Chapter 8

Ecology of Arctic Lakes and Rivers

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Lakes, rivers and their associated wetlands are prominent features of the northern landscape. They are the habitats for a diverse range of biota including migratory wildlife, and encompass a broad spectrum of physical and geochemical conditions: dilute meltwaters fed by glacial streams, large river systems draining the tundra, reticulated networks of thermokarst (melted permafrost) ponds, and a great variety of lake types (Figs 8.1 and 8.2 also see illustrations 10 and 11 in colour section between chapters 4 and 5). Their catchments are equally varied, from relatively luxuriant forest-tundra in the south, to sparsely vegetated polar desert at northernmost latitudes. Even over expanses of perennial ice, such as on the Greenland Ice Cap (lat. 60–82°N) and the Ward Hunt Ice Shelf (lat. 83°N), water accumulates each summer within shallow basins and melt-holes, and provides an ephemeral habitat for aquatic life.

In some Arctic environments the freeze-thaw cycles and low temperatures have severely limited the distribution and abundance of organisms to produce ecosystems dominated by microscopic species, sometimes to the exclusion of higher plants and animals. These extreme, highly simplified ecosystems are analogous to the lakes, ponds and streams found at equivalent latitudes in Antarctica. Throughout most of the Arctic, however, the aquatic environments are characterized by a much more developed food web including fish and waterfowl that are important as traditional foods to the indigenous peoples of the North, and for recreational fishing and hunting.

The aim of this chapter is to provide an introduction to the literature on inland aquatic ecosystems of the circumpolar Arctic and Subarctic, with emphasis on current research themes in the North American sector. These themes include traditional (and still important) limnological subjects such as habitat structure, species diversity, biological production and food web interactions. Such studies are increasingly supported by novel instruments and methodologies such as remote sensing, underwater profilers and molecular techniques, and by new research strategies. The latter includes a commitment to long term measurements at some sites to provide an accurate guide to interannual variability and climate-related trends. At the long term ecological research (LTER) site at Toolik Lake, (lat. 68.6°N, Alaska), this type of

FIGURE 8.1: TOP: LAC À L'EAU CLAIRE IN THE FOREST-TUNDRA REGION OF NORTHERN QUÉBEC; BOTTOM: KUPARUK RIVER, IN THE TOOLIK LAKE LTER SITE LOCATED IN THE SHRUB TUNDRA REGION OF NORTHERN ALASKA (ALASKAN PIPELINE IN THE BACKGROUND).

approach has also allowed investigators to run manipulation experiments over the course of several years and to resolve short versus long term responses to environmental change.

Arctic limnology developed rapidly in the 1960s and 70s because of the International Biological Program (IBP) research on tundra ponds at Barrow, Alaska (Hobbie, 1980) and on ultra-oligotrophic (i.e., extremely nutrient-poor) Char Lake in the Canadian high Arctic (Schindler *et al.*, 1974; Rigler, 1978). These and other earlier studies in polar limnology have been reviewed by Hobbie (1984), and a CD-ROM by Welch and Kling (1996) provides a more recent introduction to the subject. Freshwater studies in Alaska are summarized in Milner and Oswood (1997). Theme issues of journals relevant to Arctic freshwater ecology include volumes on high latitude limnology (Vincent and Ellis-Evans, 1989), the ecology of Toolik Lake, Alaska (O'Brien, 1992), contaminants in the northern environment (Schindler *et al.*, 1995); ecosystem studies at Taconite Inlet on Ellesmere Island with a focus on paleolimnology

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Lac À L'eau claire, Northern Quebec

Kuparuk River, Northern Alaska

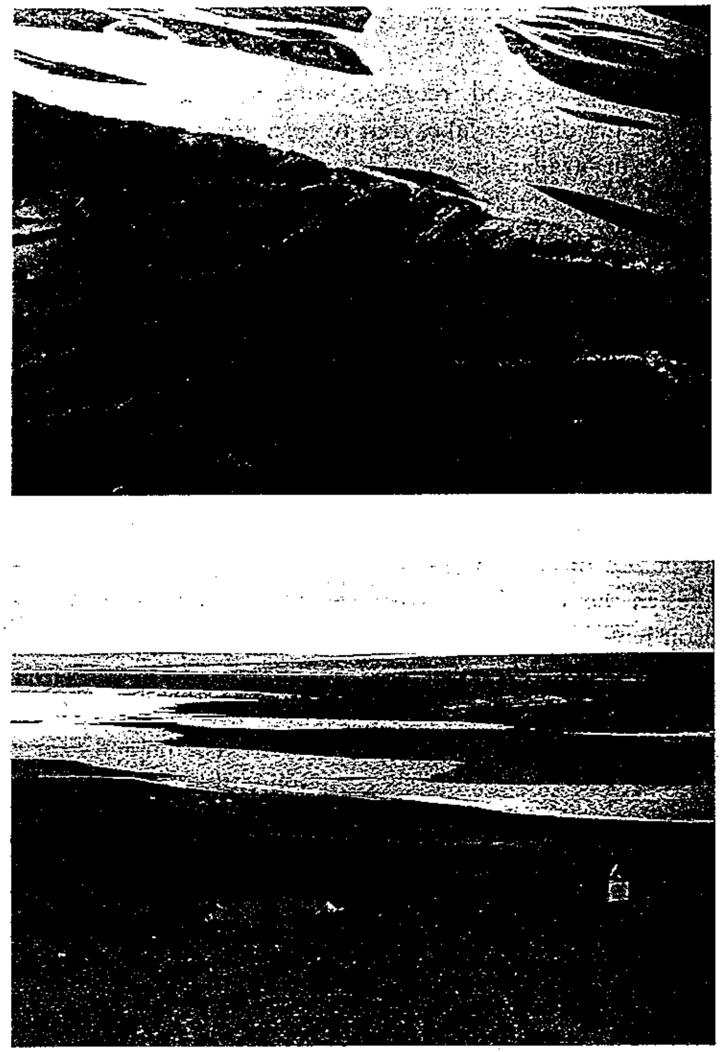

FIGURE 8.2: TOP: THERMOKARST PONDS IN THE TUNDRA, BYLOT ISLAND, LAT. 73°N; BOTTOM: LAKE HAZEN IN THE POLAR DESERT, ELLESMERE ISLAND (80°N).

(Bradley *et al.*, 1996); and a multi-disciplinary analysis of climate change issues in the Canadian Arctic environment (Burden, 1996).

HABITAT STRUCTURE AND DYMANICS

Ice cover

Four characteristics of the physical environment distinguish polar aquatic ecosystems from those at lower latitudes: persistent cold water temperatures; freeze-thaw cycles; prolonged ice-cover; and the extreme seasonality of solar radiation. Each of these features exerts a strong, controlling influence on ecosystem processes. The development and application of new remote sensing, profiling and data logging technologies is providing detailed new records of

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Thermokarst Ponds, Bylot Island

Polar Desert at Lake Hazen, Ellesmere Island these physical properties and a greatly improved understanding of their scales of variability.

The dates of ice-cover and freeze-up influence many of the physical and chemical properties of polar lakes that in turn affect the biota; for example, underwater light availability, gas transfer, solute concentrations, heat exchange and mixing processes (Welch and Bergman, 1985; Prowse and Stephenson, 1986; Rouse *et al.*, 1997). Ice duration and thickness are potential indices of long term climate change; for example, measurements in the eastern Canadian Arctic show an increased frequency of multi-year ice (Doran *et al.*, 1996) which would be consistent with a cooling trend in this region (Maxwell, 1997). Although such measurements have been mostly done in the past by ground surveys or by aerial photography, there is increasing potential to monitor lake ice from space using synthetic aperture radar (SAR). For example the SAR satellite RADARSAT has a spatial resolution of 30–100 m and can be used to monitor ice even through thick cloud cover and during the period of polar darkness. SAR techniques have been applied to tundra lakes in the Yukon and northern Alaska (Morris *et al.*, 1995) and near Hudson Bay.

High latitude river ecosystems are strongly influenced by ice formation and decay. The annual freeze-thaw cycle causes changes in water level, scouring and mechanical disturbance of the riparian zone (i.e., on and near the river-bank), while ice-formation limits the availability of habitat space for riverine biota such as fish and invertebrates (Prowse, 1994; Scrimgeour *et al.*, 1994). In the Mackenzie River, like many other northward flowing Arctic rivers, freeze-up begins in October in the northern parts of the river and causes an upstream rise in water levels behind the accumulating ice-cover. Conversely, the spring melt begins upstream in the warmer southern latitudes producing a flood wave that may progress more rapidly than the downstream melting, resulting in large ice jams and flooding (Rouse *et al.*, 1997).

Global circulation models predict that the Arctic regions should be especially sensitive to changes in greenhouse gas concentrations. A CO_2-doubling scenario predicts increases of 1–3°C in summer and 2–5°C in winter and spring (Oechel *et al.*, 1997). Temperature increases of this magnitude will influence the duration and thickness of lake ice cover which in turn will increase the availability of light for photosynthesis, the length of the growing season, and the transport of gases, nutrients and plankton through the water column by wind-induced mixing. Offset against these effects, however, will be a decrease in water transparency resulting from the release of dissolved organic carbon (DOC, see below) and particulate material from melting permafrost soils (Rouse *et al.*, 1997).

Underwater solar radiation

Most high latitude lakes are oligotrophic (nutrient-poor) waters that contain very low concentrations of phytoplankton, and unlike many lakes at lower latitudes, absorption of light by algae usually plays a negligible or minor role in the underwater distribution of photons. Apart from water itself (and in glacier fed lakes, glacial flour; i.e., fine suspensions of ground rock) the primary light-attenuating component in the majority of these lakes is chromophoric dissolved organic matter (CDOM); i.e., dissolved humic and fulvic acids that are brought in from the surrounding soils and vegetation. These compounds impart a green colour to the water at low concentration, a yellow or brown colour at moderate concentrations, and black coloured water at high concentrations (> 10 mg DOC l^{-1}). As suggested by this colour effect, CDOM influences the underwater availability of light for photosynthesis (PAR, photosynthetically available radiation) and also the spectral attenuation of solar ultraviolet radiation (UVR) through the water column. The damaging effects of UVR on aquatic biota can therefore be substantially reduced by the presence of these natural UVR-screening compounds.

