure 1.6** The typical planktonic food web in continental Antarctic lakes.

the high Arctic (Van Hove *et al.* 2008), and thin oscillators (filamentous cyanobacteria) in the deep chlorophyll maximum of Lake Fryxell, McMurdo Dry Valleys (Spaulding *et al.* 1995).

Lakes on coastal ice-free areas, like the Vestfold Hills (see Appendix 1.1), usually have a single planktonic crustacean. In freshwater and slightly brackish lakes sparse populations of the endemic Antarctic cladoceran *Daphniopsis studeri* occur (Plate 12) whereas in marine-derived saline lakes the marine copepod *Paralabidocera antarctica* is found. The McMurdo Dry Valleys lie inland and much further south (see Appendix 1.1). Here planktonic crustaceans are lacking, although a few copepod nauplii and two species of rotifers have been found in the benthos.

The great similarity between the food webs of lakes at both poles, in terms of structure and diversity, is closely related to the trophic state of the lakes (Hobbie *et al.* 1999). In this scheme, Type I lakes are ultra-oligotrophic; that is, they have very low primary productivity, and support only algae, bacteria, nanoflagellates and ciliates (e.g. ice-shelf lakes; Plates 2 and 3). Type II lakes are more productive and contain microzooplankton such as rotifers. Far northerly Arctic lakes such as Ward Hunt Lake and some McMurdo Dry Valley lakes fall into this category (Plate 4). With Type III lakes such as Char Lake, the increase in productivity allows copepods to survive. The most productive type of lake, Type IV, includes both copepods and Cladocera, much like a temperate lake. Ponds at Barrow fall into this category although they freeze completely and so have no fish. However, how can we explain the occurrence of fish (Arctic char) in the most northerly lakes that are Type I and Type II in the level of productivity? The answer is that the char are consuming the chironomid larvae of the more productive benthic food web. In contrast, continental Antarctic lakes contain neither insect larvae nor fish.

## 1.6 Polar lakes and global change

The polar regions are now experiencing the multiple stressors of contaminant influxes, increased exposure to ultraviolet radiation, and climate change (Schindler and Smol 2006; Wrona *et al.*

2006; Plates 13–16) and these impacts are likely to become more severe in the future. Global circulation models predict that the fastest and most pronounced increases in temperature over the course of this century will be at the highest latitudes (Plate 16; Meehl *et al.* 2007) because of a variety of feedback processes that amplify warming in these regions. These include the capacity for warm air to store more water vapour, itself a powerful greenhouse gas, and the reduced albedo (reflection of sunlight) as a result of the melting of snow and ice, leaving more solar energy to be available for heating. Major changes are also predicted in the regional distribution of precipitation, with increased inputs to many parts of the Arctic and Antarctica (Plate 16; Meehl *et al.* 2007), and an increased frequency of precipitation as rainfall, even at the highest latitudes where such events are unusual.

High-latitude lakes have already begun to show striking impacts of climate change. These include loss of perennial ice cover, increasing duration of open water conditions, increasing water temperatures, stronger water-column stratification, and shifts in water balance, in some cases leading to the complete drainage or drying-up of lakes and wetlands. For many polar aquatic ecosystems, small changes in their physical, chemical, or biological environment induced by climate can be amplified into major shifts in their limnological properties. Rather than slow, deterministic changes through time accompanying the gradual shift in air temperature, these threshold effects can result in abrupt step-changes in ecosystem structure and functioning.

### 1.6.1 Physical thresholds

The most critical threshold is that affecting the integrity of lake basins and the presence or absence of standing water. The degradation of permafrost soils in Siberia has resulted in collapse and drainage of many lake basins, and the complete disappearance of many waterbodies (Smith *et al.* 2005). A shift in the precipitation/evaporation balance in parts of the High Arctic has resulted in the complete drying up of ponds, perhaps for the first time in millennia (Smol and Douglas 2007a). In other regions, the accelerated melting of permafrost over

the last 50 years has created new basins for lakes and ponds, and increased development of shallow water ecosystems (Payette *et al.* 2004; Walter *et al.* 2006). An analysis of long-term changes of Mackenzie River floodplain lakes indicates that climate change is having disparate effects on their connectivity with the river. On average, the lower-elevation lakes (low-closure lakes; Figure 1.4) are being flooded for longer periods of time, whereas the highest-elevation lakes (high-closure lakes; Figure 1.4) are less flooded and may eventually dry up because of reduced ice dams and associated reductions in peak water levels in the river (Lesack and Marsh 2007).

For some polar lakes, ice dams from glaciers and ice shelves can be the primary structures retaining freshwater. Gradual warming can eventually cross the threshold of stability of these structures, resulting in catastrophic drainage. For example, the break-up of the Ward Hunt Ice Shelf in 2002 resulted in complete drainage and loss of an epishelf lake had probably been in place for several thousand years (Mueller *et al.* 2003).

The surface ice cover of polar lakes is also a feature subject to threshold effects. Many lakes in Antarctica and some Arctic lakes retain their ice covers for several years, decades, or longer. The loss of such ice results in changes in mixing regime and a complete disruption of their limnological gradients (Vincent *et al.* 2008). It also results in a massive increase in solar radiation; for example, order-of-magnitude increases in ultraviolet exposure that far exceed stratospheric ozone effects (Vincent *et al.* 2007), but also increased light supply for photosynthesis and more favorable conditions for the growth of benthic communities.

The persistent low temperatures in high-latitude lakes and ponds limit their water-column stability during open water conditions. In the coldest locations, there is insufficient heating of the water column to exceed the maximum density of water at 3.98°C, and the lakes remain free-mixing throughout summer (cold monomictic). Increased warming will result in the crossing of that threshold and a complete change in summer structure with the development of thermal stratification (dimictic conditions). These changes have far-reaching implications, including for light supply

to the phytoplankton, gas exchange, and biogeochemical processes. Recent changes in mixing and stratification patterns have been inferred from fossil diatom records in some lakes from Finnish Lapland, with evidence of increased productivity and the development of cladoceran communities (Sorvari *et al.* 2002).

### 1.6.2 Biogeochemical thresholds

The arrival of shrubs and trees in a catchment can result in a major step-increase in terrestrial plant biomass and hence the quantity of fulvic and humic materials in the soil, in turn resulting in a substantial increase in the concentration of particulate and colored dissolved organic material (CDOM) in lake waters (e.g. Pienitz and Vincent 2000). At CDOM concentrations less than 2 mgL<sup>-1</sup>, small changes in vegetation and hence CDOM can cause disproportionately large changes in the underwater light penetration and spectral regime, especially ultraviolet exposure. This vegetation change may also cause other changes that accelerate shifts in biogeochemistry, for example the increased development of root biomass, rhizosphere microbial activity, and soil weathering, and decreased albedo accompanied by increased soil heating and deepening of the permafrost active layer. Another biogeochemical threshold is that associated with water column anoxia. Once a lake fully depletes the oxygen in its bottom waters during stratification, large quantities of inorganic phosphorus, as well as iron and manganese, may be released from the lake's sediments. This increased internal loading can result in a sudden acceleration of eutrophication.

