Chapter 8

Freshwater Ecosystems and Fisheries

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Summary

Changes in climate and ultraviolet radiation levels in the Arctic will have far-reaching impacts, affecting aquatic species at various trophic levels, the physical and chemical environment that makes up their habitat, and the processes that act on and within freshwater ecosystems. Interactions of climatic variables, such as temperature and precipitation, with freshwater ecosystems are highly complex and can propagate through the ecosystem in ways that are difficult to project. This is partly due to a poor understanding of arctic freshwater systems and their basic interrelationships with climate and other environmental variables, and partly due to a paucity of long-term freshwater monitoring sites and integrated hydro-ecological research programs in the Arctic.

This chapter begins with a broad overview of the general hydrological and ecological features of the various freshwater ecosystems in the Arctic, including descriptions of each ACIA region, followed by a review of historical changes in freshwater systems during the Holocene. The chapter continues with a review of the effects of climate change on broad-scale hydro-ecology; aquatic ecosystem structure and function; and arctic fish, fisheries, and aquatic wildlife. Special attention is paid to changes in runoff, water levels, and river- and lake-ice regimes; to biogeochemical processes, including carbon dynamics; to rivers, lakes, ponds, and wetlands; to aquatic biodiversity and adaptive capacities; to fish populations, fish habitat, anadromy, and fisheries resources; and to aquatic mammals and waterfowl. Potential synergistic and cumulative effects are also discussed, as are the roles of ultraviolet radiation and contaminants.

The nature and complexity of many of the effects are illustrated using case studies from around the circumpolar north, together with a discussion of important threshold responses (i.e., those that produce stepwise and/or nonlinear effects). The chapter concludes with a summary of key findings, a list of gaps in scientific understanding, and policy-related recommendations.

8.1. Introduction

The Arctic, which covers a significant area of the Northern Hemisphere, has a number of prominent and unique climatic, geological, and biophysical features. The region is typified by extreme variability in climate and weather, prolonged darkness in the winter and continuous daylight in the summer, the prevalence of vast areas of permafrost, and the dominance of seasonal ice and snow cover. The Arctic also has a diversity of terrains that contain a significant number and diversity of freshwater ecosystems.

The Arctic has some of the largest rivers in the world (e.g., the Lena, Mackenzie, Ob, and Yenisey); numerous permanent and semi-permanent streams and rivers draining mountains, highlands, and glaciated areas; large lakes such as Great Bear, Great Slave, and Taymir; a myr-

iad of smaller permanent and semi-permanent lakes and ponds; vast areas of wetlands and peatlands; and coastal estuarine and river delta habitats. In turn, these freshwater systems contain a wide diversity of organisms that have developed adaptations to cope with the extreme environmental conditions they face. Examples include life-history strategies incorporating resting stages and diapause, unique physiological mechanisms to store energy and nutrients, an ability to grow and reproduce quickly during brief growing seasons, and extended life spans relative to more temperate species.

Thus, given the regional complexity of climate and landscape and the diversity of freshwater ecosystems and their associated biota, projecting the potential impacts of future climate change and ultraviolet (UV) radiation exposure presents significant challenges. What is certain is that the responses are likely to be quite variable and highly specific to particular freshwater ecosystems, their biota, and the ecological and biophysical circumstances in which they occur.

8.1.1. Challenges in projecting freshwater hydrologic and ecosystem responses

The first and most significant challenge in projecting responses of freshwater systems to climate change relates to the limited understanding of how the climate system is coupled to, and influences, key physical and biophysical processes pertinent to aquatic ecosystems, and in turn how these affect ecological structure and function. Figure 8.1 summarizes the complex and often hierarchi-

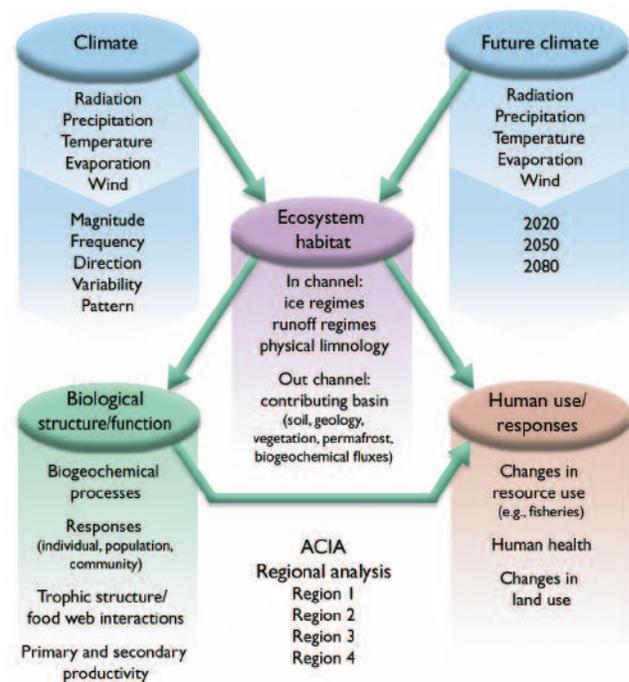**Fig. 8.1.** Climate–ecosystem interactions. The interactions among and within components tend to be sequential but complex. However, complex feedbacks also exist both within major classes of components (e.g., trophic structure linkages with biogeochemical cycling), as well as between components (e.g., ice duration and timing feedbacks to the regional climate system), but are not illustrated above for visual clarity.

cal interactions between climatic variables (e.g., radiation, precipitation, and temperature), their influence on the biophysical features of freshwater ecosystem habitat, subsequent effects on biological structure and function, and the interaction of feedbacks within and between components. Freshwater ecosystems are complex entities that consist of groups of species at various trophic levels, the hydrological and physical environment that makes up their habitat, the chemical properties of that environment, and the multiple physical, biogeochemical, and ecological processes that act on and within the system. Hence, any change in these attributes and processes as a result of changes in climate and UV radiation levels will ultimately contribute to variable and dynamic responses within freshwater systems. Even in ecosystems containing only simplified food webs (e.g., those having no predators such as fish or predatory macroinvertebrates), the interactions of environmental parameters such as temperature and precipitation with the system are still complex, and may be propagated in ways that are difficult to project (i.e., nonlinear or stepwise threshold responses in population/community dynamics and stability; see section 8.4.1, Box 8.2). Because freshwater systems receive major inputs from terrestrial systems (Chapter 7) and provide major outputs to marine systems (Chapter 9), altered states and processes within freshwater systems are intimately linked to these arctic ecosystems through feedback and transfer mechanisms.

There are a number of levels within an ecosystem where changes in climate or UV radiation levels may interact with various ecosystem components, including:

- the individual, either within it (e.g., changes in physiological processes affecting thermoregulation, or effects on life processes such as growth and reproductive rates) and/or the whole individual (e.g., behavior);
- the population (e.g., life-history traits, rates of immigration and emigration, migrations, and intra-specific competition);
- the community (e.g., changes in trophic structure and in the levels and magnitudes of food-web interactions such as inter-specific competition, predation, and parasitism); and
- the ecosystem (e.g., changes that affect the nature of the environment that the organisms occupy, such as altered biogeochemical processes and hydrologic regimes).

Hence, there are a number of considerations in assessing the effects of a change in climate or UV radiation levels on freshwater ecosystems. First, changes in the environmental parameters may occur in a variety of ways. Second, these changes may be input to the various aquatic ecosystems in a variety of ways. Third, effects within the ecosystem may manifest at various levels and in various components within the system. Fourth, the effects may propagate through the ecosystem and affect different components or processes differently within the ecosystem. The inherent complexity of such interactions greatly hampers the ability to make accurate and reasonable projections regarding such effects within arctic freshwater ecosystems with high levels of certainty. Finally, the internal complexity of potential responses makes it difficult to project output effects on key linking ecosystems such as deltas and estuaries that form the interactive zones between terrestrial, marine, and freshwater systems.

General knowledge of how the hydrology, structure, and function of arctic aquatic ecosystems are responding to past (section 8.3) and relatively recent changes in climate and UV radiation levels is gradually improving (e.g., overviews by AMAP, 1997, 1998, 2002; CAFF, 2001; Hessen, 2002; IPCC, 1996, 1998, 2001a; Prowse et al., 2001; Rouse et al., 1997; Vincent and Hobbie, 2000). However, much of the understanding of the processes and mechanics of potential impacts continues to be largely based on studies of aquatic systems outside of the Arctic (e.g., overviews by Antle et al., 2001; Carpenter et al., 1992; Meyer et al., 1999; Scheffer et al., 2001; Schindler D.W., 2001; Schindler D.W. et al., 1996a). Hence, the development of detailed projections of climate change impacts on arctic freshwater ecosystems is limited by a lack of understanding of how these impacts will cascade through arctic ecosystems and create second- and higher-order changes.

With these limitations in mind, using the approach outlined in section 8.1.2, this chapter identifies and discusses projected changes in the hydrology and ecology of

Region 1: Arctic Europe, East Greenland, Russian European North, North Atlantic
Region 2: Siberia
Region 3: Chukotka, Bering Sea, Alaska, western Arctic Canada
Region 4: Northeast Canada, Labrador Sea, Davis Strait, West Greenland

Fig. 8.2. The four ACIA regions, the southern boundary of the Arctic used in this chapter (as defined by AMAP, 1998, modified to include Québec north of the treeline), and the major river systems flowing through these regions to the Arctic Ocean (adapted from AMAP, 1998; discharge data (km³/yr) from R-ArcticNet, 2003).

arctic freshwater ecosystems in response to scenarios of future climate and UV radiation levels for three time slices centered on 2020, 2050, and 2080 generated by the ACIA-designated models (section 4.4). Where possible, similarities and/or differences in projected impacts between the four ACIA regions (Fig. 8.2; see also section 18.3) are identified.

8.1.2. Quantifying impacts and likelihood

The confidence level associated with projecting potential impacts of changes in climate and UV radiation levels is greatly hampered by the rudimentary level of understanding of arctic freshwater hydrology and ecology and their direct and indirect linkages, responses, and feedbacks to present and future climate. Moreover, the coarse spatial resolution of general circulation models (GCMs) and the uncertainty associated with complex, multi-layered, and poorly understood interactions between climate variables greatly contribute to uncertainty in projections of future climate. This is exacerbated by other complexities such as inter- and intra-regional variation driven by, for example, latitude or proximity to marine ecosystems. When combined with uncertainties about how individual species and biological communities will respond to changes in climate and UV radiation levels, the ability to forecast hydro-ecological impacts and resulting cascading effects is significantly compromised. This makes precise quantification of climate change impacts difficult and often tenuous.

To address the issue of uncertainty and to recognize the substantial inter-regional and latitudinal differences in understanding and the broad spatial extent of arctic aquatic ecosystems, climate change and UV radiation impacts have been "quantified" using a "weight-of-evidence" approach. This approach uses a hierarchy of classes that represent the range of likelihood of the impact(s)/outcomes(s) occurring based on a compilation of information available from historical data, published literature, model projections, and the expert judgment of the authors. Using the ACIA lexicon (section 1.3.3), projected likelihoods follow a progression from "very unlikely" (i.e., little chance of occurring) through "unlikely", "possible" (some chance), and "likely/probable" to "very likely/very probable".

Although not strictly quantifiable in a numeric sense (e.g., exact probabilities), this approach provides a comparative and relative measure of the likelihood that the impact(s) will occur. Hence, a greater weight-of-evidence indicates a greater confidence in the findings (i.e., an increasing convergence of evidence from a number of independent, comprehensive empirical and/or experimental studies, model projections, etc.) that allows the classification of particular impact(s)/outcome(s) as either "very unlikely" or "very likely". The designation of particular impacts as "possible" or "likely" implies the presence of significant gaps in current knowledge. These gaps must be addressed to achieve a better understanding of impacts at the level of the ecosystem and its components.

This "weight-of-evidence"-based lexicon is directly applied in the conclusions and key findings of the chapter (section 8.8.1), thereby providing a relative "quantification" of the projected responses of freshwater ecosystems to changes in climate and UV radiation levels.

8.1.3. Chapter structure

Section 8.2 provides a broad overview of the general hydrological and ecological features of the various freshwater ecosystems in the Arctic, including descriptions for each ACIA region. Section 8.3 discusses how understanding past climate regimes using paleolimnological and paleoclimatic records helps to better understand present and future responses of freshwater ecosystems. Subsequent sections discuss the climate scenarios generated by the ACIA-designated models and project impacts on the hydrology and ecology of the major types of arctic freshwater ecosystems (section 8.4), impacts on the major components of these ecosystems (section 8.5), impacts of changes in UV radiation levels (section 8.6), and the interactions of these impacts with contaminants (section 8.7). A key feature of arctic freshwater ecosystems is the biota of direct relevance to humans, especially waterfowl, mammals, and fishes that provide the basis for harvests. Species within these groups are of special interest in that they also provide direct biotic linkages between major arctic ecosystems, thus either potentially input or output effects from, or to, terrestrial and marine systems. Fish are of particular relevance since two major ecological groups are present: those wholly associated with freshwaters and those which pass parts of their life history in both fresh and marine waters (i.e., diadromous fishes further divisible into catadromous species such as eels that rear in freshwater and breed in the sea, and anadromous species such as salmon that do the opposite). Anadromous fish provide major nutrient transfers from marine systems back into freshwater systems, thus are of particular significance. A logical extension is to also consider the effects of global change on fisheries for freshwater and diadromous forms; thus, section 8.5.5 parallels the treatment of marine fisheries in Chapter 13. Section 8.8 summarizes key findings and identifies major knowledge gaps and future research needs.

8.2. Freshwater ecosystems in the Arctic

8.2.1. General features of the Arctic relevant to freshwater ecosystems

The nature and severity of climate and weather have a strong influence on the hydrology and ecology of arctic freshwater ecosystems (e.g., Murray et al., 1998a; Pielou, 1994; Prowse and Ommanney, 1990; Prowse et al., 1994; Woo, 1996, 2000). Arctic climate has several prominent features that show extensive variation along strong latitudinal gradients. These include extreme seasonality and severity in temperature extremes (i.e., long, cold winters and relatively short, warm summers, both of which persist long enough to limit biota because of physiological thresholds); high intra- and interannual

variability in temperature and precipitation; and strong seasonally driven latitudinal gradients in incident solar and UV radiation levels, to name a few. Extended low temperatures result in extensive ice cover for long periods of the year, significantly affecting physical, chemical, and biological processes in aquatic ecosystems. Extreme seasonality and low levels of incident radiation also have profound effects on aquatic ecosystems: much of this radiation may be reflected owing to the high albedo of ice and snow, especially during the critical early portions of the spring and summer. In addition, the thermal energy of a substantive portion of this incoming energy is used to melt ice, rendering it unavailable to biota. The timing of radiation is also important for some high-latitude aquatic systems that receive a majority of their annual total prior to the melting of their ice cover. Low levels of precipitation generally occur throughout the Arctic and most of this falls as snow, resulting in limited and highly episodic local runoff.

The ecological consequences of these environmental extremes are profound. For instance, overall annual productivity of freshwater systems generally tends to be low because of low levels of nutrient inputs, low temperatures, prolonged periods of ice presence compared to temperate aquatic ecosystems, and short growing seasons (Murray et al., 1998b). In most cases, this results in slower growth and some longer-lived organisms. Seasonal variations in arctic aquatic processes are relatively high, resulting in various adaptations in the organisms that thrive there. In animals, such adaptations include high rates of food consumption when it is available, rapid conversion of food to lipids for energy storage, and later metabolism of stored lipids for over-winter maintenance, growth, and reproduction (Craig, 1989). Additionally, some groups (e.g., fish) exhibit highly migratory behavior to optimize life-history functions, resulting in movements among different habitats triggered by environmental cues (e.g., dramatic temperature decreases) that usually coincide with transitions between particular seasons (Craig, 1989). Migratory organisms such as waterfowl occupy a variety of habitats both seasonally and over their lifetime (CAFF, 2001). Hence, aquatic biota display a wide range of adaptation strategies to cope with the severe environmental conditions to which they are exposed (CAFF, 2001; Pielou, 1994). A critical question is whether future changes in key climatic variables will occur at a rate and magnitude for which current freshwater species have sufficient phenotypic or genetic plasticity to adapt and survive.

8.2.2. Freshwater inputs into arctic aquatic ecosystems

The source, timing, and magnitude of freshwater inputs to arctic freshwater ecosystems has important implications for the physical, chemical and biological properties, as well as the structure, function, and distribution of river, lake, pond, and wetland ecosystems in the Arctic.