Recent bio-optical research on high latitude lakes has shown that these waters generally contain low concentrations of CDOM, and are therefore only poorly protected against the rising UV-B radiation associated with stratospheric ozone depletion in the polar regions (Vincent *et al.*, 1998b). More specifically, the CDOM concentrations lies within the range where only small changes in organic carbon loading could give rise to large shifts in the transparency of the water column to UVR relative to PAR (Laurion *et al.*, 1997). Calculations based on a 'weighted transparency' model show that a 20% change in CDOM concentration in Arctic lakes would result in a two to eight times greater increase in the exposure of aquatic biota to damaging UVR than the same 20% change in stratospheric ozone (Vincent *et al.*, 1998a). These results imply that high latitude lakes may be especially sensitive to climate-related changes in hydrology or catchment vegetation that alter their CDOM characteristics.

Hydrodynamic properties

The unusual density-temperature relationship for water is of special interest to polar limnologists because of the low temperature range which characterizes high latitude lakes. Both warming and cooling from 3.98°C give rise to a decrease in the density of surface waters leading to stratification (vertical layering of the water column). However, the change in the density of water per degree is small in the range 0–10°C (e.g., from 4 to 5°C the density change is only one thirtieth of that from 24 to 25°C), and a cool, stratified water column can therefore be readily mixed by moderate winds. The application of new fine structure (centimetre resolution) and microstructure (millimetre resolution) temperature profilers to high latitude lakes has only recently begun, but research in this area is beginning to elucidate how these lakes respond to external forcing. For example, Lac à l'Eau Claire is a large, multi-basin, impact crater lake in subarctic Québec (56°N) that remains ice-covered for all but 2–3 months of the year (Fig 8.1). Fine structure profiling showed that the central Western Basin was polymictic (i.e., mixing frequently throughout summer) despite a maximum depth of 50 m, while the shallow side arms were dimictic (i.e., stratified in winter and summer with two periods of mixing, early spring and fall), and the deep Eastern Basin was cold-monomictic, stratified under the ice in winter but unstratified and freely circulating at temperatures <3.98°C throughout summer (Fig. 8.3). These differences are important because they affect the availability of light and nutrients for algal photosynthesis, the net loss of phytoplankton by sedimentation, the thermal regime and habitat structure for zooplankton and other biota, and the potential response of the lake to changes in climate. In large lakes such as Lac à l'Eau Claire and Lake Taimyr (Robarts *et al.*, 1999), this differential heating also results in sharp horizontal gradients in temperature called fronts or thermal bars. These features may inhibit the exchange of materials between different parts of the lake, for example between the littoral zone and the central lake basin.

The near-surface trapping of solar energy in northern lakes, as in lakes elsewhere, can give rise to buoyancy fluxes (changes in density gradients) that result in a diurnal pattern of stratification and mixing. These weak, near-surface thermoclines can trap phytoplankton in the brightly lit upper water column where prolonged exposure to high UVR and PAR may cause cellular

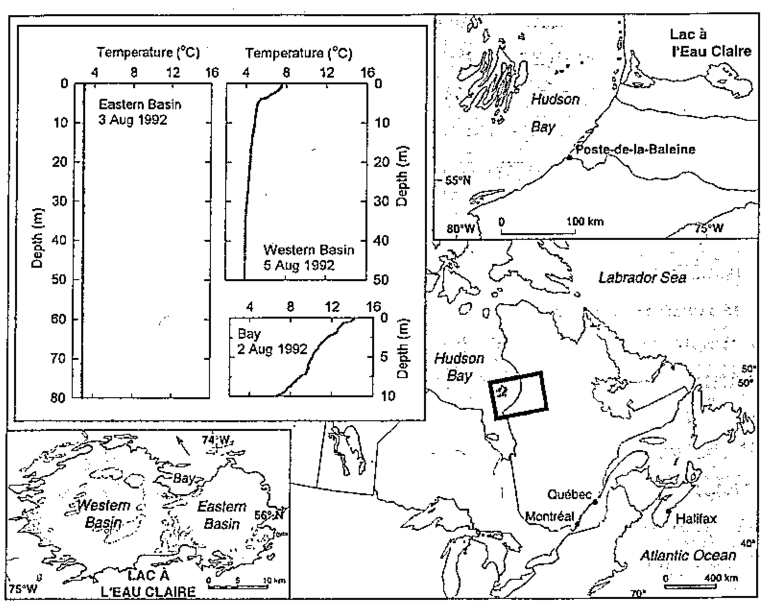

FIGURE 8.3: STRATIFICATION AND MIXING DURING SUMMER IN A COLD NORTHERN LAKE, LAC À L'EAU CLAIRE IN SUBARCTIC QUÉBEC. THE SHALLOW SIDE ARMS OF THE LAKE HEATED MORE RAPIDLY THAN THE MAIN BASINS AND WERE STRONGLY STRATIFIED BY EARLY AUGUST. THE CENTRAL WESTERN BASIN OF THE LAKE (Z_{MAX} = 50 M) STRATIFIED WEAKLY, AND WAS INTERMITTENTLY MIXED TO THE BOTTOM DURING STORM EVENTS. THE DEEP EASTERN BASIN (Z_{MAX} = 178 M) FAILED TO HEAT ABOVE 4°C, AND REMAINED CONVECTIVELY MIXING THROUGHOUT SUMMER. FINE STRUCTURE TEMPERATURES WERE RECORDED AT 5–10 CM INTERVALS WITH A BIOSPHERICAL PNF-300 (ADAPTED FROM MILOT-ROY AND VINCENT 1994).

damage (Milot-Roy and Vincent, 1994). They may also allow the near-surface accumulation of toxic photoproducts such as hydrogen peroxide that are generated by the photochemical interaction between UVR and CDOM (Scully and Vincent, 1996).

There is now a considerable literature on sub-ice lake circulation patterns. Inflows can pass through such lakes without mixing with the main waterbody because of differences in density caused by temperature or solutes (Welch and Bergman, 1985; Rouse *et al.*, 1997). For example, water balance and dye-tracer studies on Toolik Lake, Alaska, have shown that 40% of the annual inflow arrives while the lake is ice-covered, but that the streams can flow along the shore to the outlet within several days. This type of short-circuiting means that the water renewal time for this lake based on the total water budget (0.5 years) may be a misleading guide to the hydraulic flushing rate and to the nutrient loading rates for the offshore waters of the lake (O'Brien *et al.*, 1997).

Temperature changes and modelling

Lake research at the Toolik Lake LTER site has focused on long-term monitoring and whole-system experiments at several scales. Physical monitoring data, including data from a thermistor array left in place in Toolik Lake for one year, have been used to validate a physical model that simulates the year-long thermal pattern (Fig. 8.4). A 5°C increase in the average air temperature will result in a 2°C increase in the epilimnion (surface mixed layer) and a seven week longer open-water period (Hobbie *et al.*, 1999b). With an added biological module, the same model also simulates summer phytoplankton and zooplankton growth.

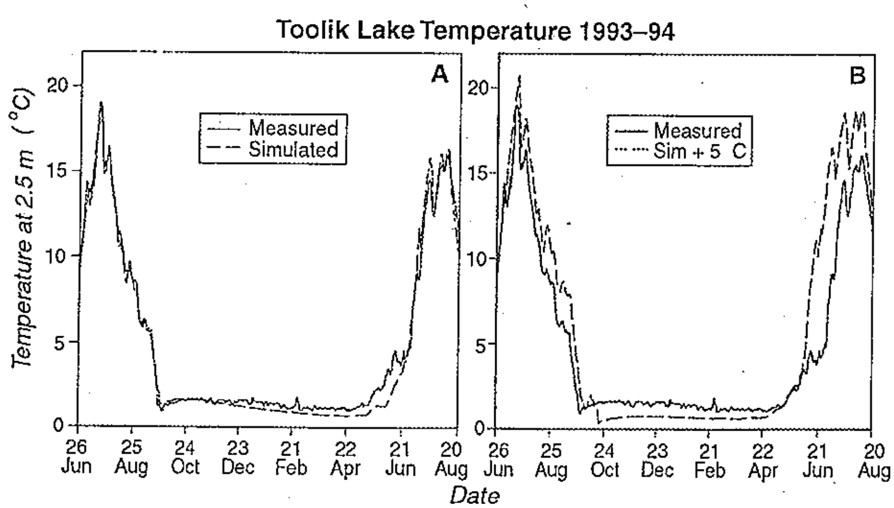

FIGURE 8.4: MEASURED TEMPERATURE DATA FOR TOOLIK LAKE AND A SIMULATION BY THE ARCTIC LAKE MODEL FOR TEMPERATURE UNDER THE CONDITION OF A 5°C INCREASE IN AIR TEMPERATURE.

Biogeochemical characteristics

With some notable exceptions such as meromictic lakes (see below) and artificially enriched streams, high latitude waters generally contain dilute concentrations of solutes. Surveys of the chemical content of northern freshwaters are gradually providing an overall picture of north-south gradients and the regional patterns of major ions, nutrients, metals and dissolved carbon in northern aquatic habitats. Recent data sets include an atlas of metal concentrations in Russian wetlands, including the Siberian tundra (Zhulidov *et al.*, 1997a) and latitudinal transects for nutrients, major ions and metals in lakes of the Canadian Arctic (Pienitz *et al.*, 1997a, 1997b; Rühland & Smol, 1998; Fallu and Pienitz, 1999). The latter studies have shown that there are strong northward gradients in the concentration of dissolved organic carbon (DOC, negatively correlated with latitude), and sometimes also in dissolved inorganic carbon (DIC, positively correlated with latitude) which reflect latitudinal gradients in vegetation, soils and parent rock type. A similar north-south gradient in DOC has been observed in lakes across the boreal forest-tundra ecotone of subarctic Quebec (Fig. 8.5).

The large rivers draining Siberia are particularly rich in dissolved organic carbon (DOC) derived from the boreal forest and northern peatlands. For example, the Lena River averages 10 mg DOC l^{-1} and is referred to as a 'black-water' system (Cauwet and Sidorov, 1996). The plumes from this and similar large rivers in Siberia extend several hundred km out into the Arctic Ocean (Olsson and Anderson, 1997) and are likely to have a broad range of effects on the marine systems, including carbon supply for microbial food web processes, the availability of PAR for photosynthesis and the underwater exposure to UVR.

A question of great interest in the context of global change is whether northern waters are a source or sink of greenhouse gases, particularly given the vast extent of high latitude wetlands. Toolik Lake and other lake and river waters sampled to date in arctic Alaska appear to be supersaturated with CO_2 and CH_4. The excess CO_2 appears to be associated with shallow CO_2-rich groundwater flows that drain the tundra, and these surface waters therefore act as a conduit for the evasion of these gases to the atmosphere (Kling *et al.*, 1991). In northern peatlands, the magnitude and direction of gas exchange is highly dependent on water balance, and interannual variations in meltwater supply can shift these systems from net sources to net sinks (Rouse *et al.*, 1997).