### 1.6.3 Biological thresholds

The extirpation of certain high Arctic taxa may occur if critical thresholds of tolerance are exceeded. Conversely new species may arrive in the catchments (e.g. the arrival of shrub and tree species as noted above) or in the rivers and lakes. For example, analyses of range distributions and climate change scenarios have shown that warm-water fish species, such as the smallmouth bass, *Micropterus dolomieu*, will shift northwards into the Arctic, with negative impacts on native fish

communities (Sharma *et al.* 2007). More subtle effects may take place through changes in animal behavior. For example, changes in the migration patterns of Arctic char may accompany increased water temperatures, with negative effects on fish productivity and size distribution, and on native fisheries (see Chapter 14).

Paleolimnological analyses of sediment cores from Cape Herschel, Ellesmere Island, showed that there was abrupt biotic change in the mid-nineteenth century at this site, as indicated by the quantity and composition of fossil diatoms (Douglas *et al.* 1994). This effect has been detected subsequently in sediment cores from many parts of the circumpolar Arctic (e.g. Antoniades *et al.* 2007), with differences in the exact timing and magnitude of change among lakes and locations, as expected (Smol *et al.* 2005; see Plate 15). These striking effects on community structure have been attributed primarily to changes in the duration and extent of lake and pond ice cover, as well as related limnological changes (Smol *et al.* 2005; Smol and Douglas 2007b; see also Chapter 3).

## 1.7 Conclusions

High-latitude lakes, rivers, and wetlands are a major focus for limnological research not only because of their remarkable diversity and intrinsic importance in polar biomes, but also because of their value as compelling models for understanding aquatic ecosystem processes in general. These environments provide habitats for plants, animals, and microbes that are adapted to or at least tolerate persistent low temperatures, freeze–thaw cycles, and marked seasonal and interannual variations in energy and nutrient supplies. However, the resilience of these biological communities is now being tested severely as they face the multiple stressors associated with local and global human impacts, notably contaminant effects, increased ultraviolet exposure, and climate change. The physical characteristics of polar lakes and rivers depend strongly on ice and the freezing and melt cycle, and small variations in air temperature can radically alter their structure and functioning. These ecosystems are therefore a sensitive guide to the magnitude and pace of global climate change, as well as key

sites for environmental research, monitoring, and stewardship.

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## References

- Antoniades, D. *et al.* (2007). Abrupt environmental change in Canada's northernmost lake inferred from diatom and fossil pigment stratigraphy. *Geophysical Research Letters* **34**, L18708, doi:10.1029/2007GL030947.
- Barnes, D.F. (1960). An investigation of a perennially frozen lake. *Air Force Surveys in Geophysics* **129**.
- Bergstrom, D., Convey, P., and Huiskes, A. (eds) (2006). *Trends in Antarctic Terrestrial and Limnetic Ecosystems*. Springer, Dordrecht.
- Bonilla, S., Villeneuve, V., and Vincent, W.F. (2005). Benthic and planktonic algal communities in a high arctic lake: pigment structure and contrasting responses to nutrient enrichment. *Journal of Phycology* **41**, 1120–1130.
- Bormann, P. and Fritsche, D. (eds) (1995). *The Schirmacher Oasis*. Justus Perthes, Gotha.
- Bowden, W.B., Finlay, J.C., and Maloney, P.E. (1994). Long-term effects of PO<sub>4</sub> fertilization on the distribution of bryophytes in an Arctic river. *Freshwater Biology* **32**, 445–454.
- Bradley, R.S. (ed.) (1996). Taconite Inlets lakes project. *Journal of Paleolimnology* **16**, 97–255.
- Brewer, M.C. (1958). The thermal regime of an Arctic lake. *Transactions of the American Geophysical Union* **39**, 278–284.
- Christoffersen, K.S., Amsinck, S.L., Landkildehus, F., Lauridsen, T.L., and Jeppesen, E. (2008). Lake flora and fauna in relation to ice-melt, water temperature and chemistry. In Meltøfte, H., Christensen, T.R., Elberling, B., Forchhammer, M.C., and Rasch, M. (eds),