Rainfall is a substantial freshwater source for ecosystems at more southerly latitudes, occurring for the most part during the extended summer season. Further north, snowfall dominates the annual freshwater budget. High-latitude polar deserts receive low levels of precipitation and as such have a pronounced moisture deficit. Maritime locations generally receive greater quantities of snow and rain than continental regions.

The most important input of freshwater into aquatic ecosystems is often snowfall. It accumulates over autumn, winter, and spring, and partly determines the magnitude and severity of the spring freshet. Snowpack duration, away from the moderating influences of coastal climates, has been documented to range from ~180 days to more than 260 days (Grigoriev and Sokolov, 1994). In the spring, elevated levels of solar radiation often result in rapid snowmelt. Consequently, this rapid melt of the snowpack translates into spring runoff that can comprise a majority of the total annual flow, and be of very short-term duration – as little as only two to three weeks (Linell and Tedrow, 1981; Marsh, 1990; Rydén, 1981). In addition, at higher latitudes, infiltration of this spring flush of water is constrained by the permafrost. Thus, spring meltwater may flow over land and enter rivers, or accumulate in the many muskegs, ponds, and lakes characteristic of low-lying tundra areas (van Everdingen, 1990). Meltwater can also have major impacts on the quality of water entering lakes and rivers. When highly acidic, it can produce "acid shock" in receiving waters. However, because the incoming meltwater is usually warmer than the lake water, it tends to pass through the lake with little mixing. The potential acidic spring pulse is therefore transient without any marked biological consequences, as documented by paleolimnological investigations (e.g., Korhola et al., 1999; Michelutti et al., 2001).

During the summer, sources of water include not only rain, but also late or perennial snow patches, glaciers, thawing permafrost, and groundwater discharges (Rydén, 1981; van Everdingen, 1990). As temperatures rise in response to climate change, these sources of water are likely to become more pronounced contributors to the annual water budgets of freshwater ecosystems, at least until their ice-based water reserves are depleted.

Groundwater can also have an important influence on the annual water budgets of arctic surface-water ecosystems. Permafrost greatly influences the levels and distribution of groundwater within the Arctic. Groundwater movement through aquifers is restricted by permafrost year-round, and by the frozen active layer for up to ten months of the year (Murray et al., 1998a). Three general types of groundwater systems occur in the Arctic: supra-permafrost, intra-permafrost, and sub-permafrost. Supra-permafrost groundwater lies above the permafrost table in the active layer during summer, and year-round under lakes and rivers that do not totally freeze to the bottom. Intra-permafrost water resides in unfrozen sections within the permafrost, such as tunnels called "taliks", which are located under alluvial flood plains and under drained or shallow lakes and swamps. Sub-permafrost water is located beneath the permafrost table. The thickness of the

permafrost determines the availability of sub-permafrost water to freshwater ecosystems, acting as a relatively impermeable upper barrier. These three types of groundwater systems, which may be located in bedrock or in unconsolidated deposits, may interconnect with each other or with surface water (Mackay D. and Løken, 1974; van Everdingen, 1990; Woo, 2000; Woo and Xia, 1995) as outflows via springs, base flow in streams, and icings. Icings (also known as aufeis or naleds) are comprised of groundwater that freezes when it reaches the streambed during winter. Groundwater interactions with surface-water systems greatly influence water quality characteristics such as cation, anion, nutrient, and dissolved organic matter concentrations, and even the fate and behavior of toxic pollutants.

8.2.3. Structure and function of arctic freshwater ecosystems

Arctic freshwater ecosystems are quite varied with respect to their type, physical and chemical characteristics, and their associated biota. Thus, the impacts of climate change and increased UV radiation levels will be variable and highly specific to particular freshwater ecosystems, their biota, and processes. Additionally, in some areas that span a wide latitudinal range (e.g., the arctic regions of Canada and Russia), similar types of freshwater systems exhibit a wide range of characteristics driven in part by latitudinal differences in the environment. These, in turn, will also respond differently to global change. Furthermore, the nature of connections between the various regions of the Arctic and non-arctic areas of the globe differ. Consequently, regional differences between the same types of aquatic systems are likely to exist, despite these being at the same latitude. In addition, historical differences in their development during recent geological time and geomorphic processes that have affected different regions (e.g., extent of Pleistocene glaciations, age, and connectivity to southern areas), will contribute to regional, subregional, and local variability in ecosystem structure and function.

Two major categories of freshwater ecosystems can be defined as lotic (flowing water) and lentic (standing water), but large variation in size, characteristics, and location is exhibited within each. Thus, large differences in response to climate change can be expected. For the purposes of this assessment, lotic ecosystems include rivers, streams, deltas, and estuaries, where flow regimes are a dominant hydrologic feature shaping their ecology. Lentic ecosystems include lakes, ponds, and wetlands (including bogs and peatlands). Although some wetland types may not have standing surface water at all times, they are considered lentic ecosystems for the purposes of this chapter.

Although the Arctic generally contains a relatively low number of aquatic bird and mammal species as compared to more temperate ecozones, it is home to most of the world's geese and calidrid sandpipers (Zöckler, 1998). Migratory birds, including geese, ducks, swans, and gulls,

can be particularly abundant in arctic coastal and inland wetlands, lakes, and deltas (Bellrose, 1980; Godfrey, 1986; Zhadin and Gerd, 1961; for comprehensive review see CAFF, 2001). Most taxonomic groups within the Arctic are generally not very diverse at the species level, although some taxonomic groups (e.g., arctic freshwater fish; see section 8.5.1.1, Box 8.6) have high diversity at and below the species level (e.g., display a large number of ecological morphs). In addition, arctic freshwater systems generally exhibit strong longitudinal gradients in biodiversity, ranging from extremely low biodiversity in high-latitude, low-productivity systems to very diverse and highly productive coastal delta–estuarine habitats (AMAP, 1998; CAFF, 2001; IPCC, 2001a). Very little is known about the biological and functional diversity of taxa such as bacteria/virus, phytoplankton, and zooplankton/macroinvertebrate communities that reside in arctic aquatic ecosystems, despite their undoubted importance as key components of freshwater food webs (Vincent and Hobbie, 2000; Vincent et al., 2000).

8.2.3.1. Rivers and streams, deltas, and estuaries

Rivers and streams

Arctic rivers and streams are most densely distributed in lowlands, including those in Fennoscandia and the Interior Plain of Canada, often in association with lakes and wetlands. Lotic ecosystems include large northward flowing rivers such as the Mackenzie River in Canada (Fig. 8.2), high-gradient mountain rivers, and slow-flowing tundra streams that may be ephemeral and flow only during short periods in the early spring. Flowing-water systems represent a continuum, from the smallest to largest, and although subdividing them at times is arbitrary, river systems of different sizes do vary in terms of their hydrology, water quality, species composition, and direction and magnitude of response to changing climatic conditions. This is particularly relevant in the Arctic, where river catchments may be wholly within the Arctic or extend southward to more temperate locations.

In general, the large rivers of the Arctic have headwaters well south of the Arctic as defined in this chapter (Fig. 8.2; see section 6.8 for a review of major arctic rivers and their historical flow trends), and as such act as conduits of heat, water, nutrients, contaminants, sediment, and biota northward (e.g., Degens et al., 1991). For such systems, not only will local effects of climate change be important, but basin-wide effects, especially those in the south, will also be critical in determining cumulative effects (e.g., see Cohen 1994, 1997). Five of the ten largest rivers in the world fall into this category: the Lena, Ob, and Yenisey Rivers in Russia, the Mackenzie River in Canada, and the Yukon River in Canada and Alaska. These rivers have substantive effects on the entire Arctic, including the freshwater budget of the Arctic Ocean and the hydro-ecology of coastal deltas and related marine shelves. Various portions of these rivers are regulated (Dynesius and Nilsson, 1994), the most affected being the Yenisey River, which is also the

largest of the group and the one projected to experience significant further impoundment (an increase of ~50%) over the next few decades (Shiklomanov et al., 2000). For northern aquatic systems, the effects of impoundment on water quantity and quality are wide-ranging, and are expected to be exacerbated by the effects of climate change (Prowse et al., 2001, 2004).

Numerous smaller, but still substantive, rivers also drain much of the Arctic and may arise from headwaters outside of the Arctic. These include the Severnaya Dvina and Pechora Rivers that drain much of the Russian European North, the Khatanga River of Siberia, the Kolyma River of eastern Siberia, and the Churchill and Nelson Rivers that drain much of central Canada and supply water to the Arctic Ocean via Hudson Bay. Although these rivers are much smaller than those in the first group, they are more numerous and in many cases are affected by a similar suite of anthropogenic factors, including agriculture, hydroelectric impoundment, industrialization, mining, and forestry, many of which occur outside of the Arctic and, as climate change progresses, may become more prominent both within and outside of the Arctic.

Still smaller types of lotic systems include medium to small rivers that arise wholly within the Arctic. Examples include the Thelon River in Canada, the Colville River in Alaska, the Anadyr River in Chukotka, many rivers throughout Siberia, and the Tana River of Scandinavia. In many cases, these rivers do not presently have the same degree of local anthropogenic impacts as the previous two types. Despite some level of anthropogenic impacts, many of these arctic rivers harbor some of the largest and most stable populations of important and widely distributed arctic freshwater species. For example, many of the most viable wild populations of Atlantic salmon (*Salmo salar*) are extant in northern systems such as the Tana River of northern Norway, despite widespread declines in southern areas (e.g., Parrish et al., 1998).

Most of the rivers noted above share an important characteristic: their main channels continue flowing throughout the winter, typically beneath ice cover, due to some type of continuous freshwater input from warm southern headwaters, lakes, and/or groundwater inflows. As such, they typically have higher levels of productivity and biodiversity than arctic rivers that do not flow during winter. This latter group consists of numerous rivers that are even smaller and found throughout the Arctic. Fed primarily by snowmelt, they exhibit high vernal flows dropping to low base flows during the summer, with perhaps small and ephemeral flow peaks during summer and autumn precipitation events prior to freeze-up. Glaciers also feed many of these smaller arctic rivers (e.g., in Alaska and Greenland), thus snowmelt feeds initial vernal flows, and glacial melt maintains flows at a relatively high level throughout the summer. Most of these small arctic rivers stop flowing at some point during the winter and freeze to the bottom throughout large reaches. Such is the case for many small rivers in Region 1, those to the

east in Region 2, and the coastal rivers of Chukotka, northern Alaska, and northwestern Canada (Region 3). This hydrology has important implications for the biota present (e.g., habitat and productivity restrictions), and climate change will have important ramifications for such ecosystems (e.g., cascading effects of changes in productivity, migratory routes).

Although the division between rivers and streams is somewhat arbitrary, as a class, local streams are numerous and found throughout the Arctic in association with all types of landforms. Streams feed water and nutrients to lacustrine environments and act as the first-order outflows from many tundra lakes, thus providing connectivity between different aquatic environments and between terrestrial and aquatic systems.

The ecology of arctic rivers and streams is as diverse as are the systems themselves, and is driven in part by size, location, catchment characteristics, nutrient loads, and sources of water. Correspondingly, biotic food webs of arctic rivers (Fig. 8.3) vary with river size, geographic area, and catchment characteristics. For example, benthic algae and mosses, and benthic invertebrate fauna associated with fine sediments, are more common in smaller, slower-flowing rivers and streams, while fish populations are limited in small rivers that freeze over the winter (Hobbie, 1984; Jørgensen and Eie, 1993; Milner and Petts, 1994; Steffen, 1971). Changes to river ecology, whether they are bottom-up (e.g., changes in nutrient loading from catchments will affect primary productivity) or top-down (e.g., predatory fish removal with habitat loss will affect lower-level species productivity and abundance), will affect not only river systems, but also receiving waters. Rivers fed primarily by glaciers are physically dynamic and nutrient-poor, and as such offer challenging environments for primary production and invertebrate communities (Murray et al., 1998a). Spring-fed streams with stable environments of clear water, year-round habitat, and higher winter temperatures exhibit greater diversity in primary producers, including mosses and diatoms, and lower trophic levels such as insects (Hobbie, 1984). Tundra streams tend to be ephemeral and low in pH and nutrients, with correspondingly low productivity. Medium-sized rivers, especially those draining lakes, typically have moderate to high levels of productivity and associated diversity in invertebrate fauna, which in turn are affected by such things as suspended sediment loads. For example, clear-flowing rivers of the Canadian Shield have higher biodiversity at lower trophic levels (e.g., invertebrates) than very turbid rivers of the lowlands of Siberia and the Interior Plain of Canada (Murray et al., 1998a). In general, fish diversity in arctic rivers appears to be related primarily to the size of the river and its associated drainage basin; thus similarly sized rivers differing greatly in suspended sediment loads tend to have a similar overall diversity of fish species. However, the suite of species present differs between clear (e.g., preferred by chars) and sediment-rich (e.g., preferred by whitefishes) rivers. Historical
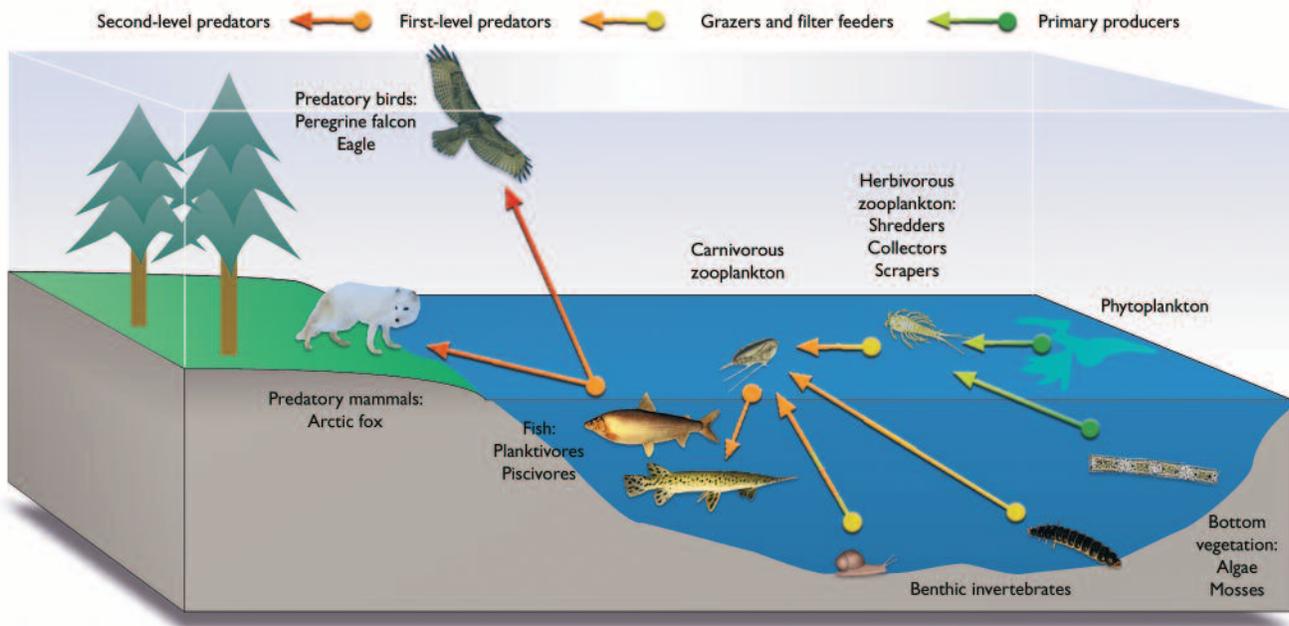
Fig. 8.3. Representative arctic river and stream food web.

factors such as deglaciation events and timing also figure prominently in determining biodiversity at higher trophic levels in these systems (Bodaly et al., 1989).

Another ecological feature of arctic rivers, and one that is likely to be significantly affected by climate change, is that of anadromy or sea-run life histories of many of the fish species present (section 8.5). That is, most of the salmonid fishes found in the Arctic, and several species of other families, use marine environments extensively for summer feeding and, in some instances, for substantial portions of their life history (e.g., much of salmon life history occurs in marine waters). These fish, and to some extent waterfowl, provide a fundamental ecological linkage between freshwater systems, estuarine systems, and marine systems of the Arctic. For such organisms, the effects of changes in climate and UV radiation levels on each environment will be integrated throughout the life of the individual and hence be cumulative in nature.