Benthic primary production (i.e., photosynthesis associated with plants, algae and cyanobacteria living on the bottom) appears to be an important carbon flux in many high latitude lakes, ponds and rivers. For example, a detailed carbon budget for one of the myriad of tundra lakes on the Tuktoyaktuk Peninsula, at the mouth of the MacKenzie River, Northwest Territories, Canada, showed that benthic photosynthesis contributed about 50% of the organic-C available to the food web while phytoplankton and

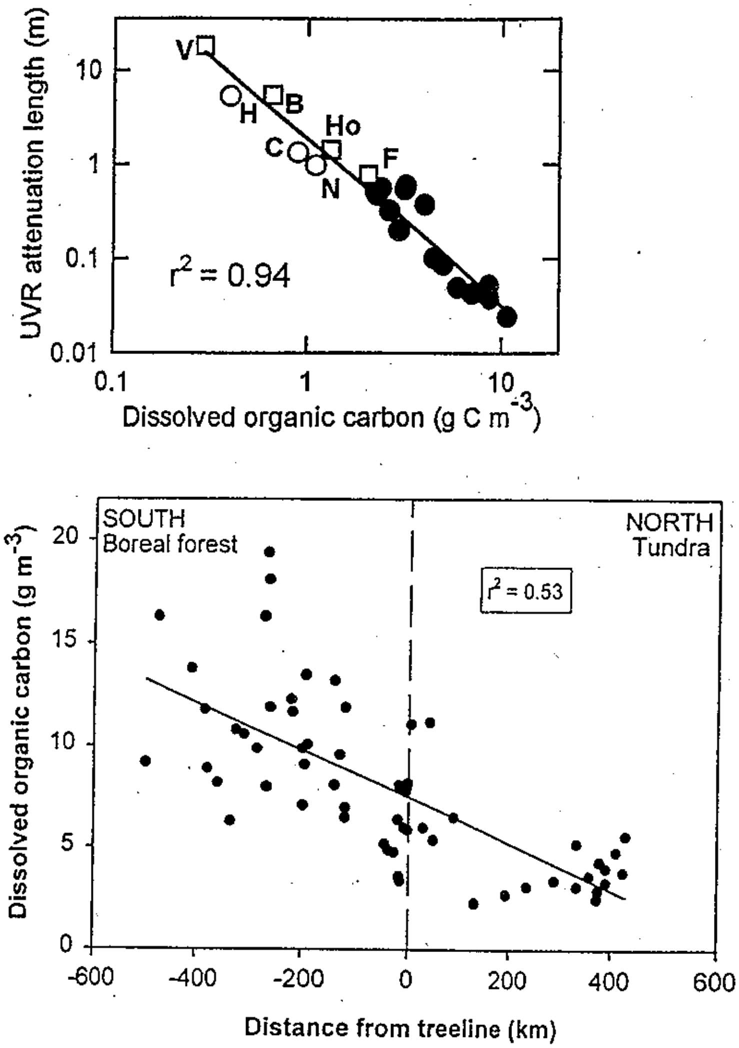

FIGURE 8.5: TRANSPARENCY OF HIGH LATITUDE LAKES TO ULTRAVIOLET RADIATION AS A FUNCTION OF DISSOLVED ORGANIC CARBON (TOP) AND THE NORTH-SOUTH GRADIENT IN DOC IN LAKES OF SUBARCTIC QUÉBEC (BOTTOM). THE UV TRANSPARENCIES ARE FOR 320 NM AND THE MEASUREMENTS ARE FROM SUBARCTIC QUÉBEC (CLOSED CIRCLES), THE CANADIAN HIGH ARCTIC (OPEN CIRCLES; C = CHAR LAKE; N = NORTH LAKE; H = LAKE HAZEN), AND FROM DRY VALLEY LAKES IN ANTARCTICA (OPEN SQUARES). ADAPTED FROM VINCENT (1997) AND VINCENT AND PIENITZ (1996).

allochthonous carbon (organic carbon from external sources such as plant detritus from the surrounding catchment) accounted for the additional 20% and 30% respectively (Ramlal *et al.*, 1994). Photosynthesis by the benthos was likely to be carbon-limited, suggesting that an increased CO_2 atmosphere would retard the degassing of CO_2 from the lake, raise pCO_2 (partial pressure of carbon dioxide) in the bulk solution and thereby enhance the absolute and proportional contribution of benthic photosynthesis to the overall C dynamics of the ecosystem (Rouse *et al.*, 1997).

Meromictic lakes

Meromictic lakes, that is waterbodies that do not completely mix to the bottom each year, are well known from lower latitudes and from around the margins of Antarctica (Vincent and Ellis-Evans, 1989). It is only recently, however, that this group of saline stratified waters has attracted limnological attention in the Arctic. Meromixis in the Arctic is thought to occur by one or more of three primary mechanisms (Bradley *et al.*, 1996; Ludlam, 1996):

1. Isostatic uplift (i.e., the rise of the land mass associated with melting and loss of an overlying ice-sheet) and entrapment of coastal marine waters. The saline bottom water of Lakes A and C in the Taconite Inlet region of Ellesmere Island, and of the many coastal lakes around Antarctica (e.g., in the Vestfold Hills, Ferris *et al.*, 1988) are believed to originate from this process.
2. Expulsion of salt-rich groundwater during permafrost formation after the land has emerged from the sea. Ouellet *et al.* (1989) attribute the origin of the bottom waters of Sophia Lake (Cornwallis Island) and Garrow Lake (Little Cornwallis Island) to this mechanism.
3. Isolation of coastal marine waters by glacial advance across a fjord, resulting in a saline, proglacial lake, for example Lake Tuborg on Ellesmere Island.

A fourth mechanism also exists in which freshwater is trapped behind an ice shelf and overlies a marine water column; these so-called epishelf lakes are well known from Antarctica, and also occur in the high Arctic (e.g., Disraeli Fjord, Ellesmere Island, Jeffries, 1987). The Taconite Inlet lakes have been the site of a comprehensive study to better understand how climate controls the formation of varves (annual bands) in the sediments (Bradley *et al.*, 1996). This information has provided a significant step towards an improved reconstruction of the Arctic environment throughout the Holocene (last 10,000 years).

Extreme Arctic habitats

There are a variety of unusual aquatic environments in the Arctic region which are receiving increasing attention because of their interesting physical and biogeochemical properties, and their colonization by novel microbial communities that can tolerate severe physical or chemical environments. These habitats include the meromictic lakes discussed in the previous section, low pH lakes (Schiff *et al.*, 1991; Doran, 1993), perennial springs (Pollard *et al.*, 1998), and meltpools on glaciers, ice-shelves and ice-caps. Over the 700 km^2 expanse of the Ward Hunt Ice Shelf, elongate, 30 m-wide channels form a parallel series of lakes, each up to 10 km long and 1–10 m deep (Jeffries, 1987). Recent studies have revealed that these lakes contain rich microbial mat communities growing in cylindrical depressions in the ice at the bottom of the stratified water column (Vincent *et al.*, 2000b). All of these habitats are the subject of ongoing microbiological studies, and are likely to yield new discoveries concerning the microbial diversity of the Arctic.

BIODIVERSITY AND COMMUNITY ECOLOGY

Polar ecosystems are typically thought of as containing simplified communities of plants, animals and microbes in which biodiversity is greatly reduced relative to temperate and tropical systems. Although this latitudinal trend applies also to Arctic lakes and rivers, these waters contain a remarkable variety of aquatic life. Current taxonomic studies are yielding new insights into the genetic diversity of these northern ecosystems.

One of the major advances in aquatic ecology over the last two decades has been the discovery that minute single-cell organisms play a major role at the base of marine and freshwater food webs (Fig. 8.6). These trophic networks contain microbial species with a diverse array of nutritional modes: heterotrophic bacteria that utilize dissolved organic carbon as their energy source; phototrophs such as picocyanobacteria that rely exclusively on photosynthesis; phagotrophic protozoa such as nanoflagellates and ciliates that engulf and ingest organic particles; and mixotrophic flagellates that obtain their carbon and energy supply partly from photosynthesis and partly by ingesting organic particles. Studies on all of these communities are still in their infancy in the northern environment, but the evidence to date indicates that aquatic microbial food webs comprise a large fraction of the total community biomass in arctic lakes and rivers, as elsewhere.

Bacteria

Research on the genetic diversity of bacterial populations in northern lakes has only recently begun and has been stimulated by the advent of molecular techniques. In the first study of this type, planktonic bacteria were isolated from Toolik Lake (Alaska) and analysed by 16S rDNA sequencing (Bahr *et al.*, 1996), that is by determining the nucleotide base sequence for the section of

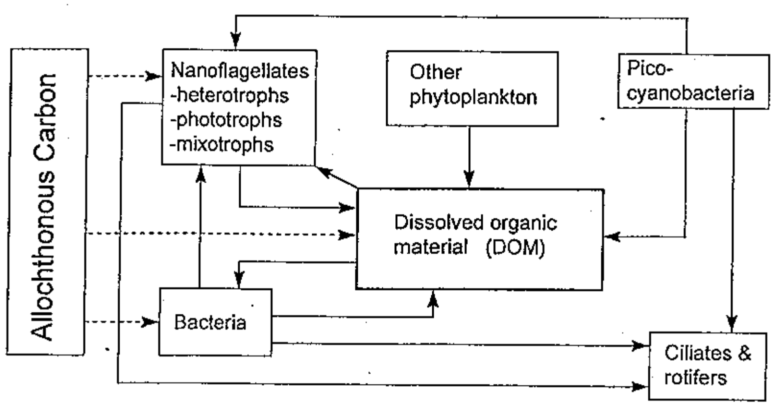

FIGURE 8.6: THE MICROBIAL FOOD WEB IN THE PELAGIC ZONE OF ARCTIC LAKES.

DNA that codes for the RNA template for ribosomal protein. Seven clones were identified spanning a broad range of phyla and physiological characteristics, including the ability to degrade organic macromolecules (*Cytophaga aquatilus*), to cause disease in plants (*Burkholderia solanacaerum*), to reduce nitrate (*Zoogloea ramigera*), to degrade low molecular weight organic compounds (*Pseudomonas mendocina*), and to metabolize relatively stable aromatic compounds (*Acinetobacter calcoaceticus*). Bacteria were also directly concentrated from the lake water and analyzed by PCR (polymerase chain reaction) of the extracted DNA. This analysis yielded 13 clones, all identified as proteobacteria. None were similar to those cultured, emphasizing the difficulty of using traditional culture assays for biodiversity studies of the microbiota. Interestingly, two of the clones were related to the SAR11 cluster, a bacterium found previously found only in tropical marine waters. The long term aim of such an approach is to develop labelled probes from these sequences that can be used with the natural bacterial communities to determine dominance and succession throughout the year.