- High-Arctic Ecosystem Dynamics in a Changing Climate. Ten years of monitoring and research at Zackenberg Research Station, Northeast Greenland*, pp. 371–390. *Advances in Ecological Research*, vol. 40, Academic Press, San Diego, CA.
- Cornwell, J.C. (1987). Phosphorus cycling in Arctic lake sediment: adsorption and authigenic minerals. *Archives für Hydrobiologie* **109**, 161–170.
- Cullen, J.J. (1991). Hypotheses to explain high nutrient conditions in the open sea. *Limnology and Oceanography* **36**, 1578–1599.
- Doran, P.T., Wharton, R.A., Lyons, W.B., DesMarais, D.J., and Andersen, D.T. 2000. Sedimentology and isotopic geochemistry of a perennially ice-covered epishelf lake in Bunger Hills Oasis, East Antarctica. *Antarctic Science*, **12**, 131–140.
- Douglas, M.S.V., Smol, J.P., and Blake, Jr, W. (1994). Marked post-18th century environmental change in high Arctic ecosystems. *Science* **266**, 416–419.
- Emmerton, C.A., Lesack, L.F.W., and Marsh, P. (2007). Lake abundance, potential water storage, and habitat distribution in the Mackenzie River Delta, western Canadian Arctic. *Water Resources Research* **43**, W05419.
- Ferris, J.M., Burton, H.R., Johnstone, G.W., and Bayly, I.A.E. (eds) (1988). *Biology of the Vestfold Hills. Hydrobiologia* **165**.
- Forel, A.-F. (1895). *Le Léman: Monographie Limnologique* Tome 2. F. Rouge, Lausanne.
- Franzmann, P.D., Roberts, N.J., Mancuso, C.A., Burton, H.R., and McMeekin, T.A. (1991). Methane production in meromictic Ace Lake, Antarctica. *Hydrobiologia* **210**, 191–201.
- Gibson, J.A.E. (1999). The meromictic lakes and stratified marine basins of the Vestfold Hills, East Antarctica. *Antarctic Science* **11**, 175–192.
- Gibson, J.A.E. and Andersen, D.T. (2002). Physical structure of epishelf lakes of the southern Bunger Hills, East Antarctica. *Antarctic Science* **14**, 253–262.
- Goldman, C.R., Mason, D.T., and Hobbie, J.E. (1967). Two Antarctic desert lakes. *Limnology and Oceanography* **12**, 295–310
- Green, W.J. and Friedmann, E.I. (eds) (1993). *Physical and biogeochemical processes in Antarctic lakes*. Antarctic Research Series vol. 59. American Geophysical Union, Washington DC.
- Heginbottom, J.A. (2002). Permafrost mapping: a review. *Progress in Physical Geography* **26**, 623–642.
- Hobbie, J.E. (1961). Summer temperatures in Lake Schrader, Alaska. *Limnology and Oceanography* **6**, 326–329.
- Hobbie, J.E. (ed.) (1980). *Limnology of Tundra Ponds, Barrow, Alaska*. US/IBP Synthesis Series vol. 13. Dowden, Hutchinson and Ross, Stroudsburg, PA. [www.biodiversitylibrary.org/ia/limnologyoftundr00hobb](http://www.biodiversitylibrary.org/ia/limnologyoftundr00hobb).
- Hobbie, J.E., Bahr, M., and Rublee, P.A. (1999). Controls on microbial food webs in oligotrophic Arctic lakes. *Archiv für Hydrobiologie, Advances in Limnology* **54**, 61–76.
- Holmgren, S.K. (1984). Experimental lake fertilization in the Kuokkel area, northern Sweden: phytoplankton biomass and algal composition in natural and fertilized subarctic lakes. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **69**, 781–817.
- Hutchinson, G.E. and Löffler, H. (1956). The thermal classification of lakes. *Proceedings of the National Academy Sciences USA*, **42**, 84–86.
- Imura, S., Bando, T., Saito, S., Seto, K., and Kanda, H. (1999). Benthic moss pillars in Antarctic lakes. *Polar Biology* **22**, 137–140.
- Izaguirre, I., Mataloni, G., Allende, L., and Vinocur, A. (2001). Summer fluctuations of microbial planktonic communities in a eutrophic lake—Cierva Point, Antarctica. *Journal of Plankton Research* **23**, 1095–1109.
- Jensen, D.B. (ed.) (2003). *The Biodiversity of Greenland—a Country Study*. Technical Report no. 55. Pinnortitaleriffik, Grønlands Naturinstitut, Nuuk, Greenland.
- Juday, C. (1920). The Cladocera of the Canadian Arctic Expedition, 1913–1918. In *Report of the Canadian Arctic Expedition 1913–1918*. Vol VII. Crustacea, Part H, Cladocera. 1–8. T. Mulvey, Ottawa.
- Kaup, E. (2005). Development of anthropogenic eutrophication in Antarctic lakes of the Schirmacher Oasis. *Verhandlungen Internationale Vereinigung der Limnologie* **29**, 678–682.
- Lesack, L.F.W. and Marsh, P. (2007). Lengthening plus shortening of river-to-lake connection times in the Mackenzie River Delta respectively via two global change mechanisms along the arctic coast. *Geophysical Research Letters* **34**, L23404, doi:10.1029/2007GL031656.
- Maciolek, J.A. (1989). Tundra ponds of the Yukon Delta, Alaska, and their macroinvertebrate communities. *Hydrobiologia* **172**, 193–206.
- Markager, S., Vincent, W.F., and Tang, E.P.Y. (1999). Carbon fixation in high Arctic lakes: Implications of low temperature for photosynthesis. *Limnology and Oceanography* **44**, 597–607.
- McKnight, D.M., Andrews, E.D., Aiken, G.R., and Spaulding, S.A. (1994). Dissolved humic substances in eutrophic coastal ponds at Cape Royds and Cape Bird, Antarctica. *Limnology and Oceanography* **39**, 1972–1979.
- Meehl, G.A. et al. (2007). Global climate projections. In Solomon, S. et al. (eds.), *Climate Change 2007: The Physical*

- Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 747–846. Cambridge University Press, Cambridge.
- Michelutti, N., Hermanson, M.H., Smol, J.P., Dillon, P.J., and Douglas, M.S.V. (2007). Delayed response of diatom assemblages to sewage inputs in an Arctic lake. *Aquatic Sciences* doi:10.1007/s00027-007-0928-8.
- Milner, A.M. and Oswood, M.W., (eds) (1997). *Freshwaters of Alaska: Ecological Synthesis*. Ecological Studies, Vol 119. Springer, New York.
- Mueller, D.R., Vincent, W.F., and Jeffries, M.O. (2003). Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake. *Geophysical Research Letters* **30**, 2031, doi:10.1029/2003GL017931.
- National Research Council. (2007). *Exploration of Antarctic Subglacial Aquatic Environments: Environmental and Scientific Stewardship*. The National Academies Press, Washington DC.
- Nolan, M. and Brigham-Grette, J. (2007). Basic hydrology, limnology, and meteorology of modern Lake El'gygytgyn, Siberia. *Journal of Paleolimnology* **37**, 17–35.
- O'Brien, W.J. *et al.* (1997). The limnology of Toolik Lake. In Milner, A.M. and Oswood, M.W. (eds.), *Freshwaters of Alaska: Ecological Synthesis*, pp. 61–106. Springer, New York.
- Payette, S., Delwaide, A., Caccianiga, M., and Beauchemin, M. (2004). Accelerated thawing of subarctic peatland permafrost over the last 50 years. *Geophysical Research Letters* **31**, L18208.
- Pearce, D.A. (2003). Bacterioplankton community structure in a maritime Antarctic oligotrophic lake during a period of holomixis, as determined by denaturing gradient gel electrophoresis (DGGE) and fluorescence in situ hybridization (FISH). *Microbial Ecology* **46**, 92–105.
- Peterson, B.J. *et al.* (2006). Trajectory shifts in the arctic and subarctic freshwater cycle. *Science* **313**, 1061–1066.
- Pienitz, R. and Vincent, W.F. (2000). Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. *Nature* **404**, 484–487.
- Pienitz, R., Douglas, M.S.V., and Smol, J.P. (eds) (2004). *Long-Term Environmental Change in Arctic and Antarctic Lakes*. Springer, Dordrecht.
- Poulsen, E.M. (1940). Freshwater Entomostraca. *Zoology of East Greenland, Meddelsor om Grønland* **121**, no. 4.
- Powell, L.M., Bowman, J.P., Skerratt, J.H., Franzmann, P.D., and Burton, H.R. (2005). Ecology of a novel *Synechococcus* clade occurring in dense populations in saline Antarctic lakes. *Marine Ecology Progress Series* **291**, 65–80.
- Priscu, J.C. (1995). Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. *Freshwater Biology* **34**, 215–227.
- Priscu, J.C. (ed.) (1998). *Ecosystem dynamics in a polar desert: the McMurdo Dry Valleys Antarctica*. Antarctic Research Series vol. 72. American Geophysical Union, Washington DC.
- Quayle, W.C., Peck, L.S., Peat, H., Ellis-Evans, J.C., and Harrigan, P.R. (2002). Extreme responses to climate change in Antarctic lakes. *Science* **295**, 645.
- Rautio, M. and Vincent, W.F. (2006). Benthic and pelagic food resources for zooplankton in shallow high-latitude lakes and ponds. *Freshwater Biology* **51**, 1038–1052.
- Riget, F. *et al.* (2000). Landlocked Arctic charr (*Salvelinus alpinus*) population structure and lake morphometry in Greenland – is there a connection? *Polar Biology* **23**, 550–558.
- Rigler, F.H. (1978). Limnology in the High Arctic: a case study of Char Lake. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **20**, 127–140.
- Røen, U.I. (1962). Studies on freshwater entomostracan in Greenland II. Locations, ecology and geographical distribution of species. *Meddelsor om Grønland* **170**, no 2.
- Schindler, D.W. and Smol, J.P. (2006). Cumulative effects of climate warming and other human activities on freshwaters of Arctic and SubArctic North America. *Ambio* **35**, 160–168.
- Schindler, D.W., Welch, H.E., Kalff, J., Brunskill, G.J., and Kritsch, N. (1974a). Physical and chemical limnology of Char Lake, Cornwallis Island (75°N lat). *Journal of the Fisheries Research Board of Canada* **31**, 585–607.
- Schindler, D.W. *et al.* (1974b). Eutrophication in the high arctic- Meretta Lake, Cornwallis Island (75°N lat). *Journal of the Fisheries Research Board of Canada* **31**, 647–662.
- Schmidt, S., Moskall, W., De Mora, S.J.D., Howard-Williams, C., and Vincent W.F. (1991) Limnological properties of Antarctic ponds during winter freezing. *Antarctic Science* **3**, 379–388.
- Schwartzman, D.W. (1999). *Life, Temperature, and the Earth: The Self-organizing Biosphere*. Columbia University Press, New York.
- Sharma, S., Jackson, D.A., Minns, C.K., and Shuter, B.J. (2007). Will northern fish populations be in hot water because of climate change? *Global Change Biology* **13**, 2052–2064.
- Shirtcliffe, T.G.L. and Benseman, R.F. (1964). A sun-heated Antarctic lake, *Journal of Geophysical Research* **69**, 3355–3359.
- Smith, L.C., Sheng, Y., MacDonald, G.M., and Hinzman, L.D. (2005). Disappearing Arctic lakes. *Science* **308**, 1429.