Deltas and estuaries

Deltas are highly diverse ecosystems that lie at the interface between rivers and lakes or oceans, providing a variety of freshwater habitats that are highly seasonal in nature. The most notable deltas in the Arctic are those of the Lena River in Russia and the Mackenzie River in Canada, where easily eroded sedimentary landscapes contribute to heavy sediment loading in rivers and deltas. Habitats include extensive wetlands, which cover up to 100% of the Mackenzie Delta (Zhulidov et al., 1997), and many ponds and lakes frequented by small mammals, fish, and waterfowl. Arctic deltas are ice-covered for the majority of the year, although flows continue in their major channels throughout the year. A critical hydrologic feature of these systems is the occurrence of ice jams and associated ice-jam floods, both of which are paramount in the maintenance of delta ecosystems

(Prowse, 2001a; Prowse and Gridley, 1993). Spring overland floods are critical to the recharge of delta lakes, such as those of the Yukon, Colville (Dupre and Thompson, 1979; Walker and McCloy, 1969), Mackenzie (Marsh and Hey, 1989, 1991), and Slave Rivers (Peterson E. et al., 1981) in North America, and the Yenisey, Lena, Kolyma, and Indigirka Rivers in Siberia (Antonov, 1969; Burdykina, 1970). Flooding during spring breakup also provides sediments and nutrients to deltas (e.g., Lesack et al., 1991), which in turn help sustain unique and highly productive habitats for plant and animal species, including fish, waterfowl, and small mammals such as muskrats (*Ondatra zibethicus*; e.g., Marsh and Ommanney, 1989). The drastic changes in delta hydrology with seasonal and interannual shifts in flow regimes, and the effect of wind-related disturbance on delta waters, have important implications for delta hydro-ecology. Hence, given the transient and sensitive nature of delta hydro-ecology, climate change is likely to have significant impacts in these areas of the Arctic.

River hydrology not only affects the hydro-ecology of deltas, but also that of estuaries. Examples of large deltas and associated estuaries include the Mackenzie River in Canada, and the Lena, Ob, and Yenisey Rivers in Russia. Arctic estuaries are distinct from those at more southerly latitudes in that their discharge is highly seasonal and ice cover is a key hydrologic variable influencing the ecology of the systems. Winter flows are typically between 5 and 10% of the annual average (Antonov, 1970), and estuarine waters are often vertically stratified beneath the ice cover. This may promote the formation of frazil ice at the freshwater–saltwater boundary. Freshwaters that flow into estuaries during winter typically retain their chemical loads until stratification deteriorates with loss of ice cover. In estuaries that are less than 2 m deep, river discharges in late winter may be impeded by ice and diverted offshore

through erosional channels or by tidal inflows (Reimnitz and Kempema, 1987). High-magnitude freshwater discharges in spring carry heavy sediment loads and flow beneath the ice, gradually mixing with saltwater as breakup progresses in the estuary; these discharges dominate estuarine waters when landward fluxes of seawater are less pronounced.

Freshwater inflows from large arctic rivers carry sediment, nutrients, and biota to coastal areas, thereby contributing to the highly productive nature of estuaries and related marine shelves. Furthermore, this production is fostered by the complex nearshore dynamics associated with mixing of water masses differing in density, which in turn, increase the complexity of biological communities (Carmack and Macdonald, 2002). Hence, estuaries provide a significant food source for anadromous species compared to what is available to them from adjacent freshwater streams (Craig, 1989). This productivity typically results in large populations of fish that are important to local fisheries (e.g., Arctic char – *Salvelinus alpinus*, Atlantic salmon) and integral to the food web supporting other arctic organisms such as waterfowl, shorebirds, and marine mammals. The fish populations are keystone components affecting energy transfer (Fig. 8.4). Many anadromous fishes in these systems (e.g., Arctic cisco – *Coregonus autumnalis*, Dolly Varden – *Salvelinus malma*, rainbow smelt – *Osmerus mordax*) overwinter in freshened coastal and estuarine waters that are often used for feeding and rearing during the summer. Fishes migrate upstream in freshwater systems to spawn, and in some cases to overwinter. Given the intimate interaction of anadromous fishes with freshwater and marine environments in these delta/estuary systems, climate-induced changes in freshwater and marine ice and hydrology will significantly affect the life histories of these fishes.

Shorebirds and seabirds that utilize freshwater and/or estuarine habitats, linking freshwater and marine environments, include the red phalarope (*Phalaropus fulicaria*), parasitic jaeger (*Stercorarius parasiticus*), red knot (*Calidris canutus*), dunlin (*C. alpina*), long-tailed jaeger (*S. longicaudus*), northern fulmar (*Fulmarus glacialis*), glaucous gull (*Larus hyperboreus*), white-rumped sandpiper (*C. fuscicollis*), western sandpiper (*C. mauri*), red-necked stint (*C. ruficollis*), Lapland longspur (*Calcarius lapponicus*), black-bellied plover (*Pluvialis squatarola*), semipalmated plover (*Charadrius semipalmatus*), and ruddy turnstone (*Arenaria interpres*). Another important feature of estuarine ecosystems is the potential for transfers (e.g., by waterfowl and anadromous fishes) of significant nutrient loads from marine to freshwater habitats (Bilby et al., 1996). Deltas and estuaries also have high rates of sedimentation and potentially significant rates of sediment suspension, and as such can be important sinks and sources of terrestrial organic carbon (e.g., Macdonald R. et al., 1995) and contaminants (e.g., Milburn and Prowse, 1998), and are thereby capable of producing both positive and negative impacts on the aquatic biota in these systems.

8.2.3.2. Lakes, ponds, and wetlands

Lentic ecosystems of the Arctic are diverse and include an abundance of lakes of varying size, shallow tundra ponds that may contain water only seasonally, and wetlands such as peatlands that are notable stores and sources of carbon. These freshwater systems provide a rich diversity of habitats that are highly seasonal and/or ephemeral.

Lakes and ponds

Arctic lakes are typically prevalent on low-lying landscapes, such as coastal and interior plains (e.g., the
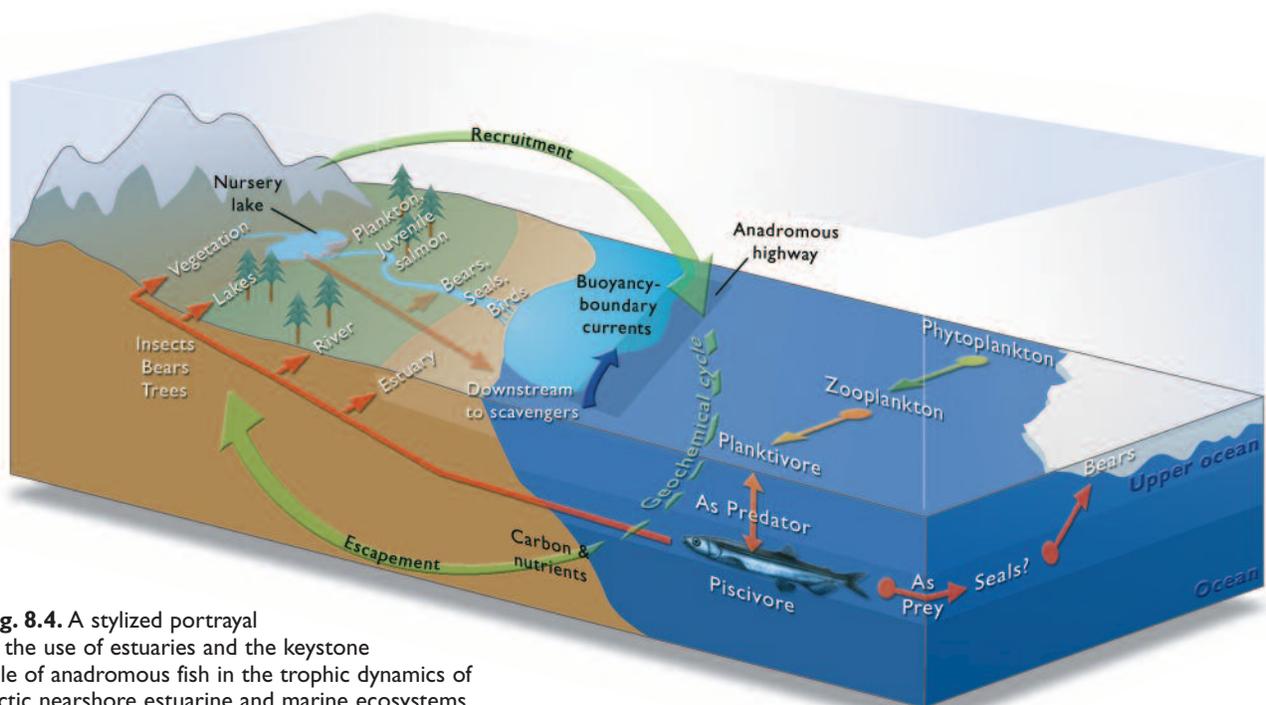

Fig. 8.4. A stylized portrayal of the use of estuaries and the keystone role of anadromous fish in the trophic dynamics of arctic nearshore estuarine and marine ecosystems (after Carmack and Macdonald, 2002).

Canadian Interior Plain and the Finnish Lowlands). There are many kettle (produced by the melting of buried glacial ice), moraine, and ice-scour lakes on the undulating terrain of postglacial arctic landscapes (e.g., the Canadian Shield, Fennoscandia, and the Kola Peninsula; Korhola and Weckström, 2005; Mackay D. and Løken, 1974). Thermokarst lakes are also quite common in the Arctic (e.g., along the Alaskan coast and in Siberia), developing in depressions formed by thawing permafrost. Small ponds also dominate portions of the Arctic landscape (e.g., the low-lying terrain of Fennoscandia); typically less than 2 m deep, these freeze solid over the winter.

Local catchments are typically the primary source of water for arctic lakes (Hartman and Carlson, 1973; Woo and Xia, 1995; Woo et al., 1981). Spring runoff originates from snow accumulation on lake ice, hillslope runoff (Woo et al., 1981), and lateral overflow from wetlands and streams (Marsh and Hey, 1989). Outlets of small lakes may be snow-dammed, and eventually release rapid and large flows downstream (Heginbottom, 1984; Woo, 1980). Arctic lakes also experience considerable evaporative water loss, sometimes resulting in the formation of athalassic (i.e., not of marine origin) saline systems. Water loss may also occur through seepage, which is common in lakes underlain by taliks in the discontinuous permafrost zone (Kane and Slaughter, 1973; Woo, 2000).

The hydro-ecology of the many small arctic lakes is intimately linked with climatic conditions. The timing and speed of lake-ice melt depend on the rate of temperature increase in late spring and early summer, wind, and inflow of basin meltwater and terrestrial heat exchanges (e.g., groundwater inflow, geothermal input, heat loss to maintain any underlying talik; Doran et al., 1996; Welch H. et al., 1987). Some lakes in the high Arctic retain ice cover throughout the year, while some thermal stratification can occur in arctic lakes where breakup occurs more quickly. In northern Fennoscandia, for example, lakes >10 m deep are usually stratified during the summer and have well-developed thermoclines (Korhola et al., 2002a). In contrast, many high-arctic lakes mix vertically, thereby reducing thermal stratification (Mackay D. and Løken, 1974; Welch H. et al., 1987). Similarly, small shallow lakes do not stratify because they warm quickly and are highly wind-mixed. Heat loss from arctic lakes tends to be rapid in late summer and early autumn and often results in complete mixing. Consequently, shallow lakes and ponds will freeze to the bottom over winter. The duration and thickness of lake-ice cover in larger lakes increases with latitude, reaching thicknesses of up to 2.5 m, and can even be perennial over some years in extreme northern arctic Canada and Greenland (Adams W. et al., 1989; Doran et al., 1996). In addition to air temperature, the insulating effect of snow inversely affects ice thickness. Any shifts in the amounts and timing of snowfall will be important determinants of future ice conditions, which in turn will affect the physical and chemical dynamics of these systems.

The abundance and diversity of biota, productivity, and food web structure in arctic lakes varies regionally with environmental conditions and locally with the physical characteristics of individual lakes (Fig. 8.5). For example, lakes across the Russian European North vary from small, oligotrophic tundra systems (having moderate phytoplankton diversity, low primary productivity and biomass, and relatively high zoobenthos abundance) to larger taiga lakes (displaying greater species diversity and higher primary and secondary productivity and biomass). Mountain lakes of the region tend to have very low phytoplankton diversity, but substantial primary and secondary productivity and biomass, similar to that of taiga lakes. In general, the abundance and diversity of phyto-
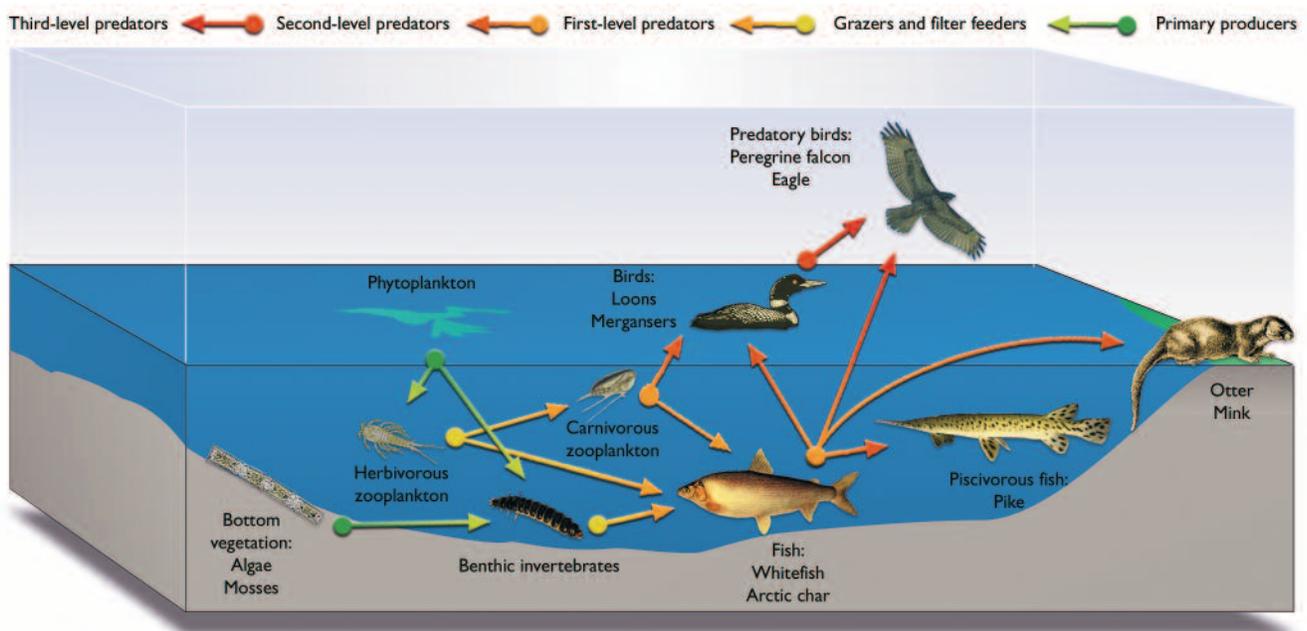

Fig. 8.5. Representative food web in arctic lakes (adapted from AMAP, 1997).

plankton and invertebrates such as rotifers, copepods, and cladocerans increase with lake trophic status (Hobbie, 1984), which is often a function of latitudinal constraints on resources for productivity. For example, some Icelandic lakes have phytoplankton production levels of >100 g C/m²/yr (Jónasson and Adalsteinsson, 1979; Jónasson et al., 1992), contrasting with extremely oligotrophic high-arctic lakes that have phytoplankton production levels of <10 g C/m²/yr (Hobbie, 1984). Although zooplankton are generally limited and at times absent in arctic lakes due to temperature and nutrient limitations, they may be quite abundant in shallow lakes where there is a lack of predators. For example, more than 30 Cladocera species have been documented in certain Finnish Lapland lakes, although generally most of them contain fewer than 10 species (Korhola, 1999; Rautio, 2001). Benthic invertebrate species diversity and abundance also display high latitudinal and inter-lake variability and may be significant in shallow lakes and ponds (Chapin and Körner, 1994; Hansen, 1983; Hobbie, 1984; Jørgensen and Eie, 1993; Vadeboncoeur et al., 2003). For example, in lakes of the Svalbard region, chironomid larvae are often numerically dominant but display low diversity (~10 species; Hirvenoja, 1967; Planas, 1994; Styczynski and Rakusa-Suszczewski, 1963), while more than 49 species have been identified in more southerly Norwegian lakes. Fish in arctic lakes are generally not very diverse, ranging from a few species (one to three) in lakes of Greenland (Riget et al., 2000), Iceland (Sandlund et al., 1992), the Faroe Islands, northwest Scandinavia, and the Kola Peninsula, up to several tens of species near the Pechora River in Russia. These fish may be anadromous or landlocked, depending on life histories and lake–river networks.