Cyanobacteria

As in Antarctic inland waters, cyanobacteria (blue-green algae) are a major element of the microbiota in Arctic lakes, ponds and streams (Vincent, 2000). Picocyanobacteria, cells less than 2 μm in diameter, are commonly found as the numerically most abundant constituent of the phytoplankton in systems ranging from shallow thermokarst ponds in the tundra to deep lakes such as Lake Hazen in the Canadian High Arctic (Fig. 8.2). Lake studies in the forest-tundra zone at the North American treeline have shown that the < 2 μm fraction of the plankton accounts for 10–80% of the total phytoplankton chlorophyll a (Milot-Roy and Vincent, 1994) and is almost exclusively dominated by *Synechococcus*-like picocyanobacteria. This fraction seems to be relatively resistant to solar ultraviolet radiation (Laurion and Vincent, 1998) and shows little response to phosphorus enrichment, implying that these cells with their high surface to volume ratios are well adapted to the low nutrient environment of northern oligotrophic lakes (Bergeron and Vincent, 1997). However, photosynthesis in the picoplankton fraction is strongly stimulated by increased temperature, to a greater extent than nanoplankton (2–20 μm) and microplankton (20–200 μm) fractions (Rae and Vincent, 1998a).

Although picocyanobacteria are usually ascribed to the genera *Synechococcus* and *Synechocystis*, recent studies indicate that there is considerable genetic variation among isolates. Evidence of such variation in the Arctic comes from studies of the lakes and ponds on Bylot Island (lat. 73°N; Plate 2). Four isolates of *Synechococcus*-like cells from waterbodies on Bylot Island showed major differences in pigmentation and growth characteristics and 16S rDNA analysis further underscored the differences between them. Three of the strains showed strongest similarity (97%) to the colonial species *Microcystis elabens* (Vincent *et al.*, 2000a).

Cyanobacteria are also common in the benthic environments of high latitude lakes, ponds and streams where they form cohesive films and mats across the bottom substrates (e.g., Sheath *et al.*, 1996; Elster *et al.*, 1997; Vézina and Vincent, 1997). These communities are a consortium of cyanobacteria, diatoms, protozoa and heterotrophic bacteria, but are typically dominated by filamentous, mucilage-producing cyanobacteria of the family Oscillatoriaceae such as *Oscillatoria*, *Phormidium* and *Schizothrix*. In tundra ponds such as those near Toolik Lake, Alaska, and thermokarst ponds in the Canadian High Arctic, these benthic layers are conspicuous by their orange surface pigmentation, with a blue-green colored underlayer. This stratified coloration is caused by the relative proportion of Chlorophyll a, phycobiliproteins and carotenoids. Studies on similar species from Antarctica have shown that this pattern is an acclimation response to bright solar radiation, including UV-radiation which can be particularly damaging at low temperatures (Roos and Vincent, 1998). All of the high latitude filamentous species examined to date have temperature optima well above their cold ambient water temperatures, and are therefore likely to be highly responsive to climate-warming trends (Tang *et al.*, 1997). For example, *Phormidium tenue* isolated from the Kuparuk River, Alaska, has an optimum temperature for growth of 30°C, whereas summer temperatures are typically in the range 8–10°C in this habitat (Tang and Vincent, 1999).

Nitrogen-fixing cyanobacteria are commonly found in shallow water habitats and may be important in the nitrogen economy of the tundra. The temperature responsiveness of high latitude cyanobacteria suggests that climate warming could favor the biogeochemical flux of nitrogen from this source. Like the benthic oscillatorians, these communities seem well adapted to high solar irradiance. For example, sheets of *Nostoc commune* from the littoral zone of Toolik Lake are rich in two classes of natural UV-screening pigments, mycosporine-like amino acids which absorb maximally around 340 nm, and scytonemin which has a broad absorbance maximum that peaks at 388 nm, but which extends well into the UVB and PAR regions of the spectrum and dominates the *in vivo* absorbance spectrum for this community (Vincent and Quesada, 1997).

Phytoplankton

The distribution of freshwater diatoms at and above the arctic treeline has been reviewed by Lotter *et al.* (1998) who provide detailed references to published and unpublished floristic records from northern North America, Fennoscandia, Siberia, the Kola Peninsula and Novaya Zemlya. These authors note that throughout the circumpolar region, northern lakes show abrupt changes in diatom species composition across the treeline that parallel the major shifts in water chemistry and physical characteristics. Diatoms have proven to be powerful indicator species for the detection of long term change in arctic ponds and lakes, in particular because of their large diversity of species, their varied environmental requirements, and their production of silicon-based cell walls (frustules) that persist as a valuable fossil record within the sediments (Smol and Douglas, 1996 and references therein).

Lakewater temperature, dissolved organic carbon (DOC), inorganic carbon (DIC), and lake morphometry (basin shape) have emerged as the most important predictors of diatom community structure. For example, Pienitz *et al.* (1995a) found that surface water temperature in summer and lake depth were the two variables explaining the greatest percentage of the variance in diatom community composition in northwestern Canada. Similarly, about 30% of the variance in diatom species composition in Labrador lakes was attributable to water colour (a correlate of DOC) and alkalinity (Allaire and Pienitz, unpubl.). Diatom community structure also tracked the DOC gradient in Siberian lakes (Laing, cited in Lotter *et al.*, 1998) and subarctic Québec lakes (Fallu and Pienitz, 1999).

Pienitz and Smol (1993) showed that a large component of the variance in diatom species composition along a lake transect through central Northwest Territories could be explained by DIC and DOC. They then derived transfer functions from the modern day assemblages and applied these to fossil diatom records contained within the sediments of two northern lakes. As shown by Pienitz *et al.* (1999), these diatom-based reconstructions of DOC can be used to infer past vegetation shifts. Since DOC is also an accurate predictor of the spectral attenuation of light in northern lakes (Laurion *et al.* 1997), these relationships can also be used to reconstruct the paleo-optical regime of lakes, that is their historical variations in the penetration and spectral quality of underwater light (Vincent and Pienitz, 1996).

Chrysophytes include mixotrophic species that can play an important role in microbial food webs, and like diatoms these species leave identifiable fossil remains in lake sediments that are useful paleolimnological markers (Pientiz *et al.*, 1995b). For the Nuussuaq/Nugssuaq region of West Greenland, Wilken *et al.*, (1995) report that the distribution of chrysophytes is controlled by pH, water colour, temperature and substratum.

Mosses and other macrophytes

Mosses and characeans (macroscopic green algae in the phylum Charophyceae) are conspicuous elements of the biota in many high latitude lakes and streams and may play an important role as the food for aquatic invertebrates and a refuge from predators, as well as a physical substrate for periphyton, the assemblage of algae and bacteria growing on surfaces. The growth rates of arctic moss communities tend to be extremely slow as a result of the low nutrient supply, low temperatures and the short period of light availability between ice break-up and freeze-up (Sand-Jensen *et al.*, 1999). However, the standing stocks of these communities can substantially increase in response to nutrient enrichment. After seven years enrichment of the Kuparuk River, Alaska, mosses increased from inconspicuous elements of the flora to dominance (Bowden *et al.*, 1994). A similar but unintentional experiment was conducted at Resolute Bay (lat. 74°N) where waste-water enrichment of the inflow to Meretta Lake from the nearby airfield has resulted in luxuriant growth of mosses along the banks of the river. Despite the probable importance of mosses and Charophytes in arctic lakes and streams, little attention has been given towards their biodiversity, genetic characteristics or community ecology. Langangen *et al.*, (1996) report that nine species of Charophytes inhabit the lakes of Greenland, with greater floristic affinity to Europe than to North America.

Microzooplankton

Little is known about the protozoan diversity of northern lakes, although they are common elements of the plankton and benthos and are likely to be the primary grazers of bacteria. The protozoa observed in the plankton of Toolik LTER lakes are heterotrophic nanoflagellates (HNF) and ciliates, the latter mostly small oligotrichs (< 50 μm in their largest dimension) of the genera *Halteria*, *Strombidium* and *Strobilidium*. A *Vorticella* sp. is also present and occasionally dominant. Common HNF genera identified microscopically from the sediments of arctic tundra ponds near Barrow, Alaska include *Monas*, *Oikomonas* and *Bodo* (Fenchel, 1980). The identity of almost all of the nanoflagellates in Toolik Lake is unknown although H. Kling has compiled a list of algal taxa identified by Utermöhl microscopy (reported in O'Brien *et al.*, 1997). Chrysophyceae are dominant and the genera *Chromulina*, *Ochromonas*, *Spiniferomonas*, *Pseudopedinella*, *Pseudokephyrion*, *Paraphysomonas* and *Kephyrion* are present. Some of these have colorless forms or are mixotrophic. The rotifer communities of the Toolik lakes are primarily composed of small-particle feeders, predominantly *Keratella cochlearis*, *Kellacottia longispina*, *Polyarthra vulgaris* and *Conochilus unicornis*. Five additional species are occasionally observed: *Keratella quadrata*, *Ascomorpha* (*Chromogaster*) *ecaudis*, *Filinia terminalis*, *Gastropus stylifer*, and an unidentified *Synchaeta* sp. (Rublee, 1992).

The highest protozoan abundance in Toolik lakes is found during late June at the beginning of the ice-free season. Initially, protozoans are more numerous than rotifers (surface concentrations of 100 to 1000 protozoa l^{-1}, compared to 10–300 rotifers l^{-1}), but rotifer biomass is usually larger than protozoan biomass because of their larger individual size. Protozoan abundance and biomass decline rapidly in all lakes after the initial peak. Secondary peaks in numbers are evident in some lakes, but protozoan biomass generally remains low (< 0.5 μg C l^{-1}). Rotifer abundance and biomass is generally low early in summer and increase to peak values during mid July to early August. The other major component of the microzooplankton in lakes of the Toolik LTER is copepod nauplii, the early life stage of a common group of crustacean zooplankton. Nauplius biomass generally equals or exceeds rotifer biomass and tends to increase during the summer (Rublee, 1992).

Some 164 species of rotifers have been reported from the arctic region, and 215 from the subarctic (Pejler, 1995). Most are benthic, cosmopolitan species with very few that are restricted to the Arctic. There is a general trend of decreasing species diversity with increasing latitude; for example Chengalath and Koste (1989) report 118 rotifer species from Canadian lakes in the latitudinal range 60–66°N, but only 21 taxa in the lakes on Bathurst Island at 75°N. There are also major east-west differences in biodiversity. For example, studies on the lakes and ponds near Kangerlussuaq on the western side of Greenland (67°N, 51°W) revealed 57 taxa including the genus *Brachionus* which is relatively rare in northern waters. A much reduced species richness was recorded at Ammassalik on the eastern side of Greenland (66°N, 38°W) with only 34 taxa and no *Brachionus*. De Smet *et al.* (1993) attribute these differences to climatic factors, with the influence of the relatively warm Western Greenland Current (branching off the Gulf Stream) on the western side and the cold Eastern Greenland Current (originating from the polar basin) along the east coast.