- Smol, J.P. and Douglas, M.S.V. (2007a). Crossing the final ecological threshold in high Arctic ponds. *Proceedings of the National Academy of Sciences of the USA* **104**, 12395–12397.
- Smol, J.P. and Douglas, M.S.V. (2007b). From controversy to consensus: making the case for recent climatic change in the Arctic using lake sediments. *Frontiers in Ecology and the Environment* **5**, 466–474.
- Smol, J.P. *et al.* (2005). Climate-driven regime shifts in the biological communities of Arctic lakes. *Proceedings of the National Academy of Sciences USA* **102**, 4397–4402.
- Sorvari, S., Korhola, A., and Thompson R. (2002). Lake diatom response to recent Arctic warming in Finish Lapland. *Global Change Biology* **8**, 153–163.
- Spaulding, S.A., McKnight, D.M., Smith, R.L., and Dufford, R. (1994). Phytoplankton population dynamics in perennially ice-covered Lake Fryxell, Antarctica. *Journal of Plankton Research* **16**, 527–541.
- Stanley, D.W. and Daley, R.J. (1976). Environmental control of primary productivity in Alaskan tundra ponds. *Ecology* **57**, 1025–1033.
- Stocker, Z.S.J. and Hynes, H.B.N. (1976). Studies on tributaries of Char Lake, Cornwallis Island, Canada. *Hydrobiologia* **49**, 97–102.
- Tanabe, Y., Kudoh, S., Imura, S., and Fukuchi, M. (2008). Phytoplankton blooms under dim and cold conditions in freshwater lakes of East Antarctica. *Polar Biology* **31**, 199–208.
- Tominaga, H. and Fukii, F. (1981). Saline lakes at Syowa Oasis, Antarctica. *Hydrobiologia* **81–82**, 375–389.
- Toro, M., Camacho A., Rochera C., *et al.* (2007). Limnological characteristics of the freshwater ecosystems of Byers Peninsula, Livingston Island, in maritime Antarctica. *Polar Biology* **30**, 635–649.
- Vadeboncoeur, Y. *et al.* (2003). From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography* **14**, 1408–1418.
- Van Hove, P., Belzile, C., Gibson, J.A.E., and Vincent, W.F. (2006). Coupled landscape-lake evolution in the Canadian High Arctic. *Canadian Journal of Earth Sciences* **43**, 533–546.
- Van Hove, P., Vincent, W.F., Galand, P.E., and Wilmotte, A. (2008). Abundance and diversity of picocyanobacteria in high arctic lakes and fjords. *Algalogical Studies* **126**, 209–227.
- Vincent, A., Mueller, D.R., and Vincent, W.F. (2008). Simulated heat storage in a perennially ice-covered high Arctic lake: sensitivity to climate change. *Journal of Geophysical Research* **113**, C04036, doi:10.1029/2007JC004360.
- Vincent, W.F. (1981). Production strategies in Antarctic inland waters: phytoplankton eco- physiology in a permanently ice-covered lake. *Ecology* **62**, 1215–1224.
- Vincent, W.F. (1988). *Microbial Ecosystems of Antarctica*. Cambridge University Press, Cambridge.
- Vincent, W.F., Downes, M.T., and Vincent, C.L. (1981). Nitrous oxide cycling in Lake Vanda, Antarctica. *Nature* **292**, 618–620.
- Vincent, W.F. and Vincent, C.L. (1982). Nutritional state of the plankton in Antarctic coastal lakes and the inshore Ross Sea. *Polar Biology* **1**, 159–165.
- Vincent, W.F. and Ellis-Evans, J.C. (eds) (1989). High latitude limnology. *Hydrobiologia* **172**.
- Vincent, W.F. and Hobbie, J.E. (2000). Ecology of Arctic lakes and rivers. In Nuttall, M. and Callaghan, T.V. (eds), *The Arctic: Environment, People, Policies*, pp. 197–231. Harwood Academic Publishers, London.
- Vincent, W.F., Rautio, M., and Pienitz, R. (2007). Climate control of underwater UV exposure in polar and alpine aquatic ecosystems. In Orbaek, J.B., Kallenborn, R., Tombre, I., *et al.* (eds), *Arctic Alpine Ecosystems and People in a Changing Environment*, pp. 227–249. Springer, Berlin.
- Walter, K.M., Zimov, S.A., Chanton, J.P., Verbyla, D., and Chapin, F.S. (2006). Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. *Nature* **443**, 71–75.
- Wand, U., Samarkin, V.A., Nitzsche, H.M., and Hubberten, H.W. (2006). Biogeochemistry of methane in the permanently ice-covered Lake Untersee, central Dronning Maud Land, East Antarctica. *Limnology and Oceanography* **51**, 1180–1194.
- West, J.J. and Plug, L.J. (2008). Time-dependent morphology of thaw lakes and taliks in deep and shallow ground ice. *Journal of Geophysical Research* **113**, F01009, doi:10.1029/2006JF000696.
- Woo, M.K. (2000). McMaster River and Arctic hydrology. *Physical Geography* **21**, 466–484.
- Woo, M.K. and Young, K.L. (2006). High Arctic wetlands: their occurrence, hydrological characteristics and sustainability. *Journal of Hydrology* **320**, 432–450.
- Wrona, F.J., Prowse, T.D., and Reist, J.D. (eds) (2006). Climate change impacts on Arctic freshwater ecosystems and fisheries. *Ambio* **35**(7), 325–415.
- Zhulidov, A.V., Headley, J.V., Robarts, R.D., Nikanorov, A.M., and Ischenko, A.A. (1997). *Atlas of Russian Wetlands: Biogeography and Heavy Metal Concentrations*. National Hydrology Research Institute, Environment Canada, Saskatoon.
- Zhulidov, A.V., Robarts, R.D., Ischenko, A.A., and Pavlov, D.F. (2008). *The Great Siberian Rivers*. Springer, New York (in press).