In general, tundra ponds tend to have very low annual primary productivity, dominated by macrophytes and benthic bacteria and algae (Hobbie, 1980). The detrital food web is highly important in these systems and phytoplankton growth is limited by nutrients and light. Zooplankton are abundant because fish are mostly absent in these shallow systems; hence, algal turnover is rapid in response to heavy grazing by herbivorous zooplankton (Hobbie, 1980). Pond vegetation typically includes horsetail (*Equisetum* spp.), water smartweed (*Polygonum*

amphibium), duckweed (*Lemna* spp.), and pondweed (*Potamogeton* spp.)(Zhadin and Gerd, 1961), and the resulting plant detritus tends to be mineralized rather than grazed upon. Figure 8.6 illustrates a typical tundra pond food web.

Ponds, as well as lakes and wetlands (discussed below), provide habitat that is critical to a wide variety of waterfowl, as well as small mammals. Typical waterfowl in the Arctic include the Canada goose (*Branta canadensis*), bean goose (*Anser fabalis)*, snow goose (*A. caerulescens*), black brent (*B. bernicla*), eider (*Somateria mollissima*), oldsquaw duck (*Clangula hyemalis*), red-throated loon (*Gavia stellata*), yellow-billed loon (*G. adamsii*), Arctic loon (*G. arctica*), tundra swan (*Cygnus columbianus*), ring-necked duck (*Aythya collaris*), canvasback duck (*A. valisineria*), greater scaup (*A. marila*), and king eider (*S. spectabilis*). Some of the most severely endangered species in the world, including the once-abundant Eskimo curlew (*Numenius borealis*), the Steller's eider (*Polysticta stelleri*), and the spectacled eider (*S. fischeri*), are dependent on arctic freshwater systems (Groombridge and Jenkins, 2002). These and other bird species have been affected by a combination of factors such as over-harvesting and changes in terrestrial habitat quality and quantity or some perturbation at sea related to climate variability and/or change (CAFF, 2001; Groombridge and Jenkins, 2002). Coastal and inland wetlands, deltas, and ponds are common feeding and breeding grounds for many species of waterfowl in the spring and summer months. Some more southerly or subarctic ponds, small lakes, and wetlands can also contain thriving populations of aquatic mammals such as muskrat and beaver (*Castor canadensis*).

Wetlands

Wetlands are among the most abundant and biologically productive aquatic ecosystems in the Arctic, and occur most commonly as marshes, bogs, fens, peatlands, and shallow open waters (Mitsch and Gosselink, 1993; Moore J., 1981). Approximately 3.5 million km² of boreal and subarctic peatlands exist in Russia, Canada, the United States, and Fennoscandia (Gorham, 1991). Arctic wetlands are densely distributed in association with river and coastal deltas (e.g., the Lena and Mackenzie Deltas), and low-lying landscapes (e.g., the Finnish and Siberian lowlands and substantive portions of the Canadian Interior Plain). Wetlands are generally less abundant in Region 4 (up to 50% in isolated areas).

Wetlands are a common feature in the Arctic due in large part to the prominence of permafrost and the low rates of evapotranspiration. Aside from precipitation and meltwater, wetlands may also be sustained by groundwater, as is the
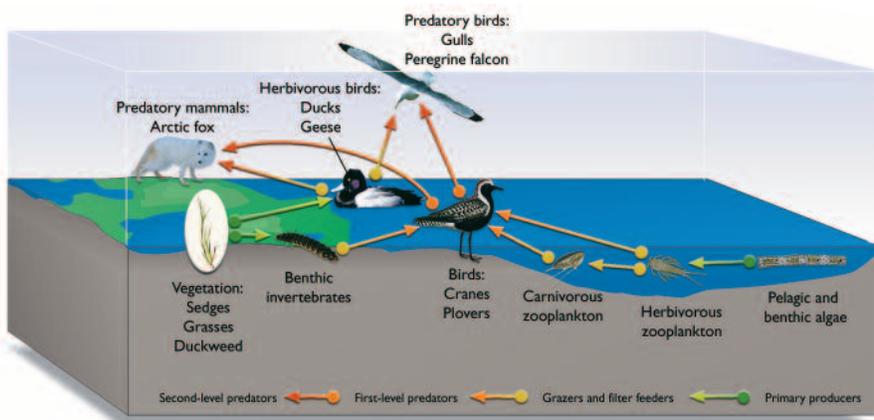

Fig. 8.6. Representative food web in arctic tundra ponds (adapted from AMAP, 1997).

case for fens, which are more nutrient-rich, productive wetland systems than bogs, which are fed solely by precipitation. Arctic wetlands may have standing water in the ice-free season or, as in the case of peatlands, may have sporadic and patchy pools. The occurrence of these pools exhibits high seasonal and interannual variability resulting from heat and water fluxes, and high spatial variability resulting from peatland microtopography. As such, arctic wetlands often have a diverse mosaic of microhabitats with different water levels, flow characteristics, and biota. The biogeochemistry of arctic wetlands is also generally distinct from other arctic freshwater systems, with lower dissolved oxygen concentrations, more extreme reducing conditions in sediments, and more favorable conditions for biodegradation (Wetzel, 2001).

Arctic wetlands are highly productive and diverse systems, as they often are important transition zones between uplands and more permanent freshwater and marine water bodies. They are typically dominated by hydrophytic vegetation, with a few species of mosses and sedges, and in some instances terrestrial species such as lichens, shrubs, and trees (e.g., forested bogs in the mountains of Siberia). Insects such as midges (chironomids) and mosquitoes are among the most abundant fauna in arctic wetlands (Marshall et al., 1999). Peatland pools in arctic Finland, for example, host thriving popu-

lations of midges that are more abundant and have greater biomass in areas of standing water than in semi-terrestrial sites, and are an important food source for many peatland bird species (Paasivirta et al., 1988).

Aside from habitat provision, river-flow attenuation, and a number of other ecological functions, wetlands also store and potentially release a notable amount of carbon, with potential positive feedbacks to climate change (e.g., radiative forcing by methane – CH_4 and carbon dioxide – CO_2). It is estimated that northern peatlands store approximately 455 Pg of carbon (Gorham, 1991), which is nearly one-third of the global carbon pool in terrestrial soils. As well, northern wetlands contribute between 5 and 10% of global CH_4 emissions (UNEP, 2003). The role of arctic and subarctic wetlands as net sinks or sources of carbon (Fig. 8.7) is highly dependent on the seasonal water budget and levels; the brief and intense period of summer primary productivity (during which photosynthetic assimilation and respiration of CO_2, and bacterial metabolism and CH_4 generation, may be most active); soil type; active-layer depth; and extent of permafrost. Methane and CO_2 production can occur beneath the snowpack and ice of arctic wetlands. Winter and particularly spring emissions can account for a significant proportion of the annual total efflux of these gases (e.g., West Siberia; Panikov and Dedysh, 2000). Arctic wetlands typically represent net sources of carbon during spring melt and as plants senesce in autumn, shifting to net carbon sinks as leaf-out and growth progress (e.g., Aurela et al., 1998, 2001; Joabsson and Christiensen, 2001; Laurila et al., 2001; Nordstroem et al., 2001). The future status of wetlands as carbon sinks or sources will therefore depend on
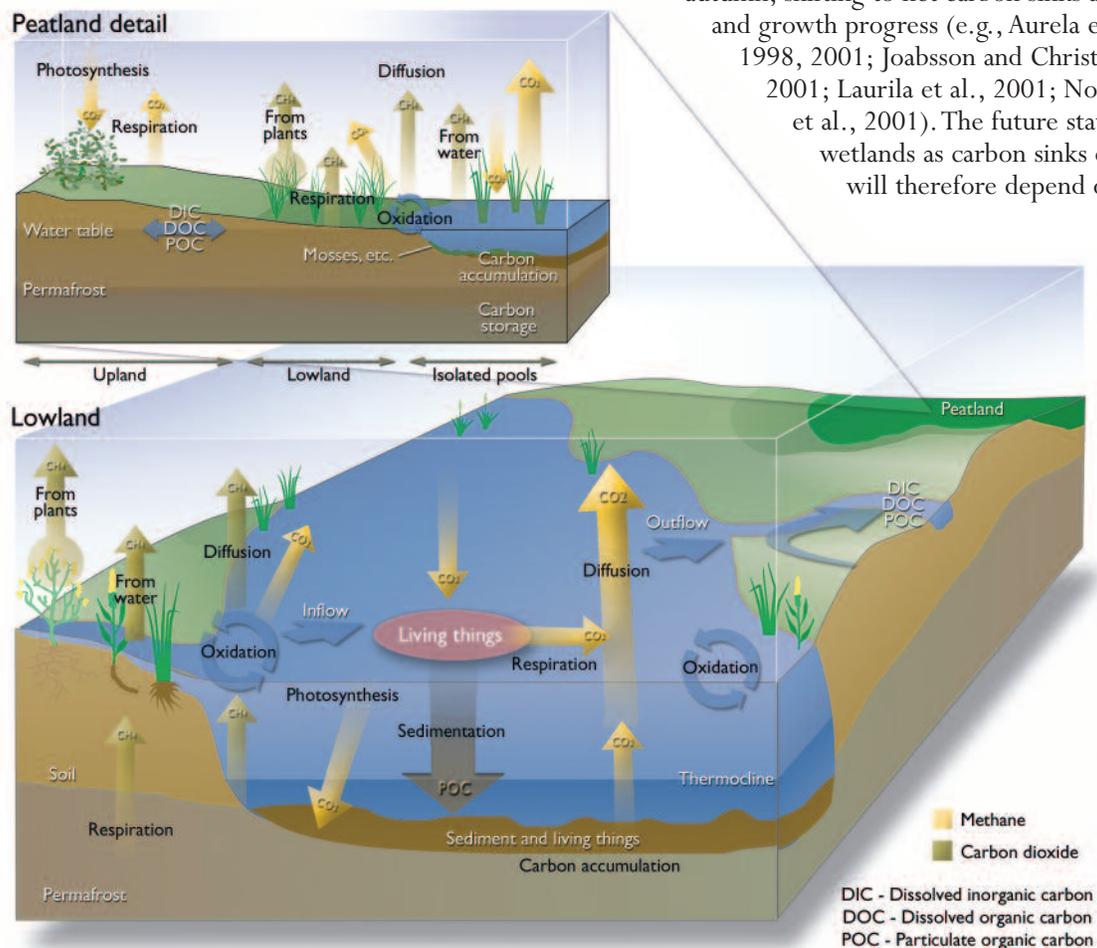

Fig. 8.7. Simplified schematic of carbon cycling in high-latitude aquatic ecosystems.

changes in vegetation, temperature, and soil conditions. Similarly, carbon cycling in lakes, ponds, and rivers will be sensitive to direct (e.g., rising temperatures affecting rates of carbon processing) and indirect (e.g., changes in catchments affecting carbon loading) effects of climate change. Section 7.5 provides a more detailed treatment of carbon cycling and dynamics in Arctic terrestrial and aquatic landscapes.

8.3. Historical changes in freshwater ecosystems

Analysis of the stability, sensitivity, rate, and mode of the response of freshwater ecosystems to past climate change has proven to be a valuable tool for determining the scope of potential responses to future climate changes. Preserved records of ecosystem variations (e.g., trees, fossils, and sedimentary deposits), combined with dating techniques such as carbon-14, lead-210, or ring/varve counting, have been a primary source of information for unraveling past environmental changes that pre-date the age of scientific monitoring and instrumental records. The application of climate change proxies in paleoclimatic analysis has traditionally relied on identification of systematic shifts in ecosystem patterns known from modern analogues or by comparison with independent instrumental or proxy climate records to determine perturbations in climate-driven environmental conditions such as growing-season length, solar insolation, temperature, humidity, ice-cover extent and duration, or hydrologic balance. Such ecosystem-based climate proxies may include the presence, distribution, or diversity of terrestrial, aquatic, or wetland species or assemblages; changes in water or nutrient balances recorded by chemical or isotopic changes; changes in growth rates or characteristics of individual plants and animals; or changes in physical environments (e.g., lake levels, dissolved oxygen content) that are known to be linked to the productivity and health of freshwater ecosystems.

The reliability of and confidence in these ecosystem indicators of climate change has been enhanced through development of spatial networks of paleoclimatic data, by comparison with instrumental climate records where available, and through concurrent examination of abiotic climate change proxies in nearby locations. Such abiotic proxy records include shifts in the isotopic composition of glacial deposits (and to some extent permafrost or pore water), which provide regional information about changes in origin, air-mass evolution, and condensation temperature of precipitation (or recharge); changes in summer melt characteristics of glacial deposits or sedimentary and geomorphological evidence such as the presence of laminated lake sediments (varves), the latter of which are indicative of water depths great enough to produce stratified water columns and meromixis; and variations in varve thicknesses in lakes and fining/coarsening sequences or paleoshoreline mapping that can be used to reconstruct shifts in lake or sea levels.

8.3.1. Ecosystem memory of climate change

The accumulation of ecosystem records of environmental change relies on the preservation of historical signals in ice caps, terrestrial deposits (soils, vegetation, permafrost), and aquatic deposits (wetlands, rivers, lakes, ice), coupled with methods for reconstructing the timing of deposition. As continuity of deposition and preservation potential are not equal in all environments, there is a systematic bias in the paleoclimatic record toward well-preserved lentic environments, and to a lesser extent wetlands, as compared to lotic systems. The following sections describe common archives and the basis of key memory mechanisms.

8.3.1.1. Lentic archives

Biological indicators of environmental change that are preserved in lake sediments include pollen and spores, plant macrofossils, charcoal, cyanobacteria, algae including diatoms, chrysophyte scales and cysts and other siliceous microfossils, biogenic silica content, algal morphological indicators, fossil pigments, bacteria, and invertebrate fossils such as Cladocera, chironomids and related Diptera, ostracods, and fish (Smol, 2002). In general, the best biological indicators are those with good preservation potential, for example, siliceous, chitinized, or (under neutral to alkaline pH conditions) carbonaceous body parts. They also must be readily identifiable in the sedimentary record, and exist within assemblages that have well-defined ecosystem optima or tolerances. Lentic records commonly extend back 6000 to 11000 years to the time of deglaciation in the circumpolar Arctic.

In general, fossil pollen and spores, plant macrofossils, and charcoal are used to determine temporal shifts in terrestrial ecosystem boundaries, notably past fluctuations in northern treeline and fire history. Pollen and spores from emergent plants may also be useful indicators for the presence and extent of shallow-water environments. Preserved remains of aquatic organisms, such as algae and macrophytes, provide additional information on aquatic ecosystem characteristics and lake-level status. Such indicators, which are used to reconstruct ecological optima and tolerances for past conditions, are normally applied in conjunction with surface-sediment calibration datasets to quantitatively compare present-day ecosystem variables or assemblages with those preserved in the sediment record (Birks, 1995, 1998; Smol, 2002). Douglas and Smol (1999) provide details on the application of diatoms as environmental indicators in the high Arctic, and Smol and Cumming (2000) provided a general treatment of all algal indicators of climate change. Biological indicators useful for lake-level reconstructions include the ratio of planktonic to littoral Cladocera as an index of the relative size of the littoral zone or water depth of northern lakes (Korhola and Rautio, 2002; MacDonald G. et al., 2000a). Chironomids and diatoms may be used in a similar manner. While such information allows for quantitative reconstruction of lake levels, errors in projecting lake water

depth from Cladocera, chironomids, and diatoms may be large (Korhola et al., 2000a; Moser et al., 2000; see also MacDonald G. et al., 2000a). Cladoceran remains may also provide evidence of changes in species trophic structure, including fish (Jeppesen et al., 2001a, b, 2003), and chironomids may be used to reconstruct changes in conductivity mediated by variations in runoff and evaporation (Ryves et al., 2002).

Due to their small volume and minimal capacity to buffer climate-driven changes, the shallow lakes and ponds characteristic of large parts of the Arctic may be well suited for hydrological and climate reconstructions. Past shifts in diatom assemblages have been used to track habitat availability for aquatic vegetation, the extent of open-water conditions, shifts in physical and chemical characteristics, and water levels (Moser et al., 2000).