Macrozooplankton

Molecular techniques that are helping establish the evolutionary relationships and origins of zooplankton at temperate latitudes (Hebert and Taylor, 1998) are now being applied to arctic populations. Attention has focused particularly on the circumpolar species of water flea *Daphnia pulex* which reproduces asexually by parthenogensis (production of offspring from unfertilised gametes), although the occasional presence of males at some sites in the Arctic implies that sexual reproduction may occur sporadically (Haney and Buchannan, 1987). PCR analysis of mitochondrial DNA from 110 populations of this species has shown a close genetic affinity between clones from Iceland and Greenland (Weider *et al.*, 1996). The present aquatic habitats on Greenland are less than 6000 years old, but the PCR data imply that colonization of both Greenland and Iceland occurred during the Pleistocene, and that ancient populations of *D. pulex* survived in areas of glacial refugia.

An interesting feature of arctic zooplankton is the high degree of polyploidy, and this has been a subject of ongoing research in genetics and population ecology. For example the cladoceran (water flea) *Bosmina* from the temperate regions of North America and Europe is typically diploid and reproduces by cyclical parthenogenesis. On the other hand, the dominant bosminid taxon in high Arctic lakes reproduces by obligate parthenogenesis and is polyploid, derived from interspecific hybridization. The hybridization process appears to produce bosminids that are more diverse than their sexual parent taxa, thus conferring an advantage to the polyploid biotype (Little *et al.*, 1997).

Benthic macroinvertebrates

There are pronounced latitudinal gradients in the taxonomic composition of stream macroinvertebrate communities, with decreasing species diversity and an increasing importance of dipterans (two-winged flies) with distance northwards. These north-south gradients are also apparent at lower taxonomic levels, in terms of families and genera (Oswood, 1997). These patterns have led to the conclusion that many high latitude species are currently at their adaptational limit and could therefore be sensitive indicators of environmental change (Danks, 1992). Climate warming is likely to cause northwards shifts in the biogeographical limits of many species, but may also result in stream environments that are thermally more stable and less subject to the disruptive effects of ice dams and break-up. Scrimgeour *et al.* (1994) suggest that if these intermediate disturbance events play a role in maintaining species richness, then climate-related changes in the severity of these events could impact on the biodiversity within arctic streams.

Fish

As with the other groups of aquatic biota, the biodiversity of the ichthyofauna is greatly reduced in arctic lakes relative to lower latitude ecosystems. Some of the species appear to be living near their limits of environmental tolerance and may therefore be especially prone to climate-related changes in the physical environment. Molecular techniques are being increasingly applied to understand the genetics of these northern communities and their relationship to lineages in the temperate zone; e.g., the postglacial dispersal of lake trout, *Salvelinus namaycush* (Wilson and Hebert, 1998).

A warmer future will likely cause elimination of lake trout populations in Toolik Lake Alaska, with concomitant impacts on the food web. A bioenergetics model predicts that a 3°C rise in July epilimnetic (surface mixed layer) temperatures could cause young-of-the-year lake trout to need to consume eight times more food than is currently necessary just to maintain adequate condition (McDonald *et al.*, 1996). This requirement greatly exceeds the current food availability in the lake. Furthermore, modeled oxygen indicates that a future combination of warmer temperatures and increased loading of P will greatly reduce the hypolimnetic habitat (bottom waters) available for lake trout. These fish require oxygen concentrations > 3 mg l^{-1} in order to thrive (Hobbie *et al.*, 1999b).

Arctic saline lakes are also proving to be interesting models for questions in evolutionary and community ecology. In Lake Garrow, a meromictic lake in northern Canada (see Section 2.6), the main fish species is an unusual four spined sculpin that is intermediate in its depth distribution and morphology between freshwater and marine forms (Dickman, 1995).

FOOD WEB STRUCTURE AND DYNAMICS

Microbial food webs

Studies on the bacteria and protozoa of Toolik Lake have begun to build up a picture of the overall microbial food web in lakes of this region of the Arctic. The number of heterotrophic nanoflagellates in Toolik Lake (HNF, 2–20 μm) is 1–3 $\times 10^3$ ml^{-1} (O'Brien *et al.*, 1997). In July 1984, a sample from the lake contained 1.2×10^6 bacteria ml^{-1} and 2.6×10^3 HNF ml^{-1}. In June 1994, a sample contained 1.1×10^6 bacteria ml^{-1} and 2.7×10^3 HNF ml^{-1} (Hobbie *et al.*, 1999a). This agrees with the generalization by Berninger *et al.* (1991) and Sanders *et al.* (1992) from aquatic ecosystems elsewhere that there are typically about one thousand times more bacteria than flagellates. A careful distinction has been made between heterotrophic and autotrophic nanoflagellates. In this lake, 25–50% of the total nanoflagellates possess some chlorophyll that fluoresces red under excitation by blue light. Some of these flagellates that possess chlorophyll are undoubtedly mixotrophic and consume bacteria; for example, the dominant alga in the lake, the chrysophyte *Dinobryon*, is known to be mixotrophic in lakes elsewhere (Bird and Kalff, 1986).

The data on the abundance of bacteria and HNFs in Toolik Lake revealed that both were more abundant than expected from the planktonic primary productivity. This abundance, related to the allochthonous DOC, illustrates the undoubted importance of the bottom-up controls. The abundance measures, however, do not allow the significance of any top-down control of bacteria by flagellates and other microbes to be determined. To address this question, parcels of water were confined in large plastic mesocosms and it was possible to follow a classic predator-prey oscillating cycle between the nanoflagellates and their bacterial prey. These cycles were especially pronounced when the phytoplankton was fertilized with inorganic nutrients, and it was found that the bacterial productivity was at its highest when the bacteria were heavily grazed (Hobbie and Helfrich, 1988).

Studies on the microbial food web in the high latitude lakes of northern Québec have focused on how global change processes may influence their structure and dynamics. A series of *in situ* microcosm assays in Lac à l'Eau Claire (Fig. 8.1 and 8.3) revealed that different components of the food web varied in their response to UVA and UVB, and that changes in the spectral composition of underwater UVR could influence microbial trophic structure as well as productivity (Bergeron and Vincent, 1997). This work was extended by replicated assays of lakewater samples in outdoor solar incubators fitted with various spectral filters and maintained at 10 and 20°C. The assays showed that UVR effects were generally small, although the concentration of actively respiring bacteria was severely (29–59%) reduced by the UV exposure in three of four experiments. The picoplankton fraction, both picocyanobacteria and heterotrophic bacteria, responded strongly to the temperature rise from 10 to 20°C, and this warming also stimulated some larger cells including ciliates and dinoflagellates (Rae & Vincent, 1998b). The strong temperature responsiveness of the picocyanobacteria is consistent with photosynthetic assays of this group in northern waters (Rae and Vincent, 1998a) and observations on high latitude cyanobacteria in general (Tang *et al.*, 1997). These bioassay results imply that shifts in lake temperature associated with climate change have the capacity to alter the species composition and size structure of northern microbial food webs.

Long term lake studies

Detailed observations and experiments at the Toolik LTER site have addressed the question of whether the simplified communities of plants, animals and microbes of polar lakes and rivers respond to external forcing and food web processes in the same way as temperate latitude systems. The overall food web structure for Toolik Lake (excluding the microbial food web) is given in Fig. 8.7 Components of this foodweb have changed substantially over the last two decades. For example, two large zooplankton species, *Daphnia middendorffiana* and *Holopedium gibberum,* have nearly disappeared from the lake. This change corresponded to a period of increasing population density of small arctic grayling, which in turn may be related to a reduction in lake trout density caused by fishing (O'Brien *et al.*, 1997).

As found for oligotrophic lakes at lower latitudes, Toolik and surrounding lakes respond strongly to the bottom-up control of added nutrients, especially phosphorus. Limnocorral assays (i.e., experimental lake enclosures, see O'Brien *et al.*, 1992) and whole-lake experiments with added nutrients triggered a dramatic increase in phytoplankton and the lake even developed cyanobacterial blooms. However, in a divided lake experiment (Fig. 8.7), the phytoplankton

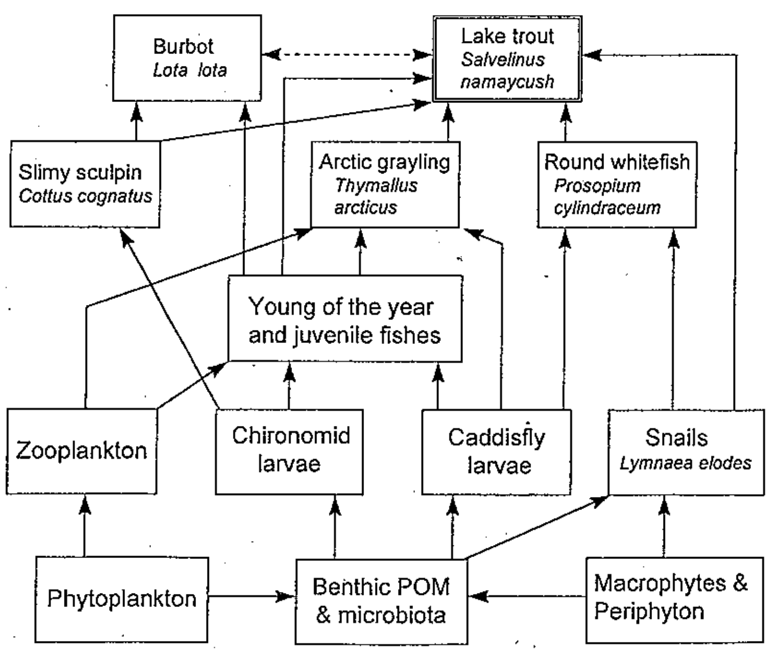

FIGURE 8.7: THE FOOD WEB OF TOOLIK LAKE IN THE NORTHERN ALASKA LTER SITE, SHOWING THE KEYSTONE POSITION OF LAKE TROUT. THE DIAGRAM OMITS THE MICROBIAL FOOD WEB (SEE FIG. 8.6) AND THE IMPORTANT INPUT OF ALLOCHTHONOUS CARBON (I.E., ORGANIC CARBON FROM EXTERNAL SOURCES SUCH AS TERRESTRIAL VEGETATION) TO THIS LAKE. (DERIVED FROM MCDONALD *ET AL.* (1996) AND ROUSE *ET AL.* (1977))

biomass response to nutrients in the P-enriched side was less than half of that expected because of nutrient sorption by sediments (Sugai and Kipphut, 1992). The reason for this was the high quantities of iron oxides in the surface layers of the sediments (Cornwell and Kipphut, 1992). After five years of fertilization the sediments reached their saturation capacity to sorb phosphorus and P began to return to the water (Fig. 8.8).