## Appendix 1.1

This section presents illustrative examples of research sites in the Arctic and in Antarctica (see Figures 1.1 and 1.2 for location maps).

### A1.1 The Toolik Lake LTER

Toolik Lake and surrounding rivers (Plate 6) and lakes lie in tussock tundra at 68°N, 149°W in the northern foothills of the North Slope of Alaska. Studies began in 1975 and continue under the Long Term Ecological Research (LTER) program (data and bibliography at <http://ecosystems.mbl.edu/ARC/>). Investigations of Toolik Lake (25m maximum depth) have included physics, chemistry, and numbers, productivity, and controls of phytoplankton, zooplankton, benthos, and fish, and cycling of carbon, phosphorus, and nitrogen. Whole lakes, large mesocosms, and streams have been treated by fertilization as well as by the introduction and exclusion of predators (O'Brien *et al.* 1997).

Toolik Lake is ice-bound for 9 months (early October until mid-June) and is ultra-oligotrophic, with an annual planktonic productivity of approximately 10 gCm<sup>-2</sup>. The low rates of organic-matter sedimentation and unusually high concentrations of iron and manganese combine with high amounts of oxygen in the water column to cause strong adsorption of soluble nitrogen and phosphorus by the metal-rich sediments (Cornwell 1987). The algae, nearly all nanoflagellates, are fed upon by seven species of crustacean zooplankton (Hobbie *et al.* 1999). Allochthonous organic matter from land produces a lake DOC level of 6 mgCL<sup>-1</sup> and Secchi disk depths of 6–7 m. The added DOC means that the microbial food web resembles that of temperate lakes (i.e. 1–2 × 10<sup>6</sup> bacterial cells ml<sup>-1</sup>). Both the microbial food web and the food web beginning with phytoplanktonic algae are truncated as the zooplankton are so rare that their grazing does not control algae or flagellates. Fish in Toolik Lake are dependent upon benthic productivity; isotopes indicate that even the top predators, lake trout, obtain most of their carbon and energy from benthic invertebrates, such as snails and chironomid larvae.

### A1.2 Thaw lakes and ponds at Barrow, Alaska

Permafrost thaw lakes (also called thermokarst lakes and ponds) are found throughout the circumpolar Arctic. A three-year integrated study of this ecosystem type took place during the IBP at Barrow, Alaska (71°N, 157°W), where the coastal plain is covered either by large lakes (2–3 m deep) and shallow ponds (≈50 cm deep) or wet sedge

tundra. The IBP investigations (Hobbie 1980) included studies on the cycling of nitrogen and phosphorus and the changes in standing stock and productivity of phytoplankton, sediment algae, zooplankton, micro- and macrobenthic invertebrates, bacteria, and emergent sedges which cover one-third of each pond. Results included annual cycles of carbon, nitrogen, and phosphorus and a stochastic model of a whole pond ecosystem.

The Barrow ponds were solidly frozen from late September until mid-June. Mean summer temperatures were 7–8°C (maximum 16°C). Primary productivity was dominated by emergent sedges and grasses (96 gCm<sup>-2</sup>year<sup>-1</sup>), while benthic algae (8.4 gCm<sup>-2</sup>year<sup>-1</sup>), and phytoplankton (1.1 gCm<sup>-2</sup>year<sup>-1</sup>) contributed lesser amounts. The grazing food webs were unimportant (annual production of zooplankton was 0.2 gCm<sup>-2</sup>) relative to the detritus food web of bacteria, chironomid larvae, and protozoans (annual production of bacteria was approximately 10–20 gCm<sup>-2</sup>, of macrobenthos 1.6 gCm<sup>-2</sup>, and of protozoans 0.3 gCm<sup>-2</sup>).

The phytoplankton productivity of Barrow ponds was phosphorus-limited (Stanley and Daley 1976). Concentrations in the water were extremely low, 1–2 µg PL<sup>-1</sup>, despite high amounts (25 gPm<sup>-2</sup>) in the top 10 cm of sediments. The concentrations in the water were controlled by sorption on to a hydrous iron complex. Nitrogen was supplied mostly from the sediments as ammonium at a turnover rate of 1–2 days. The smallest life forms of the ponds did not seem to have any special adaptations to the Arctic. Concentrations and even species of bacteria and protists resembled those of temperate ponds. Metazoans were different in that many forms were excluded (e.g. fish, amphibia, sponges, many types of insects).

Permafrost thaw lakes are widely distributed throughout the tundra. They are formed by the thawing of permafrost and subsequent contraction and slumping of soils. In this way, they are particularly sensitive to present and future climate change. At some northern sites (e.g. Siberia; Smith *et al.* 2005) they are appear to be draining, drying up, and disappearing, whereas in some discontinuous permafrost areas they are expanding (Payette *et al.* 2004). Recent attention has focused especially on their abundant zooplankton populations, value as wildlife habitats, striking optical characteristics (see Plates 8 and 9), and biogeochemical properties, especially production of greenhouse gases (Walter *et al.* 2006).

### A1.3 Canadian Arctic Archipelago

A diverse range of lake ecosystem types occur throughout the Canadian high Arctic, ranging from rock basin

ponds at Cape Herschel (Smol and Douglas 2007a), to large deep lakes such as Lake Hazen (542 km<sup>2</sup>; Plate 5) on Ellesmere Island, and Nettilling Lake (5542 km<sup>2</sup>) and Amadjuak Lake (3115 km<sup>2</sup>), both on Baffin Island. The most northerly lakes in this region resemble those in Antarctica, with perennial ice cover, simplified food webs and polar desert catchments (e.g. Ward Hunt Lake, 83°05'N, 74°10'W; Plate 4). Meromictic lakes (saline, permanently stratified waters) are found at several sites, including Cornwallis Island, Little Cornwallis Island, and Ellesmere Island (Van Hove *et al.* 2006), and several of these have unusual thermal profiles that result from solar heating, as in some Antarctic lakes (Vincent *et al.* 2008; Figure 1.3).