Isotopic analysis (e.g., $\delta^{13}C$, $\delta^{18}O$, $\delta^{15}N$) of fossil material, bulk organic sediments, or components such as cellulose or lignin can provide additional quantitative information. For example, carbon and oxygen isotope analysis of sediment cellulose has been applied in many parts of the circumpolar Arctic (MacDonald G. et al., 2000a). It relies on the key assumptions that fine-grained cellulose in offshore sediments (excluding woody material, etc.) is derived from aquatic plants or algae and that the cellulose–water fractionation is constant (Wolfe B. et al., 2002). Often the source of material (aquatic versus terrestrial) can be confirmed from other tests such as carbon–nitrogen ratios (Wolfe B. et al., 2002), although these two assumptions may not be applicable in all arctic systems (Sauer et al., 2001). Under ideal conditions, the $\delta^{18}O$ signals in aquatic cellulose are exclusively inherited from the lake water and therefore record shifts in the water balance of the lake (i.e., input, through-flow, residency, and catchment runoff characteristics; Gibson J.J. et al., 2002). Studies of ice cores from Greenland and arctic islands support the interpretation of $\delta^{18}O$ signals and other climate proxies across the circumpolar Arctic (Smol and Cumming, 2000). Ice-core records of past precipitation ($\delta^{18}O$, δ^2H) can help to distinguish climatically and hydrologically driven changes observed in lake sediment records.

Stratigraphic reconstructions using $\delta^{13}C$, $\delta^{14}C$, or $\delta^{15}N$ measured in aquatic cellulose and fossil material can likewise be used to examine changes in ecosystem carbon and nitrogen cycles and ecosystem productivity. Trends in chemical parameters such as dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and total nitrogen can also be reconstructed from fossil diatom assemblages as demonstrated for lakes in the treeline region of the central Canadian Arctic (Rühland and Smol, 2002), Fennoscandia (Seppä and Weckström, 1999), and elsewhere.

While lakes are nearly ideal preservation environments, lake sediment records may not always offer unambiguous evidence of climate-induced ecosystem changes. Other factors not driven by climate, including selective preser-

vation of some organisms (Rautio et al., 2000), erosion or deepening of outlets, damming by peat accumulation, or subsequent permafrost development, can alter lake records (Edwards et al., 2000). Such problems are overcome to some extent by using multi-proxy approaches, by comparing multiple lake records, and by using spatial networks of archives. Further research on modern ecosystems, especially processes controlling the preservation and modification of proxy records, is still required in many cases to reconcile present and past conditions.

8.3.1.2. Lotic archives

Sedimentary deposits in lotic systems are often poorly preserved compared to lentic systems, owing to the relatively greater reworking of most riverine deposits. However, preservation of at least partial sediment records can occur in fluvial lakes, oxbow lakes, estuaries, and artificial reservoirs. Past river discharge can also be studied by tracking the abundance of lotic diatoms in the sediments of lake basins, such as demonstrated for a lake in the high Arctic (Douglas et al., 1996; Ludlam et al., 1996).

8.3.1.3. Terrestrial and wetland archives

Tree rings are a traditional source of climate change information, although there are obvious difficulties in applying the method to tundra environments with sparse vegetation. Conifers are, however, abundant within the circumpolar Arctic (particularly in northwestern Canada, Alaska, and Eurasia), with the northernmost conifers in the world located poleward of 72º N on the Taymir Peninsula, northern Siberia (Jacoby et al., 2000). Tree-ring widths increase in response to warm-season temperatures and precipitation/moisture status and have been used to reconstruct climate changes, in many cases for more than 400 years into the past (Jacoby et al., 2000; Overpeck et al., 1997).

Diatoms, chrysophytes, and other paleolimnological indicators are also preserved in peatlands and may be used to reconstruct peatland development and related water balance and climatic driving forces (Moser et al., 2000). Records of $\delta^{13}C$ and $\delta^{18}O$ from peat cellulose also provide information on climatic variability (Hong et al., 2001), although this method has not been widely applied to date in the Arctic. Selective use of pore water from within peat and permafrost has also been utilized to reconstruct the isotopic composition of past precipitation (Allen et al., 1988; Wolfe B. et al., 2000), although dating control is often imprecise.

8.3.2. Recent warming: climate change and freshwater ecosystem response during the Holocene

The climate of the earth has continuously varied since the maximum extent of ice sheets during the late Pleistocene (e.g., Gajewski et al., 2000). The most recent climate warming trend during the industrial peri-

od overprints Holocene climate shifts that have occurred due to orbit-induced variations in solar insolation, as well as oscillations produced by local to regional shifts in sea surface temperatures, atmospheric and oceanic circulation patterns, and the extent of land-ice cover (MacDonald G. et al., 2000a). During the early Holocene (10 000–8000 years BP), orbital variations (the Milankovitch (1941) theory of a 41 000-year cycle of variation in orbital obliquity) resulted in approximately 8% higher summer insolation and 8% lower winter insolation compared to present-day values poleward of 60° N (Kutzbach et al., 1993). This directly altered key factors controlling arctic freshwater systems, including precipitation, hydrology, and surface energy balance. Sea level was also 60 to 80 m below present-day levels, providing an expanded zone (up to several hundred kilometers wide) of nearshore freshwater environments.

During the Holocene, rapidly melting ice sheets presented a shrinking barrier to major airflows, and variations in insolation altered the spatial distribution of atmospheric heating (MacDonald G. et al., 2000a). Several climate heating episodes between 11 000 and 7700 years BP are attributed to the catastrophic drainage of Lake Agassiz and the Laurentide glacial lakes in North America. Paleogeographic data from this interval suggest that the Laurentide Ice Sheet was almost completely gone, with the possible exception of residual ice masses in northern Québec. In general, most of the Arctic experienced summers 1 to 2 °C warmer than today during the early to middle Holocene (Overpeck et al., 1997). A common assumption is that decreases in summer insolation resulted in cooler summers in the late Holocene, which culminated in the Little Ice Age (ca. 1600). This cooling trend ended sometime in the 18th century. Detailed reconstructions of climate and ecosystems in North America at 6000 years BP (Gajewski et al., 2000) confirm that the Holocene was also a time of increased moisture, resulting in the spread of peatlands. In the European Arctic, combined evidence from oxygen isotope and pollen-inferred precipitation records, cladoceran-inferred lake levels, diatom-inferred lake-water ionic strength, and elemental flux records of erosion intensity into lakes, all suggest more oceanic conditions in the region during the early part of the Holocene than today, with a shift towards drier conditions between approximately 6000 and 4500 years BP (Hammarlund et al., 2002; Korhola et al., 2002c). In the late Holocene, there has been a general tendency towards increased moisture, resulting in more effective peat formation (Korhola, 1995).

Despite pervasive orbit-driven forcings, climate changes during the Holocene varied significantly between regions of the Arctic due to differences in moisture sources (Overpeck et al., 1997). In general, arctic Europe, eastern Greenland, the Russian European North, and the North Atlantic were dominated by Atlantic moisture sources; Siberia was dominated by Nordic Seas moisture; Chukotka, the Bering Sea region, Alaska, and the western Canadian Arctic were dominated by Pacific moisture; and northeastern Canada, the
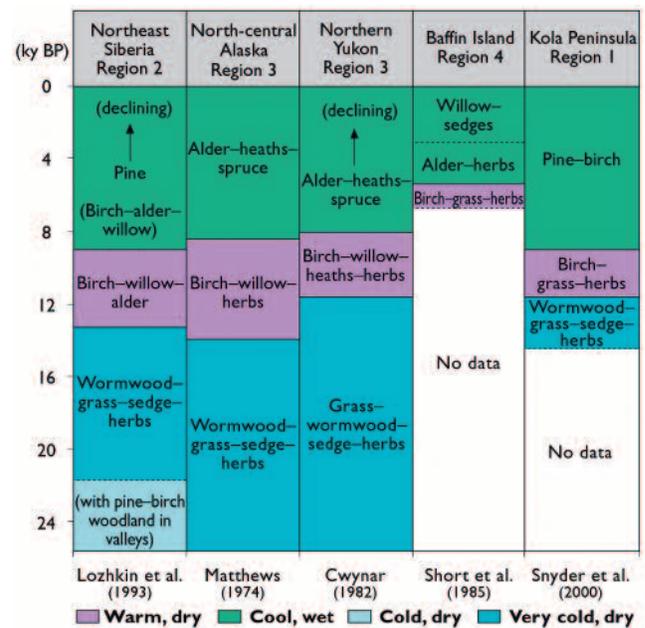
Fig. 8.8. Pollen record of regional arctic climate change (after I. Hutchinson, Simon Fraser University, British Columbia, pers. comm., 2004).

Labrador Sea and Davis Strait regions, and western Greenland were dominated by Labrador Sea and Atlantic moisture. The following sections describe significant regional differences in climate and ecosystem evolution during the Holocene (Fig. 8.8). Much of the subsequent discussion focuses on historical changes in hydroclimatology (e.g., atmospheric moisture sources) and terrestrial landscape features (e.g., vegetation) in the context of their primary control over the water cycle affecting freshwater ecosystems. More details about these changes can be found in sections 2.7 and 7.2.

8.3.2.1. Region 1: Arctic Europe, eastern Greenland, the Russian European North, and the North Atlantic

The present-day climate in northern Fennoscandia is dominated by westerly airflow that brings cyclonic rains to the area, especially during winter (see Seppä and Hammarlund, 2000). The Scandes Mountains of mid-central Sweden mark the boundary between oceanic climate conditions to the west and more continental conditions to the east, especially in northern Finland and Russia, which are strongly influenced by the Siberian high-pressure cell that allows easterly air flow into northern Fennoscandia during winter. Climate and freshwater ecosystem changes during the Holocene have been attributed largely to fluctuations in the prevailing air circulation patterns in the region. Pollen, diatom, chironomid, and oxygen isotope records from lake sediments have been used to reconstruct climate conditions and ecosystem responses during the Holocene (e.g., Korhola et al., 2000b, 2002c; Rosén et al., 2001; Seppä and Birks, 2002; Seppä and Hammarlund, 2000). These studies suggest that northern Fennoscandia was a sparse, treeless tundra environment following final disintegration of the Scandinavian Ice Sheet (10 000–9000

years BP) until birch (*Betula* spp.) forests spread to the shores of the Arctic Ocean and to an altitude of at least 400 m in the mountains between 9600 and 8300 years BP (see section 7.2 for discussion of changes in terrestrial vegetation). Increased moisture during this period has been attributed to strengthening of the Siberian High which may have enhanced sea-level pressure gradients between the continent and the Atlantic Ocean, strengthened the Icelandic Low, and produced greater penetration of westerly winter storms and increased snowfall over western Fennoscandia (see also Hammarlund and Edwards, 1998). Associated strengthening of westerlies and northward shifts in the Atlantic storm tracks may also have produced higher snowfall in Greenland during this period (MacDonald G. et al., 2000a).

The decline of birch forests was accompanied by rapid increases in pine (*Pinus* spp.) forests between 9200 to 8000 years BP in the extreme northeast and 7900 to 5500 years BP in the western and southwestern parts of the region, signaling a shift toward drier summers and increased seasonality (Seppä and Hammarlund, 2000). Pollen evidence suggests that the late-Holocene treeline retreat in northern Norway and Finland started about 5000 years BP, and included southward retreat of treeline species of both pine and birch, which were subsequently replaced by tundra vegetation. This retreat has been attributed to decreased summer insolation during the latter part of the Holocene. It has also been suggested that later snowmelt and cooler summers gradually favored birch at the expense of pine along the boreal treeline. Similar climate changes may explain peatland expansion in the late Holocene within both boreal and tundra ecozones (Seppä and Hammarlund, 2000).

The response of aquatic ecosystems to the climate-induced changes during the Holocene has been inferred from lake-sediment and peat stratigraphic records. The very dry period corresponding to shifts from birch to pine corresponds to increasing frequency of diatom and cladoceran taxa indicating lake-level reduction and vegetation overgrowth of numerous lakes (Seppä and Hammarlund, 2000). Likewise, diatom and cladoceran evidence suggest dry warm summers during the period dominated by pine (~7000–3500 years BP).

There have been a variety of recent quantitative reconstructions of Holocene changes and variability in climatic and environmental variables through analysis of isotopic records and sedimentary remains of pollen, diatom assemblages, and/or chironomid head capsules from arctic and subarctic lakes in northern Sweden (Bigler and Hall, 2002, 2003; Bigler et al., 2002, 2003; Korhola et al., 2000b, 2002c; Rosén et al., 2001; Seppä et al., 2002; Shemesh et al., 2001). Comparative analyses revealed that the timing and scale of development of historical biotic assemblages were attributable to local geology, site-specific processes such as vegetation development, climate, hydrological setting, and in-lake biogeochemical and ecological processes. Several general climate-related trends were deduced for the region: a decrease in the

average annual temperature of approximately 2.5 to 4 °C from the early Holocene to the present; summer temperatures during the early Holocene that were 1.7 to 2.3 °C above present-day measurements; winter temperatures that were 1 to 3 °C warmer than at present during the early Holocene; and a decrease in lake-water pH since the early Holocene.

Collectively, proxy records for closed-basin (i.e., a basin that has very little continuous surface outflow so that water-level variations strongly mirror changes in precipitation or moisture status) lakes suggest that water levels were high during the early Holocene, declined during the mid-Holocene dry period (~6000–4000 years BP), and rose again during the latter part of the Holocene. During the culmination of the Holocene dry period, many shallower water bodies in this region decreased greatly in size or may have dried up entirely (Korhola and Weckström, 2005).

In contrast to often quite distinct changes in physical limnology, changes in chemical limnological conditions have been relatively moderate during lake development in the Fennoscandian Arctic and on the Kola Peninsula (Korhola and Weckström, 2005; Solovieva and Jones, 2002). Because of changing climate and successional changes in surrounding vegetation and soils, lakes close to the present treeline are typically characterized by a progressive decline in pH, alkalinity, and base cations, and a corresponding increase in DOC over the Holocene. In contrast, lakes in the barren arctic tundra at higher altitudes manifest remarkable chemical stability throughout the Holocene. Excluding the initial transient alkaline period following deglaciation evident at some sites, the long-term natural rate of pH decline in the arctic lakes of the region is estimated to be approximately 0.005 to 0.01 pH units per 100 yr. This is a generally lower rate than those of more southerly sites in boreal and temperate Fennoscandia, where rates between 0.01 and 0.03 pH units per 100 yr have been observed. No evidence of widespread recent "industrial acidification" is apparent from extensive paleolimnological assessments in arctic Europe (Korhola and Weckström, 2005; Korhola et al., 1999; Sorvari et al., 2002; Weckström et al., 2003). However, fine-resolution studies from a number of remote lakes in the region demonstrate that aquatic bio-assemblages have gone through distinct changes that parallel the post-19th century arctic temperature increase (Sorvari et al., 2002).

8.3.2.2. Region 2: Siberia

Siberian climate was affected by increased summer insolation between 10 000 and 8000 years BP, which probably enhanced the seasonal contrast between summer and winter insolation and strengthened the Siberian High in winter and the Siberian Low in summer (Kutzbach et al., 1993). Following final disintegration of the Scandinavian Ice Sheet approximately 10 000 to 9000 years BP, cool easterlies were replaced by predominantly westerly flows from the North Atlantic, which now could penetrate

western Russia and Siberia (Wohlfarth et al., 2002). Warm, wet summers and cold, dry winters probably dominated the early to mid-Holocene, with more northerly Eurasian summer storm tracks, especially over Siberia (MacDonald G. et al., 2000a). Warm periods were generally characterized by warmer, wetter summer conditions rather than by pronounced changes in winter conditions, which remained cold and dry. Pollen reconstructions from peatlands across arctic Russia suggest that temperatures were 1 to 2 °C higher than at present during the late glacial–Holocene transition, which was the warmest period during the Holocene for sites in coastal and island areas. The warmest period of the Holocene for non-coastal areas (accompanied by significantly greater precipitation) occurred between 6000 and 4500 years BP, with notable secondary warming events occurring at about 3500 and 1000 years BP (Andreev and Klimanov, 2000).