An experimental fertilization of one of the highly oligotrophic Toolik Lakes (Lake N-1) was carried out for five summers in 1990–1994. Inorganic nitrogen and phosphorus were added to the lake at approximately four times ambient loading rates. This increased nutrient load mimics effects that increased human impact may have in the region. The manipulation allowed an assessment of species abundance and community structure as populations changed in response to the addition over several years. Protozoa increased significantly in both number and biomass following fertilization, and community structure shifted from dominance by oligotrichs (planktonic ciliates) prior to fertilization to dominance by the bacteria-eating peritrich (another type of ciliate) *Epistylis rotans* in the second and third years of the fertilization (Rublee and Bettez, 1995). The numbers of the predatory rotifers *Synchaeta* and *Polyarthra* also increased in response to fertilization. However, the largest increase in numbers did not occur until the fourth year, when the Trichocercidea rotifers first appeared and accounted for 68% of the rotifer biomass. Trichocercidea have been found in a wide variety of periphytic environments (i.e., on the surface of rocks and

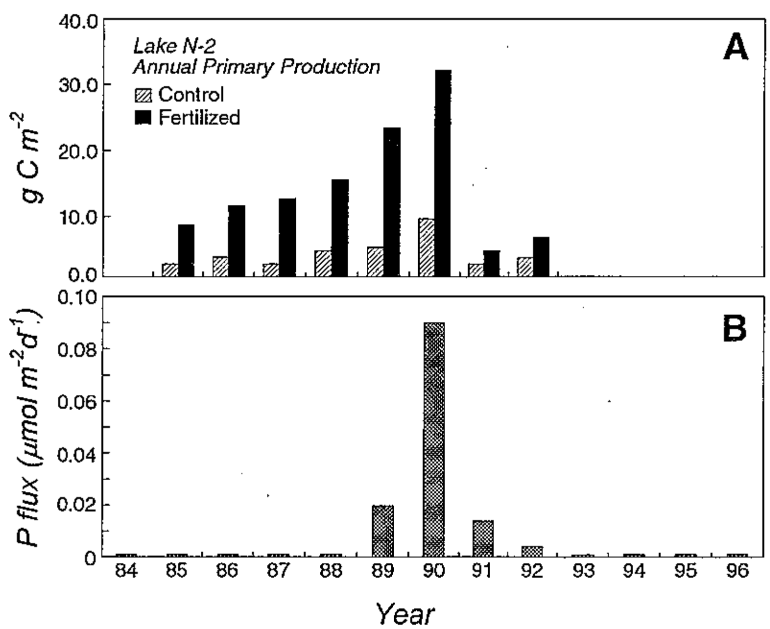

FIGURE 8.8: RESULTS OF THE DIVIDED LAKE EXPERIMENT AT THE TOOLIK LAKE LTER SITE. A. PRIMARY PRODUCTIVITY (ANNUAL) IN THE FERTILIZED AND CONTROL SIDES. B. PHOSPHATE FLUX (AVERAGE PER DAY) FROM THE SEDIMENTS INTO THE WATER OF THE FERTILIZED HALF. (FROM HOBBIE *ET AL.* (1999B) WITH PERMISSION)

bottom-dwelling plants) with a few species that are found also in the plankton. These species can act as indicators of eutrophy (nutrient-rich conditions) and usually invade due to increased primary productivity (Pejler and Berzins, 1993). The average number of zooplankton nauplii increased four fold over the course of the fertilization, although the response was species dependent. For example, *Heterocope septentrionalis* increased, while *Cyclops scutifer* had lower values post treatment. The overall increase in crustacean zooplankton nauplii abundance suggests the emergence of top-down regulatory controls as the lake became eutrophic.

Top down control is exerted at several levels in arctic lake foodwebs. In large lakes at the Toolik site, the top predator, lake trout, plays a keystone role (Fig. 8.7) and controls the size and density of the zooplankton *Daphnia* (Hobbie *et al.*, 1995), the snail *Lymnaea elodes* (Merrick *et al.*, 1992), and the density and habitat distribution of slimy sculpin (Hanson *et al.*, 1992, McDonald and Hershey, 1992). When the hypothesis concerning predator control of sculpin was tested by removal of all large lake trout from a lake, burbot suddenly moved from a minor member of the community to become very abundant. Instead of freeing the sculpin from predation, the experiment substituted another effective predator and so the sculpin became even more concentrated in rocky littoral habitats. Slimy sculpin are also effective predators and when free from predation they can reduce their prey of chironomids to low densities (Cuker *et al.*, 1992, Goyke and Hershey, 1992).

An added level of control of fish distribution is by geomorphology, acting through stream gradients. A too-steep gradient in outlet streams as well as shallow depth and small area will keep lake trout out of a lake. A model based on a Geographic Information System (GIS) that incorporated this type of data, in part from remote sensing images, successfully predicted lake trout distribution in a wide area around Toolik Lake with 86% accuracy.

Long term stream studies

In addition to the work on lakes, studies at the Toolik Lake LTER have included the long-term monitoring and whole-stream fertilization experiments in two tundra streams, the Kuparuk River and Oksrukuyik Creek. As of 2000, the Kuparuk River experiment was in its seventeenth year of phosphorus fertilization. Here, the structure and function of the stream processes and populations are controlled by geomorphology, climate, fluxes of resources from land and by biotic interaction among components of the stream community. Climatic variation in summer precipitation controls stream discharge which in turn controls stream insect and fish production (Deegan *et al.*, 1999; Hershey *et al.*, 1997). Landscape geomorphology dictates the presence of springs which are nutrient-rich, highly productive habitats (Craig and McCart, 1975). Long-term fertilization experiments (17 years) have demonstrated strong stream responses to increased nutrient inputs, including increases in primary production, insect abundance and fish production (Peterson *et al.*, 1993; Harvey *et al.*, 1998) (Fig. 8.9). The response of the stream ecosystem to different combinations of geomorphology, climate and nutrient fluxes from land is moderated by biotic interactions such as top-down control by consumers (Gibeau and Miller, 1989) and competition for space by primary producers (Bowden *et al.*, 1994).

Manipulations of adult and young-of-the-year fish indicate that production in these rivers is largely controlled by bottom-up nutrient supply and flood disturbance (Deegan *et al.*, 1997; Golden and Deegan, 1998). Over a period of about 8 or 9 years, the dominant primary producer shifted from diatoms to moss in the fertilized reach of the Kuparuk River (Bowden *et al.*, 1994). The change in primary producer and habitat structure has also changed the abundance and distribution of insects (Bowden *et al.*, 1999). In 1997, adult fish in the fertilized reach of the Kuparuk River did not grow any faster than fish from the control reach which suggests that the long-term change in food web structure from diatoms to moss may be adversely affecting the efficiency of transfer from primary production to fish.

Stable isotope studies

Use of ^{13}C, ^{15}N and other natural isotopic tracers is proving to be a powerful approach towards understanding food web relationships in high latitude lakes. Kling *et al.* (1992) examined the natural ^{15}N abundance in phytoplankton and zooplankton from 8 oligotrophic lakes in the Toolik Lake LTER site and found large variations between lakes. In some lakes the planktonic food web followed the typical three-tiered pattern: plankton $\rightarrow$ the herbivorous copepod *Diaptomus pribilofensis* $\rightarrow$ the predaceous copepod *Heterocope septentronatis*, with a 3‰ enrichment at each trophic level. In other lakes, however, there was a continuum in $\delta^{15}N$ between *Diaptomus* and *Heterocope*, showing that the latter species was omnivorous and feeding to a varying degree on phytoplankton as well as *Diaptomus*. Stable isotopes have also been used to discern migration patterns, for example for northern pike and broad whitefish populations in lakes on the Tuktoyaktuk Peninsula (Hesslein *et al.*, 1991), and the drift of benthic invertebrates in Alaskan rivers (Hershey *et al.*, 1993).

These same, nonradioactive isotopes may safely be added to lakes and streams to follow the pathways of carbon and nutrients. Kling (1994) carried out a one-time addition of ^{15}N to a divided lake near Toolik and was able to follow the pathway of nitrogen into both planktonic and sediment animals over several years. The data will be used to test the lake model of nutrient flux. Peterson *et al.* (1997), in contrast, have continuously added ^{15}N to streams of different orders to measure the uptake length of NH_4^+. This is the average distance a molecule of NH_4^+ travels before it is removed from the water, and for the Kuparuk River was estimated as 0.8 km. Theoretical estimates of uptake length from a model that divides the river into 100 m segments corresponds well with the field data. The model (Fig. 8.10), is being