Around 1970, Char Lake, a 27-m-deep (74°43'N, 94°59'W) lake on Cornwallis Island, was the site of a 3-year IBP comprehensive study (Schindler *et al.* 1974a; Rigler 1978), with comparative studies on nearby Meretta Lake that had become eutrophic as a result of sewage discharge into it (Schindler *et al.* 1974b). The average yearly air temperature was -16.4°C and summer temperatures averaged 2°C. Although Char Lake is usually ice-free for 2–3 months, the weather is often cloudy so the water temperature rarely exceeds 4°C. Because of the extreme conditions, the lake lies in a polar desert catchment with sparse vegetation, resulting in an unusually low loading of phosphorus. This, plus cold water temperatures and low light levels beneath the ice, results in planktonic production of approximately 4 g C m<sup>-2</sup> year<sup>-1</sup>, one of the lowest ever measured. However, benthic primary production of mosses and benthic algae is four-fold higher. One species of copepod dominates the planktonic community; the seven species of benthic Chironomidae account for half of the energy through the zoobenthos. Most animal biomass is found in the Arctic char that feed mainly on the chironomids. Rigler (1978, p. 139) concluded that 'There is little sign of Arctic adaptation in the classical sense. The species that live in Arctic lakes merely develop and respire more slowly than they would at higher temperatures'. However, this study was undertaken before the advent of molecular and other advanced microbiological techniques, and little is known about the microbial food web of Char Lake.

#### A1.4 Greenland lakes and ponds

The tremendous latitudinal extent of Greenland, from 60° to 83°N, includes a great variety of lakes, ponds, rivers, and streams (Poulsen 1940; Røen 1962; Jensen 2003). Very special features exist, such as saline lakes with old seawater in the bottom and hot and/or radioactive springs. In North Greenland, some lakes are permanently covered

with ice while the lakes in South Greenland have open water for 6 months of the year. There is a gradient of biodiversity and, as expected, the fauna and flora are much reduced in the north. For example, 21 species of vascular aquatic plants are found in southern Greenland and three in northern Greenland. Only 672 species of insects are present in Greenland while over 20 000 are found in Denmark. There is, furthermore, an east–west gradient as exemplified by the zooplankton diversity that decreases from south to north and from west to east. The largest number of freshwater entomostracans is found around Disko Island and at the southern west coast (around 45 species according to Røen 1962). A gradient study of primary productivity in Greenland, Danish, and US lakes showed that the Greenland lakes were all highly oligotrophic and that more than 80% of their total primary productivity took place on benthic surfaces (Vadeboncoeur *et al.* 2003). Arctic char are found throughout Greenland, sometimes with dwarf forms (3–8 cm), medium forms, and large forms (>30 cm) in the same lake (Riget *et al.* 2000). The large forms are often piscivorous on sticklebacks and young char. Medium-sized fish fed mainly on zooplankton while dwarf forms fed mainly on chironomid and trichopteran larvae.

Several areas have been sites of detailed limnological studies during the last few decades because there are field stations and associated infrastructure: Kangerlussuaq (Sønder Strømfjord) and Disko Island in West Greenland, and Pituffik (Thule Airbase) and Peary Land in North Greenland (Jensen 2003). The Danish BioBasis 50-year monitoring program in the Zackenberg Valley in northeastern Greenland (74°N) includes two shallow lakes (<6 m in depth), one with Arctic char. These lakes have been monitored for 10 years and it is evident that phytoplankton and zooplankton biomass is greatest in warm summers when there is deep thawing of the active layer of the soil and more nutrients enter the lakes (Christoffersen *et al.* 2008).

#### A1.5 Maritime Antarctic lakes

Islands to the north and along the western side of the Antarctic Peninsula experience a climate regime that is wet and relatively warm by comparison with continental Antarctica, and their limnology reflects these less severe conditions. Byers Peninsula (62.5°S, 61°W) on Livingston Island is an Antarctic Specially Protected Area under the Antarctic Treaty and is one of the limnologically richest areas of maritime Antarctica. This seasonally ice-free region contains lakes, ponds, streams, and wetlands. The lakes contain three crustacean species: *Boeckella poppei*, *Branchinecta gaini*, and the benthic cladoceran *Macrothrix*

*ciliate*. The chironomids *Belgica antarctica* and *Parochlus steinenii*, and the oligochaete *Lumbricillus* sp., occur in the stream and lake zoobenthos. Cyanobacterial mats occur extensively, and epilithic diatoms and the aquatic moss *Drepanocladus longifolius* are also important phyto-benthic components. The Antarctic Peninsula region is currently experiencing the most rapid warming trend in the Southern Hemisphere, and Byers Peninsula has been identified as a valuable long-term limnological reference site for monitoring environmental change (Toro *et al.* 2007).

Signy Island (60°43'S, 45°38'W) is part of the South Orkney Islands and also experiences the relatively warm, wet maritime Antarctic climate. It has a number of lakes that have been studied for many years by the British Antarctic Survey. The largest is Heywood Lake (area 4.3 ha, maximum depth 15 m), which has undergone eutrophication because its shores provide a wallow for an expanding population of fur seals. The lakes are cold monomictic (Figure 1.3) and contain the planktonic zooplankton species *Bo. poppei* and benthic crustacean species such as *Alona rectangularis*. These waters are proving to be excellent study sites for molecular microbiology (e.g. Pearce 2003), and there is limnological evidence that they are responding to recent climate change (Quayle *et al.* 2002). Phycological and limnological studies have also been made at many other sites in the maritime Antarctic region, including King George Island and Cierva Point, an Antarctic Specially Protected Area on the Antarctic Peninsula (e.g. Izaguirre *et al.* 2001).