Pollen evidence from permafrost and peat sequences suggests that boreal forest development commenced across northern Russia and Siberia by 10000 years BP, reached the current arctic coastline in most areas between 9000 and 7000 years BP, and retreated south to its present position by 4000 to 3000 years BP (MacDonald G. et al., 2000b). Early forests were dominated by birch, but larch (*Larix* spp.), with some spruce (*Picea* spp.) became prevalent between 8000 and 4000 years BP. The northward expansion of the forest was facilitated by increased solar insolation at the conclusion of the Scandinavian glaciation, and by higher temperatures at the treeline due to enhanced westerly airflow (MacDonald G. et al., 2000b). The eventual southward retreat of the treeline to its present-day position is likewise attributed to declining summer insolation towards the late Holocene, as well as cooler surface waters in the Norwegian, Greenland, and Barents Seas (MacDonald G. et al., 2000b).

Increases in precipitation in some portions of northern Russia occurred during the interval from 9000 to 7000 years BP, followed by gradual drying to 6000 years BP (Andreev and Klimanov, 2000; Wolfe B. et al., 2000). This has been attributed to strengthening of the sea-level pressure gradients that also affected climate and ecosystems in Region 1 at this time (see MacDonald G. et al., 2000a).

Northward migration of the treeline also had a systematic impact on the ecosystem characteristics of some Siberian lakes. For a lake in the Lena River area, diatom assemblages dated prior to treeline advance were found to be dominated by small benthic *Fragilaria* species, and diatom indicators also suggest high alkalinity and low productivity at this time. Following the treeline advance, lakes shifted to stable diatom assemblages dominated by *Achnanthes* species and low alkalinity, attributed to the influence of organic runoff from a forested landscape. Re-establishment of *Fragilaria*-dominated assemblages and higher alkalinity conditions accompanied the subsequent reversion to shrub tundra. Laing et al. (1999) attributed recent declines in alkalinity and minor changes in diatom assemblages to the influx of humic substances from catchment peatlands.

8.3.2.3. Region 3: Chukotka, the Bering Sea, Alaska, and western Arctic Canada

The Laurentide Ice Sheet strongly influenced early Holocene (10000–9000 years BP) climate in northwestern North America, particularly in downwind areas. High albedos, cold surface conditions, and ice-sheet height apparently disrupted westerly airflows (or may possibly have maintained a stationary surface high-pressure cell with anticyclonic circulation), which promoted the penetration of dry, warm air from the southeast (MacDonald G. et al., 2000a). Dry conditions were also prevalent at this time in unglaciated areas such as northwestern Alaska and portions of the Yukon, where a 60 to 80 m reduction in sea level increased distances to marine moisture sources by several hundred kilometers. Biological indicators from Alaskan lakes suggest dry, more productive conditions, with lower lake levels between 11000 and 8000 years BP, followed by a gradual shift to modern moisture levels by 6000 years BP (Barber and Finney, 2000; Edwards et al., 2000).

Terrestrial vegetation (and the northern treeline) clearly indicates a warmer-than-present early Holocene (e.g., Spear, 1993). Vegetation shifts reconstructed mainly from fossil pollen evidence reveal the northward advance and southward retreat of the boreal forest in western North America, which has been attributed mainly to short-term changes in atmospheric circulation and associated storm tracks (i.e., shifts in the mean summer position of the Arctic Frontal Zone; MacDonald G. et al., 1993). Higher temperatures and increased moisture during the mid-Holocene (especially between about 5000 and 3500 years BP) also produced episodes of 250 to 300 km northward advances of the treeline that are recorded in the isotopic, geochemical, diatom, and fossil-pollen records of lakes near present-day treeline in the Yellowknife area of Canada (MacDonald G. et al., 1993). Additional evidence for significant changes in diatom community structure (shifts from planktonic to benthic forms) and increased productivity is recorded in lake sediments during this mid-Holocene warming interval (ca. 6000 to 5000 years BP) in the central Canadian subarctic (Pienitz and Vincent, 2000; Wolfe B. et al., 2002). This period was also accompanied by significant increases in DOC in lakes, lower water transparency, and less exposure to photosynthetically active radiation (PAR) and UV radiation in the water column. On the Tuktoyaktuk Peninsula (near the Mackenzie Delta), forest limits were at least 70 km north of the current treeline between 9500 and 5000 years BP (e.g., Spear, 1993). Permafrost zones were also presumably located north of their present-day distribution during this period. In general, present-day forest types were established in Alaska by 6000 years BP and northwestern Canada by approximately 5000 years BP.

Prolonged development and expansion of peatlands in North America commencing between 8000 and 6000 years BP have been attributed to progressive solar-insolation driven moisture increases towards the late Holocene (MacDonald G. et al., 2000a).

## Box 8.1. Northern Québec and Labrador: Long-term climate stability

Northern Québec and Labrador in the eastern Canadian Low Arctic is a landscape dominated by lakes, wetlands, and streams. Few studies have addressed the effects of recent climate change in this region, but a variety of paleolimnological studies have provided insights into long-term change.

This region is comprised of four terrestrial ecozones: "taiga shield" with bands and patches of wetland forest, forest-tundra, and lichen-woodland vegetation; "southern arctic" consisting of shrub tundra; "northern arctic" consisting of true tundra; and "arctic cordillera" (the Torngat Mountains). Major changes in the chemical and biological characteristics of lakes are associated with the transition between these different vegetation types, notably changes in alkalinity and, in particular, colored dissolved organic matter (CDOM; see section 8.6.1, Box 8.10). The darkest water color (greatest CDOM concentrations) is associated with the heavily vegetated wetland-forest catchments, while much lower values occur in lakes completely surrounded by drier lichen woodland and tundra (see figure). As dissolved organic matter has a broad range of effects on high-latitude aquatic ecosystems (Vincent and Pienitz, 1996), this implies that any climate-related shift in catchment vegetation is very likely to have major impacts on the limnology of these eastern Canadian lakes.

Colored dissolved organic matter (measured by relative water color) in lakes from different vegetation zones in Labrador. Values shown represent the mean of between 7 and 20 lakes (data from Fallu et al., 2002).

In the western Canadian subarctic, variations in climate over the last 5000 years caused large shifts in the position of the northern treeline. These shifts resulted in substantial changes in water color, the underwater light regime (including biologically damaging UV radiation exposure), and in the relative importance of benthic versus pelagic production (as indicated by their diatom communities; MacDonald G. et al., 1993; Pienitz and Vincent, 2000; Pienitz et al., 1999). In contrast, the eastern Canadian subarctic seems to have experienced relatively little change in vegetation structure at the millennial timescale. The stable forest–tundra of northern Québec and Labrador has been referred to as "an ecological museum" (Payette et al., 2001), and is partly a consequence of the extremely slow pace of northward migration and colonization by black spruce (*Picea mariana*) during periods of warming. This region also appears to be less prone to temperature change owing to the strong marine influence of the Hudson Strait and Labrador Current outflows from the Arctic. Like much of the eastern Canadian Arctic and southern Greenland, this region has shown little temperature change or even cooling from the mid-1960s to the mid-1990s, while most other sectors of the circumpolar Arctic have shown strong warming trends over the same period (Capellen and Vraae Jørgensen, 2001; Weller, 1998).

The paleolimnology of the region also reflects this long-term stability in climate and vegetation. Diatom assemblages in the sediment cores taken from Labrador lakes show very little change over the last 200 years, while there were major shifts in community structure elsewhere in the Arctic (Laing et al., 2002). Similarly, in a lake at the northern Québec treeline, CDOM and other inferred limnological variables remained relatively stable over the last 3000 years. For example, the mean inferred DOC concentration over this period is 5 mg/l, with a coefficient of variation for 107 strata of only 8% (Ponader et al., 2002). Coastal lakes in this region exhibited major changes associated with plant succession immediately after deglaciation, and isostatic uplift causing the severing of connections with the sea, but relatively constant conditions over the last 1000 years (Pienitz et al., 1991; Saulnier-Talbot and Pienitz, 2001; Saulnier-Talbot et al., 2003).

This remarkable stability at timescales of decades, centuries, and millennia suggests that northern Québec and Labrador lakes are likely to experience less short-term climate change relative to other regions of the circumpolar Arctic. Projections from the ACIA-designated climate models, however, suggest that these east–west differences in climate change will largely disappear by 2080 (see section 4.4.2), by which time the lakes, rivers, and wetlands of northern Québec and Labrador will begin experiencing the climate impacts that are well advanced in other regions.
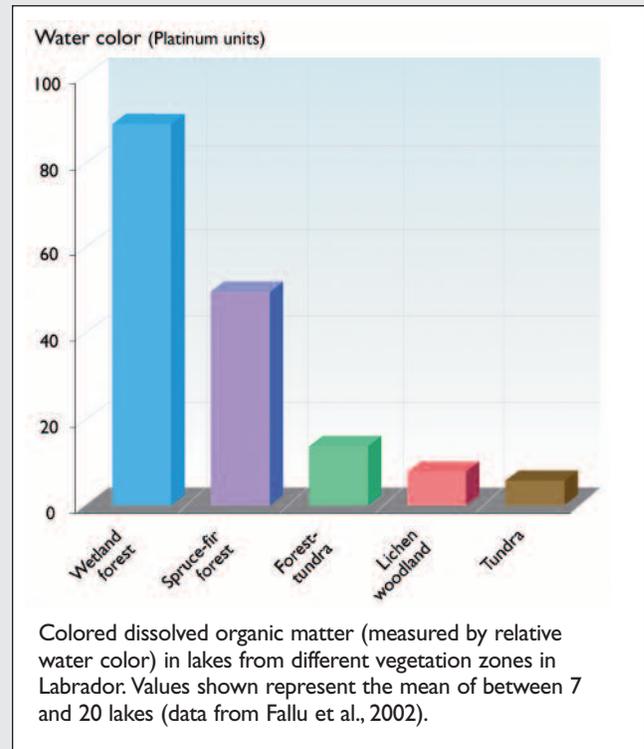
8.3.2.4. Region 4: Northeastern Canada, Labrador Sea, Davis Strait, and West Greenland

The climate change and ecosystem response in northeastern Canada is distinguished from northwestern regions by generally colder conditions during the early Holocene because of delayed melting of ice sheet remnants until close to 6000 years BP. Consequently, tundra and taiga with abundant alder (*Alnus* spp.) covered more of Labrador and northern Québec than at present (Gajewski et al., 2000). Shrub tundra and open boreal forest were also denser than at present (Gajewski et al., 2000). Warming in the eastern Arctic reached a maximum shortly after 6000 years BP, with higher sea surface temperatures and decreased sea-ice extent. Peatland expansion was apparently similar to that of northwestern Canada, and is likewise attributed to insolation-driven increases in moisture and cooler conditions in the late Holocene. In contrast with other parts of the circumpolar north, this region has had a relatively stable climate over the last few thousand years but may experience significant temperature increases in the future (see Box 8.1 and projections of future temperature increases in section 4.4.2).

8.3.3. Climate change and freshwater ecosystem response during the Industrial Period

An abrupt shift in the rate of climate and related ecosystem changes occurred around 1840 that distinguish these impacts from those due to climate change observed during the preceding part of the Holocene. A compilation of paleoclimate records from lake sediments, trees, glaciers, and marine sediments (Overpeck et al., 1997) suggests that in the period following the Little Ice Age (~1840 until the mid-20th century), the circumpolar Arctic experienced unprecedented warming to the highest temperatures of the preceding 400 years. The last few decades of the 20th century have seen some of the warmest periods recorded, thus continuing this early industrial trend. The effects of this increase in temperature include glacial retreat, thawing permafrost, melting sea ice, and alteration of terrestrial and aquatic ecosystems. These climate changes are attributed to increased atmospheric concentrations of greenhouse gases, and to a lesser extent shifts in solar irradiance, decreased volcanic activity, and internal climate feedbacks. Examples of profound responses to the recent temperature increases relevant to freshwater systems are numerous. Selected examples are given below.

Sorvari and Korhola (1998) studied the recent (~150 years) environmental history of Lake Saanajärvi, located in the barren tundra at an elevation of 679 m in the northwestern part of Finnish Lapland. They found distinctive changes in diatom community composition with increasing occurrences of small planktonic diatoms starting about 100 years ago. Since no changes in lake water pH were observed, and because both airborne pollution and catchment disturbances are known to be almost nonexistent in the region, they postulated that recent arctic temperature increases are the main reason for the observed ecological change.

To further test the hypothesis that temperature increases drove the system, Korhola et al. (2002b) analyzed additional sedimentary proxy indicators from Lake Saanajärvi. The biological and sedimentological records were contrasted with a 200-year climate record specifically reconstructed for the region using a compilation of measured meteorological data and various proxy sources. They found synchronous changes in lake biota and sedimentological parameters that seemed to occur in parallel with the increasing mean annual and summer temperatures starting around the 1850s, and hypothesized that the rising temperature had increased the metalimnion steepness and thermal stability in the lake, which in turn supported increasing productivity by creating more suitable conditions for the growth of plankton.

Sorvari et al. (2002), using high-resolution (3–10 yr) paleolimnological data from five remote and unpolluted lakes in Finnish Lapland, found a distinct change in diatom assemblages that parallels the post-19th century arctic temperature increase detected by examination of regional long-term instrumental data, historical records of ice cover, and tree-ring measurements. The change was predominantly from benthos to plankton and affected the overall diatom richness. A particularly strong relationship was found between spring temperatures and the compositional structure of diatoms as summarized by principal components analysis. The mechanism behind the change is most probably associated with decreased ice-cover duration, increased thermal stability, and resultant changes in internal nutrient dynamics.

Douglas et al. (1994), using diatom indicators in shallow ponds of the high Arctic (Ellesmere Island), found relatively stable diatom populations over the past 8000 years, but striking successional changes over the past 200 years. These changes probably indicate a temperature increase leading to decreased ice- and snow-cover duration and a longer growing season (Douglas et al., 1994). Although temperature changes are difficult to assess, they were sufficient to change the pond communities. In these ponds, there are no diatoms in the plankton; however, a shift occurred from a low-diversity, perilithic (attached to rock substrates) diatom community to a more diverse periphytic (attached to plants) community living on mosses.

Diatom indicators in lakes also show shifts in assemblages, most likely caused by temperature increases over the past 150 years. Rühland et al. (2003) documented changes in 50 lakes in western Canada between 62° and 67° N, spanning the treeline. Shifts in diatoms from *Fragilaria* forms to a high abundance of the planktonic *Cyclotella* forms are consistent "with a shorter duration of ice cover, a longer growing season, and/or stronger thermal stratification patterns", such as a shift from unstratified to stratified conditions.

Char Lake on Cornwallis Island, Canada (74° N) is the most-studied high-arctic lake. Recent studies (Michelutti et al., 2002) show no change in water quality over time but do show a subtle shift in diatom assemblages as evidenced in the paleolimnological record. These changes are consistent with recent climate changes (1988–1997) and are probably a result of "reduced summer ice cover and a longer growing season". Section 6.7.2 reviews recently documented observations of the general, although not ubiquitous, decline in the duration of lake and river ice cover in the Arctic and subarctic.

Chrysophyte microfossils show changes that parallel diatom changes (Wolfe A. and Perren, 2001) and are also probably related to reduced ice-cover duration. For example, chrysophyte microfossils were absent or rare in Sawtooth Lake (Ellesmere Island, 79° N) over the past 2500 years but suddenly became abundant 80 years ago. Similarly, in Kekerturnak Lake (Baffin Island, 68° N), planktonic chrysophytes increased greatly in the upper sediments dated to the latter part of the 20th century. In contrast, lakes in regions without tem-

perature increases show no change in sediment-based indicators. For example, Paterson et al. (2003) found no change in chrysophyte and diatom indicators over the past 150 years in the sediment of Saglek Lake (northern Labrador, Canada).

This section has provided documented changes in some aspects of freshwater ecosystems driven by climate shifts in the recent past. As such, it provides a baseline against which future effects of climate change can be both projected and measured.

8.4. Climate change effects

8.4.1. Broad-scale effects on freshwater systems

Arctic freshwater systems are particularly sensitive to climate change because numerous hydro-ecological processes respond to even small changes in climate. These processes may adjust gradually to changes in climate, or abruptly as environmental or ecosystem thresholds are exceeded (Box 8.2). This is especially the case for cryo-

Box 8.2. Thresholds of response: step changes in freshwater systems induced by climate change

Some climate change effects projected for arctic freshwaters are likely to result in small, slow responses in the environment; other changes are likely to exceed environmental or ecosystem thresholds and cause a dramatic switch in organisms or a change of state of the system. Thresholds may be physical (e.g., permafrost is likely to begin to slowly thaw when the mean annual air temperature approaches 0 °C); chemical (e.g., the bottom waters of a lake are likely to lose all oxygen when lake productivity increases or allochthonous carbon increases); or biological (e.g., insect larvae frozen in the bottom of tundra ponds will die when their temperature falls below -18 °C; Scholander et al., 1953). While thresholds are only a part of the whole picture of response, they are critical to the understanding and assessment of the full scope of climate change impacts.