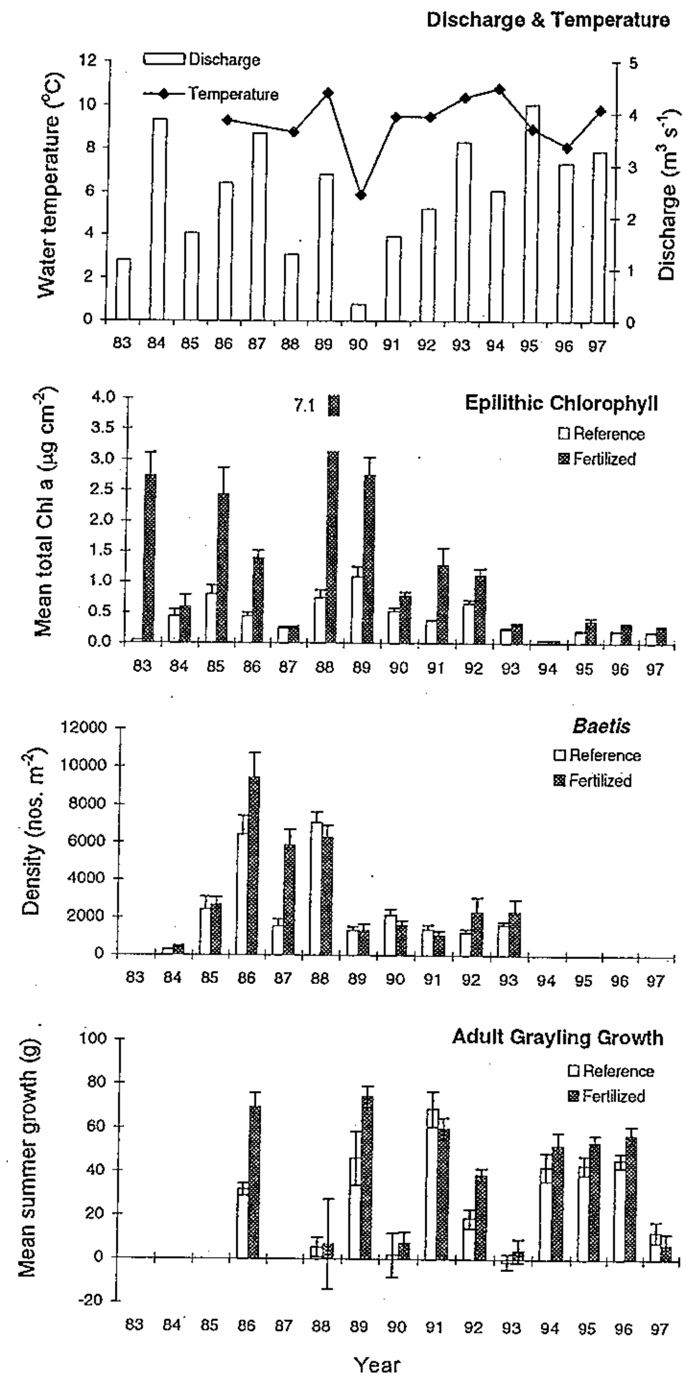

FIGURE 8.9: LONG TERM RESPONSE OF THE KUPARUK RIVER TO FERTILIZATION. THE NUTRIENT ENRICHMENT STIMULATED ALGAL BIOMASS ON THE STREAM BED (EPILITHIC CHLOROPHYLL *A*), INSECT ABUNDANCE (ILLUSTRATED BY THE MAYFLY *BAETIS*) AND FISH GROWTH (ARCTIC GRAYLING, *THYMALLUS ARCTICUS*). (FROM HOBBIE *ET AL.* (1999B) WITH PERMISSION)

used to synthesize existing information on stocks (the amount of nitrogen in each biotic and abiotic compartment) and fluxes (rate of transfer between compartments), and to explore the characteristics of N-cycling in high latitude aquatic ecosystems (Wollheim *et al.*, 1999).

LAND-WATER-ATMOSPHERE INTERACTIONS

Catchment studies

Measurements of dissolved and particulate materials in surface waters have now been carried out at many locations in the Arctic, but such measurements need to be extended throughout the annual cycle to quantify the overall flux of carbon, nutrients and other substances from land to water. Detailed records of this type are now available for sites near Toolik Lake, specifically the Kuparuk River (Peterson *et al.*, 1986; 1992; Fig. 8.1), Imnavait Creek (Everett *et al.*, 1989; Marion and Everett, 1989), and the inlet to Toolik Lake (Cornwell, 1992). Most of the C, N, and P transported is in the organic form. From these and other studies, it is evident that water flow, vegetation and soil uptake and release, and landscape heterogeneity are likely to control the exports of materials to surface waters. Much of the Toolik Lake LTER research is aimed at quantifying these controls.

As water moves across a landscape its chemistry is modified by vegetation and soil processes. Some of the most complete research on the role of vegeta-

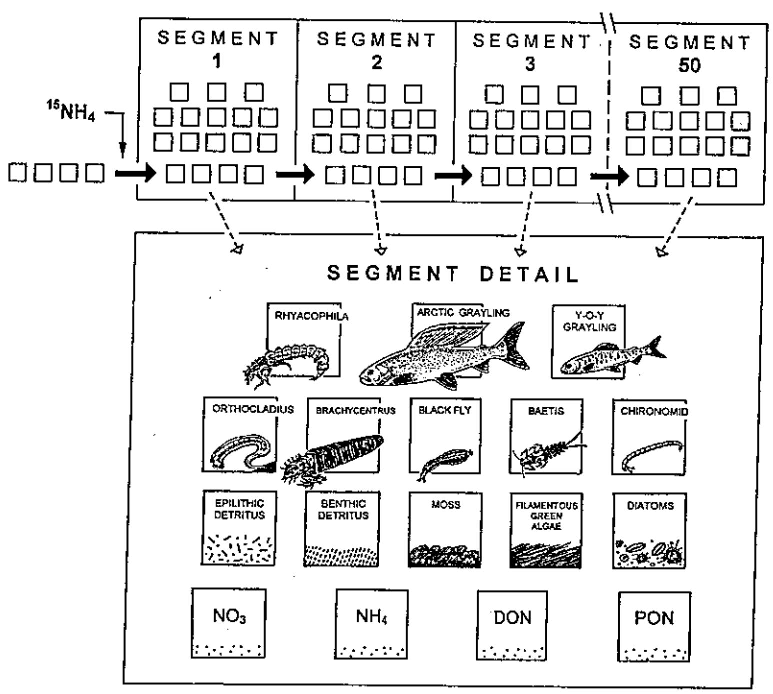

FIGURE 8.10: SCHEMATIC DIAGRAM OF THE RIVER MODEL USED TO CALCULATE NITROGEN TRANSFORMATIONS, TRANSPORT AND RETENTION. EACH SEGMENT OF THE RIVER HAS A COMMUNITY MODEL EMBEDDED WITHIN IT. (FROM WOLLHEIM *ET AL.* (1999) WITH PERMISSION)

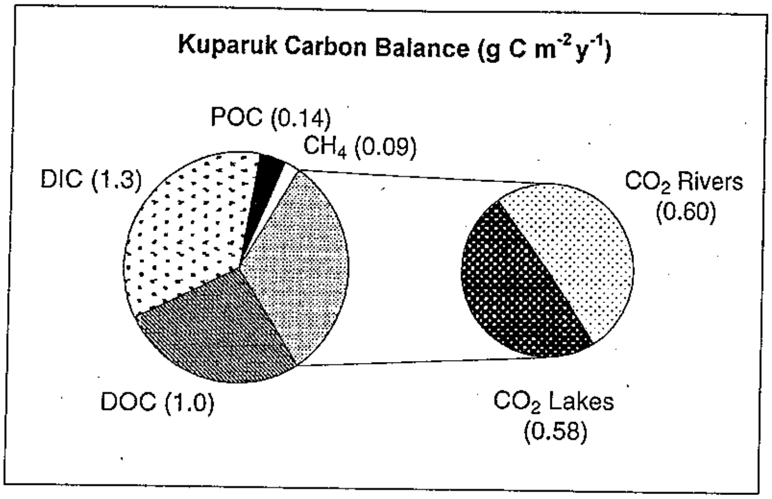

FIGURE 8.11: CARBON LOSS FROM THE KUPARUK BASIN FROM 1994–1996, SHOWING THE RELATIVE IMPORTANCE OF EACH BUDGET TERM. THE DOC (DISSOLVED ORGANIC CARBON) DIC (DISSOLVED INORGANIC CARBON) AND POC (PARTICULATE ORGANIC CARBON) ARE EXPORTED IN RIVER FLOW TO THE ARCTIC OCEAN, WHILE METHANE (CH_4) AND CARBON DIOXIDE (CO_2) ARE RELEASED DIRECTLY FROM THE LAKES AND RIVERS TO THE ATMOSPHERE (THIS IS 32 % OF THE TOTAL 3.73 G C M^{-2} Y^{-1}). (FROM DATA PROVIDED BY G.W. KLING)

tion in modifying inorganic nutrients in soil waters was done in the Arctic at Imnavait Creek (Marion and Everett, 1989) and at the Sagavanirktok River near Toolik (Shaver *et al.*, 1990; Giblin *et al.*, 1991). This latter work studied inorganic N and P dynamics in a toposequence of tundra soils, and showed that different vegetation types and locations differ strongly in their soil water chemistry. There are also abrupt temporal changes; for example, NH_4^+ and NO_3^-concentrations increase strongly just as soil waters begin to flush into the river during the initial stages of a storm event.

Monitoring and synoptic measurements revealed that the lakes and streams near Toolik Lake, and throughout the 9200 km^2 Kuparuk basin, were supersaturated with CO_2 (Kling, 1994). The source of the excess CO_2 is soil respiration; the CO_2 is transported in soil water into streams and lakes and eventually to the atmosphere or ocean. This aquatic conduit is a major pathway for gaseous transfer from land to the atmosphere for both CO_2 and CH_4 (Kling *et al.*, 1996; Reeburgh *et al.*, 1998) (Fig. 8.11). Most of the aquatic flux of carbon is through movement of dissolved organic carbon (DOC), originating from land, through lakes and streams. This DOC export is influenced by vegetation cover and watershed position (Kling, 1995) but the use of that DOC by organisms is controlled strongly by the material quality as well as the quantity. The highest quality DOC (in terms of biological availability) DOC arises from leaching of overwintering plant detritus and reaches streams and lakes by surface flow during the spring runoff. Soon thereafter, the soils thaw and the DOC from leaching percolates through soils where the high-quality material is metabolized by soil bacteria before it can reach streams and lakes. Experiments showed that differences in the quality of the organic carbon were related to its place of origin on the landscape and to the time of season, and this controlled the rate of conversion of organic carbon to CO_2 (Michaelson *et al.*, in press). Mesocosm experiments (Kling, 1995) and bioassays show that this material is accessible to lake bacteria. To gain a better understanding of the processes involved within the soil, a recent experiment has used a ^{14}C label to estimate the production rate in soil waters of DOC, CO_2, and CH_4 in soil-plant microcosms. To synthesize these data, a process model has been constructed that combines a soil-energy column and water balance routine with topographic statistics of the watershed (Ostendorf *et al.*, 1996; Stieglitz *et al.*, 1997). The model predicts well the surface runoff and soil temperatures in Imnavait Creek near Toolik. The next step will be to incorporate DOC and gas production in the soil and predict export from the basin under various conditions.

Photochemical processes

There is increasing evidence that photochemical reactions play a major role in the flux and biological availability of materials entering rivers and lakes from their surrounding catchments. Such processes may be especially important in high latitudes where the long daylength offsets the effect of reduced maximum irradiances caused by the large solar zenith angle. Photochemical research began in the Arctic in the 1970s (Strome and Miller, 1978), but only recently has emerged as an important theme in high latitude limnology. As noted above, CDOM is a link between catchment hydrology, soils and vegetation, and ecosystem function in the downstream receiving waters. These materials strongly absorb in the UV region of the solar spectrum and in the process undergo photochemical degradation to products that can have positive (e.g., increased C, N, P and Fe availability to microbiota) and negative effects (e.g., production of reactive oxygen species such as peroxides) on aquatic communities. In two subarctic lakes, for example, hydrogen peroxide concentrations in the surface waters tracked the diurnal radiation and mixing cycle (Scully and Vincent, 1997). Photochemical reactions may also influence the efflux of materials that have been derived from the catchment. For example, photochemical degradation of DOC to CO_2 and CO during the continuous summer daylight, and the subsequent evasion (transfer from the water to the atmosphere) of these gases, could result in a significant carbon loss from high latitude aquatic ecosystems. In high Arctic lakes, the photochemical interaction between solar radiation (particularly UVR) and photoreducible Hg(II) compounds results in the production of dissolved gaseous mercury and could be a major loss mechanism for such waters (Amyot *et al.*, 1997). The implications of stratospheric ozone depletion for surface water photochemistry (e.g., Scully *et al.*, 1997) are of particular interest for northern lake environments given the rising levels of UV-B in this region.