### A1.6 McMurdo Dry Valleys LTER

First discovered by Captain Robert Falcon Scott in 1903, this is the largest ice-free region (about 4800 km<sup>2</sup>) of continental Antarctica (77°30'S, 162°E). It is best known for its deep lakes that are capped by thick perennial ice (Goldman *et al.* 1967; Green and Friedmann 1993; Prisco 1998). In the most extreme of these, Lake Vida (Victoria Valley), the ice extends almost entirely to the sediments; its 19 m of ice cover overlies a brine layer that is seven times the salinity of seawater with a liquid water temperature of -10°C. Most of the lakes are capped by 4–7 m of ice and are meromictic, with a surface layer of freshwater overlying saline deeper waters. These include Lake Fryxell, Lake Hoare, and Lake Bonney (Plate 4) in the Taylor Valley, Lake Miers in the Miers Valley, and Lake Vanda in the Wright Valley. The latter has a complex water column with thermohaline circulation cells and a deep thermal maximum above 20°C (Figure 1.3). The lakes contain highly stratified microbial communities, often with a deep population maximum of phytoplankton,

and a benthic community of thick microbial mats, but no crustacean zooplankton. The lakes also contain striking biogeochemical gradients and extreme concentrations at specific depths of certain gases and other intermediates in elemental nutrient cycles (see Chapter 8). Ephemeral streams are also common through the valleys (Plate 6), and are fed by alpine or piedmont glaciers. The largest of these, the Onyx River, flows 30 km inland, ultimately discharging into Lake Vanda (see Chapter 5 in this volume). Most of the streams contain pigmented microbial mats dominated by cyanobacteria, typically orange mats largely composed of oscillatorioid taxa and black mats composed of *Nostoc commune* (details in Vincent 1988). The valleys are polar deserts that are largely devoid of vegetation, with dry, frozen soils that are several million years old. New Zealand and the USA have conducted research in the region from the 1957/1958 International Geophysical Year onwards, and in 1993 the Taylor Valley was selected as an NSF-funded long term ecological research site (LTER; data and bibliography are given at: [www.mcmlter.org](http://www.mcmlter.org)). In recognition of the environmental sensitivity of this region, the McMurdo Dry Valleys have been declared an Antarctic Specially Managed Area under the terms of the Antarctic Treaty System.

### A1.7 Vestfold Hills

This lake-rich area lies in east Antarctica, at 68°30'S, 78°10'E (Ferris *et al.* 1988). The proximity of Davis Station permits year-round investigations, and consequently the lakes of the Vestfold Hills are among the few polar water bodies for which there are annual data-sets. Unlike most of the lakes of the McMurdo Dry Valleys, the lakes of the Vestfold Hills usually lose all or most of their ice cover for a short period in late summer. Saline lakes carry a thinner ice cover and the most saline, such as Deep Lake (about eight times the salinity of seawater), cool to extreme low temperatures in winter (Figure 1.3) but never develop an ice cover. The meromictic lakes (Gibson 1999) have well-oxygenated mixolimnia (upper waters), whereas the monimolimnia (lower waters that never mix) are anoxic. In contrast, the larger freshwater lakes are fully saturated with oxygen throughout their water columns at all times in the year. Compared with the lakes of the McMurdo Dry Valleys, the lakes of the Vestfold Hills are relatively young; the saline lakes are derived from relic seawater by evaporation, or where they are brackish by dilution. Sulphate reduction occurs in the meromictic lakes, as it does in those of the Dry Valleys. The high reducing capacity of sulphide serves to maintain anoxic conditions in the monimolimnia of these lakes. Large populations of photosynthetic sulphur bacteria

and chemolithotrophic thiosulphate-oxidizing bacteria occur in the anoxic waters, and use sulphide or its oxidation product, thiosulphate, as an electron donor (Ferris *et al.* 1988). Methanogenesis occurs in these sulphate-depleted waters (Franzmann *et al.* 1991), with rates up to  $2.5 \mu\text{mol kg}^{-1} \text{day}^{-1}$ . Ace Lake (Plate 5) is the most studied lake in the Vestfold Hills, largely because it is easily accessed both in summer and winter from Davis Station. It contains stratified microbial communities including flagellates, ciliates and high concentrations of picocyanobacteria (Powell *et al.* 2005). Unlike the McMurdo Dry Valley lakes, it also has crustacean zooplankton.

### A1.8 Larsemann Hills

This oasis of ice-free land is an Antarctic Specially Managed Area that lies at  $69^{\circ}25'S$  and  $76^{\circ}10'E$  between the Sørsdal Glacier and the Amery Ice Shelf, about 80 km south of the Vestfold Hills. It has about 150 lakes and ponds, most of which are freshwater. They vary in size from Progress Lake (10 ha in area and 38 m deep) to small ponds of a few square metres in area and a depth around 1 m. Geomorphologically the lakes can be classified as supraglacial ponds, lakes and ponds in large glaciated rock basins, and ponds dammed by colluvium (loose sediment that accumulates at the bottom of a slope). Most of them are fed by meltwater from snow banks and a number of them have distinct inflow and outflow streams which flow for around 12 weeks each year in summer. Like the freshwater lakes of the Vestfold Hills, the Larsemann Hills lakes contain sparse phytoplankton populations that are likely to be phosphorus-limited. Most of these clear waters contain luxuriant benthic mats dominated by cyanobacteria.

### A1.9 Bunger Hills

This site lies at  $66^{\circ}S$ ,  $100^{\circ}E$  in Wilkes Land, adjacent to the Shackleton Ice Shelf to the north. It has an area of  $950 \text{ km}^2$ , making it one of the largest oases in Antarctica. It contains hundreds of lakes, both freshwater and saline, in valleys and rock depressions. The freshwater lakes (the largest being Figurnoye, area  $14.3 \text{ km}^2$ ) are concentrated in the southern part of the oasis and at its periphery, while the saline lakes are located in the north and on the islands (Gibson and Andersen 2002). Most lakes in the centre of the Bunger Hills lose their ice-cover in summer, whereas those at its margins in contact with glaciers (epiglacial lakes) retain perennial ice caps. Geochemical and sedimentological studies have been conducted on White Smoke Lake, an epishelf lake in the region that is capped by 1.8–2.8 m of perennial ice (Doran *et al.* 2000).