One obvious physical threshold is the amount of heat necessary to melt the ice cover of a lake. At the northern limit of the terrestrial Arctic, such as on Ellesmere Island, there are lakes that have only recently begun to have open water during the summer; other lakes now have open water for more summers every decade than in the past. Sediment records of algae, in particular diatom species and chrysophyte abundance, show that in Finland and northern Canada, lakes were ice-bound for thousands of years but conditions began to change about 150 years ago. With open water, the algal community shifts from a predominance of benthic diatoms to planktonic forms, and chrysophytes begin to occur. This is the result of an increase in summer air temperatures caused by climate change and the earlier onset of melt. Some scientists believe that the likely increase in growing-season length may also be important in controlling algal species. Shifts in species composition at the level of primary producers are also likely to have consequences for higher trophic levels through the alteration of food pathways. This could possibly lead to local extirpation of benthic and planktonic animals, as well as overall shifts in productivity.

Another physical threshold is the onset of stratification in lakes. Once lakes begin to have open water, wind-driven water circulation becomes one of the controls of biological processes. Almost all lakes have a period of complete mixing of the water column immediately after the ice cover disappears. Very cold waters may continue to circulate for the entire summer so that each day algae spend a significant amount of time in deep waters where there is not enough light for growth. When a lake stratifies (i.e., when only the uppermost waters mix), algae have better light conditions and primary production increases. The higher temperatures in the upper waters increase the rates of all biotic processes. There is a threshold, probably tied to increased primary production, when entirely new trophic levels appear. For example, the sediment record from a lake in Finland shows that Cladocera, a type of zooplankton, began to appear around 150 years ago. Most lakes in the Arctic already exhibit summer stratification, so this threshold will apply mostly to lakes in the far north.

When air temperatures increase above a mean annual air temperature of -2 °C, permafrost begins to thaw. When the upper layers of ice-rich permafrost thaw, the soil is disturbed; lakes may drain, and ponds form in

spheric components that significantly affect the water cycle of lakes, rivers, and ponds; the habitat characteristics of these freshwater systems; and the flora and fauna that occupy them. In the case of large arctic rivers (e.g., the Lena, Mackenzie, Ob, and Yenisey), the effects of climate change must be evaluated for areas outside of as well as within the Arctic. The dynamics of such large systems depend on hydrologic processes prevailing within their water-rich headwaters in more temperate southern latitudes. In addition, many of these headwater areas are regulated in some way, a factor that may interact in some way with downstream arctic climate change impacts.

Prior to considering the specific effects of climate change on arctic freshwater systems, it is useful to place the climate projections generated by the five ACIA-designated atmosphere–ocean general circulation models (AOGCMs) for the Arctic as a whole into a more suitable freshwater context. For the most part, this requires focusing on model projections for the major arctic terrestrial landscapes, including some extra-arctic headwater areas, since these are the domains of freshwater

systems. The following paragraphs review the ACIA-designated model projections (primarily for the final time slice, 2071–2090, to illustrate the most pronounced changes) and, through additional processing of the model projections, provide a perspective on how such changes may be important to broad-scale features of arctic freshwater ecosystems, and a background template for the subsequent discussions of specific effects.

For the area north of 60º N, the five ACIA-designated models project that the mean annual temperature will increase by 3.7 ºC (five-model average) between the 1981–2000 baseline and the 2071–2090 time slice, or approximately twice the projected increase in global mean annual temperature (section 4.4.2). At a global scale, AOGCMs used in the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2001b) project that it is very likely that nearly all land areas, which include freshwater systems, will warm more rapidly than the global average, particularly during the cold season at northern high latitudes. Within the Arctic, the spatial distribution of the projected tempera-

depressions. In eastern Siberia, newly thawed soils that are rich in organic matter slump into lakes. Microbial action depletes the oxygen in the lake allowing the bacteria to produce so much methane that the lakes and ponds become a significant source of this greenhouse gas, and enhance an important feedback to the climate system. This threshold is likely to affect lakes in the more southerly regions of the Arctic.

It is well known that lakes surrounded by shrubs and trees contain much more colored dissolved organic matter (CDOM; see section 8.6.1, Box 8.10) than lakes in the tundra zone. The CDOM comes from the organic matter produced by plants and modified by soil microbes. It strongly absorbs light, such that the algae of the upper waters become light limited and primary production is reduced. This may also be accompanied by a shift towards increasing primary production by attached algae in the shallow inshore zone relative to offshore planktonic production. The threshold described here is related to the treeline, often demarcated by patches rather than a continuous zone of vegetation. As air temperatures increase over the 21st century these patches are likely to expand, fuse, and move further north, resulting in a slowly moving band of affected lakes. Extreme polar-desert catchments in the high Arctic are very likely to experience their first arrival of higher plants, and a sudden increase in the transfer of organic materials from land to water.

As lakes warm, some species or populations of species will probably reach a temperature threshold for survival. This threshold is linked to increases in the rate of metabolism and growth. For example, a bioenergetic model based on laboratory studies projects that the young-of-the-year lake trout in northern Alaska will not obtain enough food for growth if their metabolic rate rises in response to a temperature increase of a degree or so. Evidence from field studies of a stream fish, the Arctic grayling (*Thymallus arcticus*), also suggests that a population at the northern limit of its distribution is unlikely to survive an increase of only a few degrees in summer water temperatures. Both these examples are of fish species at the northern limit of their distribution. Other types of widely distributed fish, such as whitefish and Arctic char, are less likely to be affected unless new competing species arrive from southerly regions.

A different type of threshold involves a shift in the ecological behavior of migratory fish such as the Arctic char. In many arctic rivers, char migrate to the sea for some months every year; the productive marine food web allows them to grow to a large size. Local fishers harvest many of these sea-run fish in the rivers each time the fish congregate and migrate. When freshwaters become more productive, migrations to the sea are projected to decrease and may eventually cease, thus the char are likely to remain in freshwater rivers and lakes for the entire year. These freshwaters are much less productive than the marine ecosystems; therefore, adult freshwater char are likely to be much smaller than are migrating char. As a result of climate change, a valuable food resource for arctic peoples is likely to change with respect to sizes available, and could possibly be lost.

ture increases in terrestrial areas is associated with even greater projected temperature increases over the central Arctic Ocean. For example, the five-model average projects that autumn (October–December) temperatures over large areas of the Arctic Ocean will increase by up to 9 °C by 2071–2090 compared to the 1981–2000 baseline (section 4.4.2). Adjacent to the Arctic Ocean, the models project substantial temperature increases for extensive terrestrial areas, with the largest projected temperature increases closest to the coastal margins and decreasing to the south.

This pattern of temperature increases is likely to have serious implications for high-latitude coastal areas such as the Russian polar desert and northern tundra, where

temperature and associated species distribution gradients are steep (e.g., vascular species abundance increases five-fold from north to south on the Taymir Peninsula; see section 7.3.1.1). Figure 8.9a shows the spatial pattern of October warming projected for the 2071–2090 time slice. (Note the spatial congruence of warming between the ocean and the adjacent arctic coastal zone and the extension to more southerly latitudes.) Areas where projected temperature increases are particularly pronounced include northern Siberia and the western portions of the Canadian Archipelago. Notably, however, the maximum projected air temperature increases in these areas are about 5 °C (greatest near the coasts), compared to the almost two-fold greater projected increases in temperature over the Arctic Ocean. Such pronounced potential temperature increases in freshwater systems in October are particularly important because this is typically the time when freshwater lake and river systems along the coastal margins currently experience freeze-up. Employing a typical rate of change for freeze-up of 1 day per 0.2 °C increase in temperature (Magnuson et al., 2000), the projected temperature increases could cause delays of up to 25 days in freeze-up by 2071–2090. This is likely to have the greatest effect on higher-latitude, near-coastal freshwater systems (see also sections 8.4.3.1 and 6.7.3).

Even more dramatic temperature increases are projected for coastal land areas in November (Fig. 8.9b). Significant temperature increases are projected for most coastal areas in Region 3 and more southerly latitudes in Region 2, including the headwater regions of the major Siberian Arctic rivers below 60° N. Latitudinal gradients of temperature increases are especially important for arctic freshwater systems because of the influence of extra-arctic basins on the timing and magnitude of flow in the major northward-flowing arctic rivers. In the case of Region 2, projected temperature increases in November south of 60° N are significant because this is typically the month that marks the beginning of major snow accumulation. Similar to the delay in freeze-up, such higher temperatures would effectively decrease the length of time available to accumulate a winter snowpack. This would subsequently be reflected in the magnitude of the spring snowmelt that forms the major hydrologic event of the year at northern latitudes and is known to significantly affect downstream arctic river and delta systems. The effect of a reduced period of winter snow accumulation on the freshet magnitude, however, is likely to be offset by the projected increase in winter precipitation. The terrestrial regions of North America and Eurasia are among the areas with the greatest projected precipitation increases; similar to temperature, the largest increases are projected for autumn and winter (section 4.4.3). Although caution must be used in interpreting regional trends from the simulated precipitation patterns because of large variations in model projections, the average of the five ACIA-designated model projections also shows winter increases in precipitation for the extra-arctic headwater regions of the large northern rivers (Fig. 8.10). The degree to which this would compensate for

Fig. 8.9. Change in mean monthly air temperature between 1981–2000 and 2071–2090 projected by the ACIA-designated models (five-model average) for (a) October and (b) November.
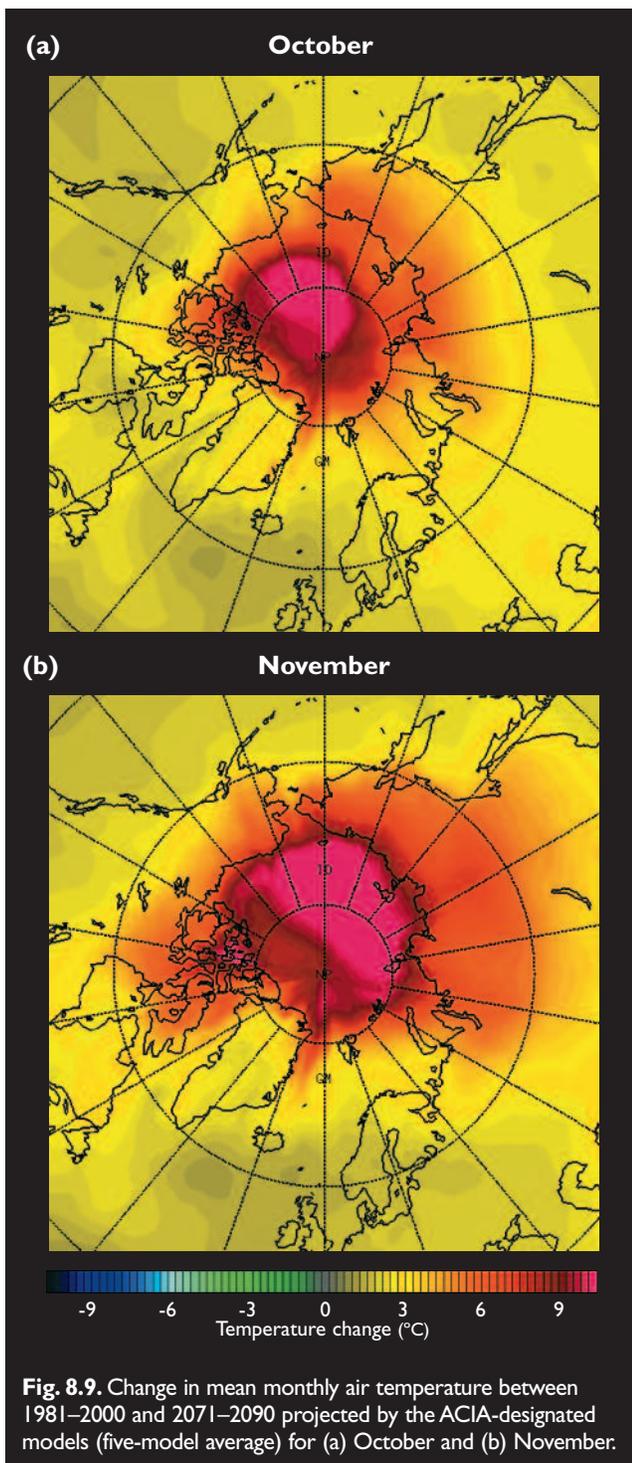
the reduced duration of winter snow accumulation, however, requires detailed regional analysis.

Over the terrestrial regions of the northern latitudes, it is the cold season (defined here as October to May, the current period of dominant snow and ice cover for freshwater systems) that is characterized by the steepest latitudinal gradients in projected temperature increases. Figure 8.11 displays the projected changes in average temperature (from the ACIA 1981–2000 baseline) over terrestrial areas for the four ACIA regions broken into three latitudinal bands of 70°–85°, 60°–70°, and 50°–60° N. The latter represents the zones of higher precipitation that feed the major arctic rivers in Region 2 (Lena, Ob, and Yenisey) and eastern Region 3 plus western Region 4 (Mackenzie River). The steepest latitudinal gradients in projected cold-season temperature increases are evident in Regions 1 and 3, becoming particularly magnified in the latter by 2071–2090, whereas Region 4 shows a slight decrease in the level of warming with latitude. Hence, except for Region 4, it appears that with continued temperature increases the higher-latitude zones will continue to experience the relatively highest degree of warming. This would lead to a reduction in the thermal gradient along the course of some of the major arctic rivers. If such reductions prevail during particular parts of the cold season, they are likely to have major implications for the dynamics of particular hydrologic events such as the spring freshet and ice breakup.

In general, the most severe spring floods on cold-regions rivers are associated with a strong climatic gradient between the headwaters and the downstream reaches –
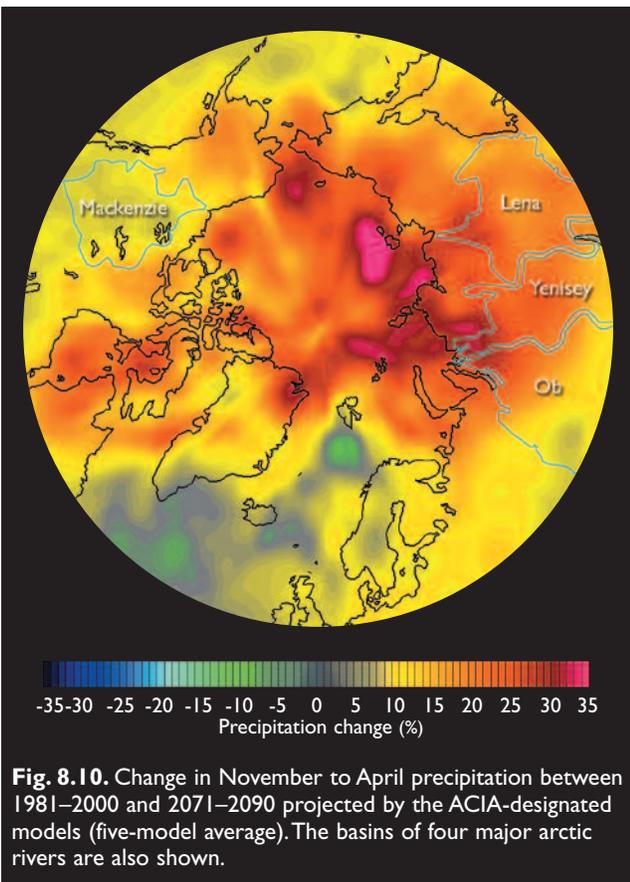
typically from south to north on most large arctic rivers (e.g., Gray and Prowse, 1993). In such cases, the spring flood wave produced by snowmelt must "push" downstream into colder conditions, and hence towards a relatively competent ice cover that has experienced little thermal decay. Changes in the strength of this climatic gradient would alter the severity of breakup and the associated flooding. Figure 8.12a illustrates the change in average air temperature projected for April 2071–2090. This is currently the month of freshet initiation, with May the primary month of freshet advance, in the southern headwaters of the major arctic rivers. With projected advances in the timing of ice and flow conditions (see also section 6.7.3), April should become the primary month of freshet advance by 2071–2090. Of particular note in Fig. 8.12a are the substantial projected temperature increases in the downstream areas of the major Russian rivers. Such high-latitude temperature increases are likely to lead to less severe ice breakups and flooding as the spring flood wave pushes northward. A comparable degree of high-latitude temperature increase is absent for the Mackenzie River. Of additional note in Fig. 8.12 is the degree of warming projected to occur in the headwater regions of the three large Russian
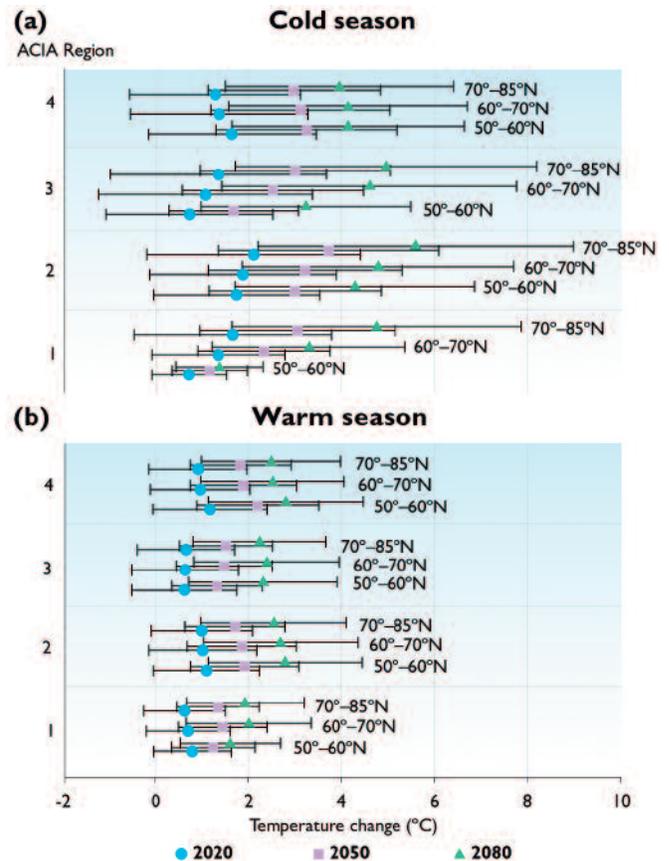
Fig. 8.11. Changes in mean air temperature projected by the ACIA-designated models (five-model average) for the land areas of the four ACIA regions at three time slices in three latitudinal bands. Error bars represent standard deviation from the mean. The (a) cold season (October–May) and (b) warm season (June–September) were divided based on approximate ice-covered and open-water conditions prevailing in the current climate for major freshwater systems located in the 60°–70° N band. Longer (shorter) duration ice-covered periods prevail in the more northerly (southerly) latitudinal band.