CONTAMINANT DISTRIBUTION AND IMPACTS

Long range transport

During the 1980s the surprising discovery was made that many of the apparently pristine environments in the north and their biota were highly contaminated with metals and persistent organic chemicals. Although some of the organic contaminants entering the Arctic are from local sources (see below) the primary inputs appear to be via long range transport in the atmosphere (see Reiersen, this volume). The main source regions for the Canadian Arctic are believed to lie several thousand kilometres away in Eurasia, carried in by atmospheric circulation from this direction in winter. The materials are transported in the gas phase and aerosols, deposited on the snow pack, vegetation and soils, and then washed off, buried or revolatilized. This latter process is greatly reduced by cold temperatures, and the contaminants are therefore likely to become less mobile with increasing latitude—a process referred to as global distillation or the cold condensation effect (MacKay and Wania, 1995).

An analysis of lake sediments across a south-north transect in Arctic Canada has provided evidence consistent with global distillation (Muir *et al.*, 1996): the depositional flux of total PCBs decreased with increasing latitude north while the proportion of lower chlorinated, more volatile congeners increased. Further support was provided by the depositional trend over the last five decades which shows that the PCB flux was delayed and prolonged in lakes at higher latitudes. PCB deposition began in the 1950s–60s in the high Arctic, but in the 1930s and 40s in the low Arctic. Maximum concentrations are currently found at the very surface of high Arctic lake sediments, but in the sediments of low Arctic lakes maximum concentrations occur below the surface, at depths corresponding to the 1960s and 70s.

Local effects

Local contamination originates from a variety of sources at high northern latitudes. Industrial activities have caused deterioration of the environment at many locations in the Arctic. For example, SO_2 emissions from smelters on the Kola Peninsula have resulted in high levels of sulphur deposition onto nearby lakes, including those in the Sor-Vanger region of Norway (71°N). There has been sufficient acid neutralizing capacity in most of these systems to reduce the toxic effects of this input, however fish damage has been observed in a small number of the lakes, including loss of some populations of Arctic charr and brown trout (Hesthagen *et al.*, 1998). Industry and mining have resulted in heavy metal contamination at some sites, for example in wetlands of the Russian Arctic (Zhulidov *et al.*, 1997b). The metal concentrations at these sites was well above those measured in more isolated regions of Siberia, for example relative to Lake Taymyr which is some 1000 km from the nearest city (Robarts *et al.*, 1999). Military activities, particularly those associated with the Cold War, have left a legacy of contamination throughout the circumpolar Arctic, for example PCBs released from military radar stations in Arctic

Canada (Bright *et al.*, 1995). In Canada and elsewhere, these contaminated soils and waters have been the subject of ongoing monitoring and remediation measures.

For some pollutants, the contamination of high latitude lakes and rivers is a combination of local and long range effects. Mercury contamination has been the subject of intense scrutiny in northern Canada because of findings in the 1970s and 1980s that some native communities had been exposed to methyl mercury at levels that posed a long term risk for human health. Some of the mercury input can be associated with local industrial or urban waste sources, however long range dispersal has had more general influence throughout the Arctic. In a paleolimnological study on a lake on the Belcher Islands, southern Canadian Arctic, Hermanson (1998) showed that anthropogenic mercury inputs started to appear in the mid 18th century, apparently the result of atmospheric transport, and continued to the present. This region has no history of local industrial or agricultural sources of contaminants. However, a second lake in this region received domestic sewage input from an Inuit community established in the 1960s, and the sediments of this lake showed an increased level of Hg contamination from the 1960s onwards.

Mercury contamination and biomagnification through aquatic food webs (Fig. 8.12A) has been widely observed in remote subarctic lakes (Langlois *et al.*, 1995), further indicating the importance of long range transport. Such contamination, however, is greatly accelerated in the lakes produced by flooding of northern lands for hydro-electric reservoirs. In the La Grande complex in northern Quebec, some 11,500 km^2 of land were flooded for the creation of a series of large reservoirs. Soon after this event, increased mercury levels were recorded in their resident fish populations, ultimately rising to 3.5–5 times the pre-impoundment levels (Fig. 8.12B). Consistent with food web relationships and longevity, planktivorous species such as lake whitefish (*Coregonus clupeaformis*) showed a faster rise in concentrations than piscivorous species (predators on other fish) such as northern pike (*Esox lucius*). From the seventh year following impoundment onwards, concentrations in lake whitefish have slowly declined. Monitoring data for northern Québec Cree communities have shown that Hg concentrations in hair significantly decreased over the period 1984–94, but this may reflect a reduction in fish consumption and a switch in diet towards the less contaminated non-piscivorous fish, i.e., fish lower in the food web than top predators (Chevalier *et al.*, 1997).

CONCLUSIONS

Northern lakes and rivers were until quite recently thought of as part of a remote, pristine wilderness unlikely to be affected by human activities. Over the last few decades this earlier perception has proven to be ill founded. Mining, oil and gas exploitation, hydroelectric development, military installations and urbanization have placed increasing pressure on these ecosystems,

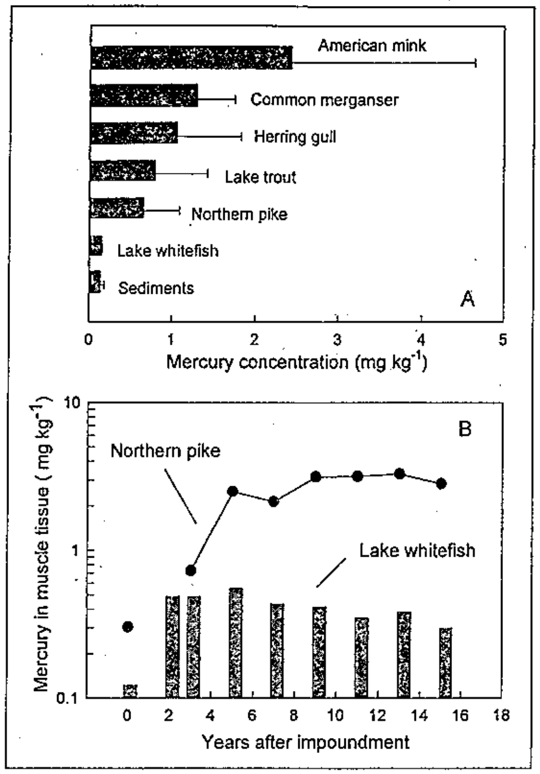

FIGURE 8.12: MERCURY CONTAMINATION IN SUBARCTIC LAKES. A. BIOACCUMULATION OF MERCURY IN THE FOOD WEB OF REMOTE LAKES IN NORTHERN QUÉBEC (PLOTTED FROM THE DATA IN LANGLOIS *ET AL.* 1995). B. CHANGE IN MERCURY IN THE MUSCLE TISSUE OF PLANKTIVOROUS (LAKE WHITEFISH, STANDARDIZED LENGTH OF 400 MM) AND PISCIVOROUS FISH (NORTHERN PIKE, 700 MM LENGTH) IN THE LA GRANDE 2 RESERVOIR SUBSEQUENT TO IMPOUNDMENT (REPLOTTED FROM CHEVALIER *ET AL.* 1997). THE YEAR 0 DATA ARE MEANS FOR 21 NATURAL, UNIMPOUNDED LAKES OF THE REGION.

with severe local impacts at some sites. There is also mounting evidence that these high latitude environments are especially vulnerable to human impacts operating at a planetary scale such as climate change, stratospheric ozone depletion and the global transport of contaminants. This trend of increasing human-induced change in the arctic environment, coupled with the need to better manage these land and water resources, has highlighted the need for an improved understanding of northern lakes and rivers.

The detailed IBP studies during the 1970s at Char Lake, Canada, and on the tundra ponds at Barrow, Alaska, provided a solid foundation for arctic limnology. Since that time, the aquatic sciences have continued to evolve rapidly, and much of the current research on northern freshwater ecosystems reflects the emergence of new themes in international limnology; for example, the dynamics of the microbial food web, the multiple roles of dissolved organic matter and the molecular genetics of high latitude biota. New global issues of particular relevance to the polar regions have also set the agenda for recent and ongoing research on arctic lakes and rivers; in particular the distillation of contaminants towards the polar regions, rising UV-B radiation, and climate change.

The earliest limnological studies in the Arctic tended to view the freshwater environments of this region as discrete, isolated systems. Today there has been a shift of emphasis towards a 'whole ecosystem' perspective whereby streams, lakes and their catchments are viewed as coupled systems. Many of their physical (e.g., light penetration) and biogeochemical (e.g., carbon availability) properties are determined by landscape processes in the surrounding watershed. These waters continue to have a large downstream influence after they discharge into the Arctic Ocean, affecting the marine physics, chemistry and biology (Vincent *et al.*, 1999b) and acting as a conduit for pollutants from terrestrial systems to the sea (e.g., Yunker and Macdonald, 1995). The arctic region must also be viewed at the broader level, as an interacting component of the planet Earth system. The wetlands of the arctic tundra, for example, contain globally significant organic carbon reserves and can be an important source or sink for carbon exchanges with the Earth's atmosphere.

The extended research programs at Toolik Lake, Alaska, and in northern Canada have allowed arctic limnology to move beyond descriptive data collection to experiments and process studies. These studies, however, are restricted in their geographical coverage, and an improved understanding of polar freshwaters is required at a much broader array of sites, notably Greenland, Siberia, northern Scandinavia, and Svalbard. Lakes and streams are also an important element of the Antarctic environment (Vincent and Ellis-Evans, 1989; Ferris *et al.*, 1988; Priscu, 1998) and much is to be learned by comparing the fascinating similarities (e.g., extreme seasonality) and differences (e.g., in biodiversity) between the two polar regions. These circumpolar and bipolar approaches have the potential to yield valuable new tools for environmental management in the Arctic, as well as new insights into the structure and function of aquatic ecosystems within and outside the polar regions.

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