### A1.10 Schirmacher and Untersee Oases

The Schirmacher and Untersee Oases lie in Dronning Maud Land at  $71^{\circ}S$ ,  $11\text{--}13^{\circ}E$  (Bormann and Fritsche 1995). The Russian Antarctic Station *Novolazarevskaya* and the Indian Station *Maitri* are located in this region. The largest lake, Lake Untersee, has an area of  $11.4 \text{ km}^2$  and a maximum depth of 167 m. The lakes are fed by under-water melting of glaciers, and lose water by sublimation from their perennial ice surfaces. Within the Schirmacher Oasis there are over 150 lakes ranging in size from  $2.2 \text{ km}^2$  (Lake Ozhidaniya), to small unnamed water bodies of less than  $0.02 \text{ km}^2$  in area. These lakes are small and shallow compared with some of the lakes which occur in the McMurdo Dry Valleys and the Vestfold Hills. The geomorphological diversity of lakes in the Schirmacher Oasis is considerable. There is a supraglacial lake (Taloye,  $0.24 \text{ km}^2$ ), which is around 5 m in depth. A number of relatively small epishelf lakes have formed on the northern edge of the oasis (Lake Prival'noye,  $0.12 \text{ km}^2$ ; Lake Zigzag,  $0.68 \text{ km}^2$ ; Lake Ozhidaniya,  $2.2 \text{ km}^2$ ; and Lake Predgornoye,  $0.18 \text{ km}^2$ ). Several lakes have formed in tectonically developed glaciated basins, for example Lake Sbrosovoye ( $0.18 \text{ km}^2$ ) and Lake Dlinnoye ( $0.14 \text{ km}^2$ ). Glacier-dammed and ice-wall-dammed lakes such as Lakes Iskristoye and Podprudnoye also occur as does one morainic lake (Lake 87). All of the lakes are freshwater and carry ice cover for most of the year. The majority become ice-free for a period in summer. The lakes have high transparency with several allowing light penetration to considerable depth; for example, Lakes Verkheneye and Untersee. Apart from several lakes that are subject to anthropogenic influences, the surface waters of the lakes of both oases are nutrient-poor. Total phosphorus levels are low, ranging between 4 and  $6 \mu\text{g l}^{-1}$  in surface lakewaters of the Schirmacher Oasis and less than  $1 \mu\text{g l}^{-1}$  in the upper water column of Lake Untersee. However, the bottom waters (>80 m depth) of Lake Untersee are anoxic, with extraordinarily high methane concentrations (around  $22 \text{ mmol l}^{-1}$ ) that are among the highest observed in natural aquatic ecosystems (Wand *et al.* 2006). Lake Glubokoye receives waste water from the Soviet Station and now has elevated dissolved reactive phosphorus levels of  $300 \mu\text{g l}^{-1}$  in its deepest water (Kaup 2005).

### A1.11 Syowa Oasis

This site lies on the Sôya Coast at  $69^{\circ}S$ ,  $39^{\circ}30'E$ . Like the Vestfold Hills and Bunger Hills it carries freshwater, saline, and hypersaline lakes. A number of the saline lakes have been studied in some detail (Tominaga and Fukii 1981). Lake Nurume is a meromictic lake (maximum

depth 16.6m) with two distinct haloclines, which makes it similar to well-studied Ace Lake in the Vestfold Hills. The upper waters are brackish and overly waters with a salinity similar to seawater, which in turn overly more saline waters with a salinity equivalent to 1.5 times that of seawater. Summer water temperatures are close to 10°C at the surface, decreasing in the more saline lower waters to 8°C. A temperature maximum occurs at around 3–4m (15°C). There are several hypersaline lakes (Lake Suribati at six times seawater and Lake Hunazoko at 5.5 times seawater), which are monomictic. Like the hypersaline lakes of the Vestfold Hills they are mixed in winter and develop a stratified water column during the summer. The freshwater lakes of this region are renowned for their luxuriant moss communities. These rise from the cyanobacterial mat-coated benthos at depths from 3 to 5m and form ‘moss pillars’ about 40cm in diameter and up to 60cm high (Imura *et al.* 1999; see Plate 10). Continuous data-logging in two of the freshwater lakes has shown that phytoplankton biomass increases under the ice with the arrival of first light in spring, drops to low values during summer open water conditions, and may then show a second peak during the fall ice-up period (Tanabe *et al.* 2008).

### A1.12 Subglacial aquatic ecosystems

Many liquid-water lakes are now known to occur beneath the Antarctic Ice Sheet (Plate 1; see Chapter 7 in this volume). The first of these to be discovered was Lake Vostok, a deep waterbody nearly the area of Lake Ontario (but more than three times deeper) lying beneath 3700m of ice. A total of 145 lakes have now been identified, and there are likely to be more. There is evidence that many may be connected either by films of flowing water between the basement rock and ice sheet or by larger subglacial rivers and streams. Lake Vostok, Lake Ellsworth, and Lake Concordia are the main sites of current research activities. There is intense interest in how these environments may act as a lubricant for movement of the overlying ice sheet, as well as their outstanding value for climate records, as potential habitats for microbial growth and evolution, and as astrobiological models for the search for life on icy moons and planets. There is much concern about how they may be explored without contamination or other impacts, and a first set of guidelines has been prepared for their long-term stewardship (National Research Council 2007).

### A1.13 Supraglacial aquatic ecosystems

The Arctic and Antarctica contain numerous regions where water lies on glaciers, ice sheets, and ice shelves.

These range from small cryoconite holes, first discovered on the Greenland ice cap and now compelling models for biogeochemical studies, to the extensive systems of meltponds on the Arctic and Antarctic ice shelves (thick landfast ice that floats on the sea) that are a habitat for rich microbial mat communities that are of great interest to astrobiologists (see Chapter 6 in this volume). The major sites of limnological study of ice shelves have been the Ward Hunt and Markham ice shelves in the Canadian High Arctic (Plate 2) and the McMurdo Ice Shelf, Antarctica (Plate 3).

### A1.14 Arctic rivers and floodplains

The Arctic contains six large rivers (Pechora, Ob, Yenisei, Lena, and Kolyma rivers in Siberia; the Mackenzie River in Canada, Plate 7) that flow into the Arctic Ocean, with a total discharge that amounts to 11% of the total freshwater drainage into the World Ocean. These rivers flow across extensive fluvial deltas that are underlain by permafrost. The uneven thawing of these regions results in tens of thousands of lake basins that become filled with snow melt and with ice-jammed flood waters from the river (Figure 1.4; Plate 8). These floodplain lakes provide a rich habitat for aquatic plants, animals, and microbes, and play a key role in the biogeochemical processing of river water before its discharge to the Arctic Ocean (see Chapter 5 in this volume). Climate change is affecting the flow regime of many Arctic rivers (Petersen *et al.* 2006) and the connectivity between the flood-plain lakes and their river source waters (Lesack and Marsh 2007).

### A1.15 High Arctic wetlands and flowing waters

The Arctic also contains many wetlands and lower-order flowing-water ecosystems. The inflows to Char Lake were examined during the IBP program on Cornwallis Island in the Canadian high Arctic, and were found to contain a low-diversity benthos dominated by cold-water chironomids, notably *Diamesa*; insect groups that are commonly found in temperate-latitude streams such as *Simuliidae* and *Ephemeroptera*, were conspicuously absent from the fauna (Stocker and Hynes 1976). Hydrological studies on McMaster River, also on Cornwallis, showed that infiltration and storage of meltwater into the frozen ground was limited compared with total melt. Much of the meltwater ran down the slopes, and streamflow was high during the melt season, followed by low summer flows influenced by active layer processes (Woo 2000). This has implications for impact of climate warming on high Arctic wetlands, which are dependent upon sustained water input throughout summer. Most of the

snow accumulated over 9–10 months is released as meltwater over 2–3 weeks and floods the wetlands while they are still frozen. Patchy wetlands occur where local water sources, especially late-lying snow banks, river flooding, or groundwater inflow into topographic depressions,

permit a high water table. The development of vegetation and accumulation of peat at these locations helps preserve the wetland by providing insulation over the permafrost and a porous medium for water infiltration and storage (Woo and Young 2006).