Fig. 8.10. Change in November to April precipitation between 1981–2000 and 2071–2090 projected by the ACIA-designated models (five-model average). The basins of four major arctic rivers are also shown.

rivers during April and March. This is very likely to result in an early onset of snowmelt along these rivers. Again, however, a comparable degree of headwater warming and hence snowmelt runoff is not projected for the Mackenzie Basin. This regional dichotomy is likely to produce future differences in the spring timing of lake- and river-ice breakup and associated freshet, including the ultimate export of freshwater to the Arctic Ocean.

Although the smallest temperature increases are projected for the open-water warm season in all regions and at all latitudes (Fig. 8.11b), even the projected ~1 to 3 °C temperature increase is likely to significantly increase evaporative losses from freshwater systems, especially

with a shortened ice season, and via evapotranspiration from the terrestrial landscape that feeds them. Similar to changes in winter snowpack, increases in precipitation could offset such temperature-induced evaporative losses, but the five-model average projects that precipitation increases will be smallest during the summer. More detailed consideration of the changes and effects on cold-regions hydrology that could result from the changes in climate projected by the ACIA-designated models are provided in subsequent sections and in Chapter 6.

8.4.2. Effects on hydro-ecology of contributing basins

The regional patterns of projected changes in temperature and precipitation reviewed in the previous section are useful to understand some of the broad-scale effects that may occur. Specific effects, however, will be much more diverse and complex, even within regions of similar temperature and precipitation changes, because of intra-regional heterogeneity in freshwater systems and the surrounding landscapes that affect them. For example, elevational difference is one physical factor that will produce a complex altered pattern of snow storage and runoff. Although warmer conditions are very likely to reduce the length of winter, snow accumulation could either decrease or increase, with the latter most likely to occur in higher-elevation zones where enhanced storm activity combined with orographic effects will probably increase winter snowfall. Increased accumulation is likely to be most pronounced at very high elevations above the elevated freezing level, where the summer season is likely to remain devoid of major melt events, thereby creating the conditions for the preservation of more semi-permanent snowpacks at high altitudes (Woo, 1996). In contrast, temperature increases at lower elevations, especially in the more temperate maritime zones, are likely to increase rainfall and rain-on-snow runoff events. Snow patterns will be affected by a number of other factors, including vegetation, which is also projected to be altered by climate change (section 7.5.3.2). For example, shifts from tundra vegetation to trees have led to greater snow interception and subsequent losses through sublimation (e.g., Pomeroy et al., 1993), whereas shifts from tundra to shrubs have been shown to reduce snow losses (Liston et al., 2002), thereby affecting the magnitude of the snowpack available for spring melt.

An advance of the spring warming period means that snowmelt will occur during a period of lower insolation, which, other things being equal, will lead to a more protracted melt and less intense runoff. Traditional ecological knowledge indicates that through much of northern Canada, including the western Canadian Arctic and Nunavut, spring melt is already occurring earlier than in the past, and spring air temperatures are higher (Krupnik and Jolly, 2002), although observations near eastern Hudson Bay indicate a delay in the initiation of spring melt (McDonald M.A. et al., 1997). See Chapter 3 for local accounts of such changes in the Arctic. The effects of early and less intense spring melt will be most
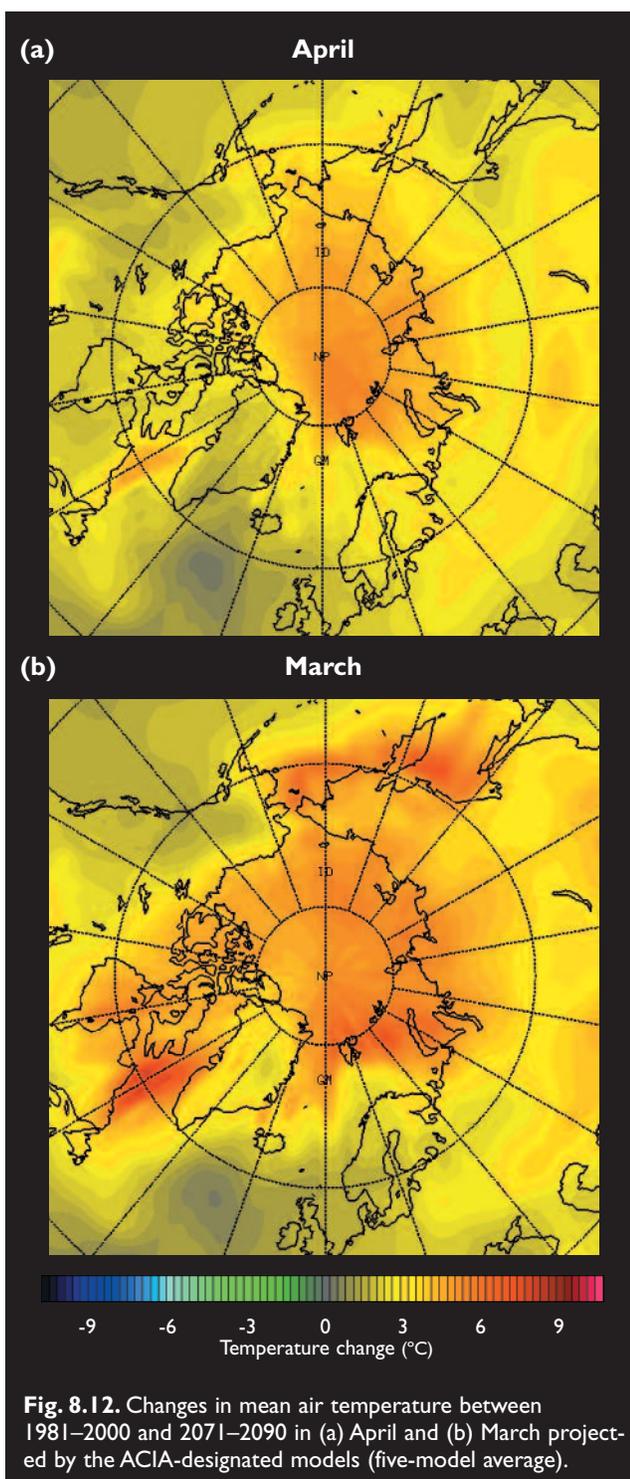

Fig. 8.12. Changes in mean air temperature between 1981–2000 and 2071–2090 in (a) April and (b) March projected by the ACIA-designated models (five-model average).

dramatic for catchments wholly contained within the northern latitudes, where snowmelt forms the major and sometimes only flow event of the year. Reductions in the spring peak will be accentuated where the loss of permafrost through associated warming increases the capacity to store runoff, although there will also be a compensating increase in summer base flow. Overall, the magnitude and frequency of high flows will decline while low flows will increase, thereby flattening the annual hydrograph. This impact is similar to that observed as a result of river regulation, and hence will tend to compound such effects.

Loss of permafrost or deepening of the active layer (seasonal melt depth; see section 6.6.1 for changes in permafrost) will also reduce the peak response to rainfall events in summer, increase infiltration, and promote groundwater flow. This is consistent with the analogue of northern basins where those with less permafrost but receiving comparable amounts of precipitation have a lowered and smaller range of discharge (Rouse et al., 1997). Changes in the rate of evapotranspiration and its seasonal duration will also directly affect stream runoff from permafrost basins. As suggested by the modeling results of Hinzman and Kane (1992) for areas of Alaska, the greatest reduction in summer runoff is likely to occur in years experiencing light, uniformly spaced rainfall events whereas in years characterized by major rainfalls comprising most of the summer precipitation, total runoff volume is likely to be affected least.

Changes in the water balance will vary by regional climate and surface conditions, but particular areas and features are believed to be especially sensitive to such alterations. Such is the case for the unglaciated lowlands of many arctic islands where special ecological niches, such as found at Polar Bear Pass on Bathhurst Island or Truelove Lowland on Devon Island, are produced by unique hydro-climatic regimes and are largely dependent on ponded water produced by spring snowmelt. On a broad scale, arctic islands and coastal areas are likely to experience significant changes in local microclimates that will probably affect water balance components, especially evaporation rates. Here, longer open-water seasons in the adjacent marine environments are likely to enhance the formation of fog and low clouds and reduce associated solar radiation. Increased water vapor and lower energy flux would thereby offset any potential increase in evaporation resulting from higher air temperatures (Rouse et al., 1997).

Large regional differences in water balance will also occur because of differences in plant communities (see also section 7.4.1). For example, surface drying of open tundra is restricted when non-transpiring mosses and lichens overlie the tundra. Over the longer term, a longer growing season combined with a northward expansion of more shrubs and trees will very probably increase evapotranspiration. Quite a different situation is very likely to exist over the multitude of wetlands that occupy so much of th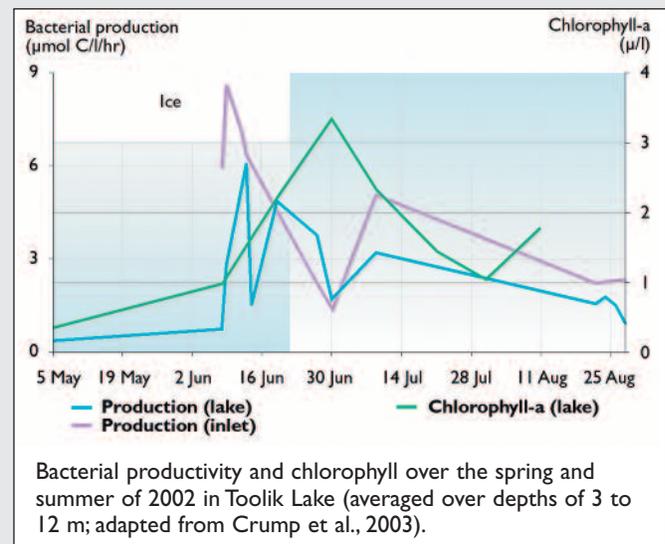e northern terrain. Although evaporation is inhibited after initial surface drying on those wetlands covered by sphagnum moss or lichen, evapotranspiration continues throughout the summer in wetlands occupied by vascular plants over porous peat soils, and only slows as the water table declines. Higher summer temperatures have the ability to dry such wetlands to greater depths, but their overall storage conditions will depend on changes in other water balance components, particularly snowmelt and rainfall inputs.

As the active layer deepens and more unfrozen flow pathways develop in the permafrost, an enhancement of geochemical weathering and nutrient release is very likely (e.g., phosphorus; Hobbie et al., 1999; see also section 6.6.1.3). Ultimately, this is very likely to affect productivity in arctic freshwater systems such as Toolik Lake, Alaska (Box 8.3). In the short term, the chemical composition of surface runoff and groundwater flows is very likely to change. In addition, suspended sediment loads will very probably increase as a result of thermokarst erosion, particularly in ice-rich locations. Suspended sediment and nutrient loading of northern freshwater systems will probably also increase as land subsidence, slumping, and landslides increase with permafrost degradation, as traditional ecological knowledge has documented in the western Canadian Arctic where the depth of the active layer has increased (Krupnik and Jolly, 2002). Thermokarst erosion is very likely to continue until at least the large near-surface ice deposits are depleted and new surface flow patterns stabilize. Such fluvial-morphological adjustment is likely to be very lengthy, of the order of hundreds of years, considering the time that has been estimated for some northern rivers to reach a new equilibrium after experiencing a major shift in their suspended-sediment regimes (e.g., Church, 1995). A major reason for such a protracted period is the time it takes for new vegetation to colonize and stabilize the channel landforms. The stabilization that will occur in the Arctic under climate change is further complicated by the projected change in vegetation regimes, particularly the northward advance of shrubs and trees (see section 7.5.3.2). Such vegetation shifts will cause further changes in stream water chemistry by altering DOC concentrations. Current data indicate that DOC is negatively correlated with latitude (Fallu and Pienitz, 1999; Rühland and Smol, 1998) and decreases with distance from treeline (Korhola et al., 2002b; Pienitz and Smol, 1994) and along gradients from boreal forest to tundra (Vincent and Hobbie, 2000). Hence, as vegetation shifts from mosses and lichens to grasses and woody species, runoff is very likely to contain increasing concentrations of DOC and particulate detrital material. Verification of enhanced DOC supply associated with northward treeline advance is provided by various paleolimnological and paleoclimatic studies (e.g., Korhola and Weckström, 2005; Seppä and Weckström, 1999; Solovieva and Jones, 2002). Although such increases will be long-term, given the slow rates of major vegetation shifts (see also section 7.5.3.2), earlier increases in DOC and DIC are very likely to result from the earlier thermal and mechanical erosion of the

Box 8.3. Ecological transitions in Toolik Lake, Alaska, in the face of changing climate and catchment characteristics

Toolik Lake (maximum depth 25 m, area 1.5 km^2) lies in the foothills north of the Brooks Range, Alaska, at 68° N, 149° W. The river study site is the headwaters of the Kuparuk River. Details of the research project and related publications are available on the Arctic Long-Term Ecological Research site (http://ecosystems.mbl.edu/ARC/). The mean annual temperature of the area is -9 °C, and annual precipitation is approximately 300 to 400 mm. Permafrost is 200 m thick with an active layer up to 46 cm deep. Acidic tussock tundra covers the hillslopes. Sedges dominate a small area of wetlands in the study site, while the dry uplands have a cover of lichens and heaths. Lakes and streams are ultra-oligotrophic, and are ice-free from July to September with strong summer stratification and oxygen saturation. Stream flow is nival, and carries DOC-enriched spring runoff from peaty catchments to Toolik Lake. Primary producers in Toolik Lake consist of 136 species of phytoplankton, dominated by chrysophytes with dinoflagellates and cryptophytes, as well as diatoms. Annual primary productivity averages 12 g C/m^2 and is co-limited by nitrogen and phosphorus. Zooplankton are sparse.

Fish species are lake trout, Arctic grayling, round whitefish (*Prosopium cylindraceum*), burbot, and slimy sculpin (*Cottus cognatus*), which feed on benthic chironomid larvae and snails, the latter controlling epilithic algae in the lake. Dissolved organic carbon drives microbial productivity (5–8 g C/m^2/yr).

The average air temperature of northern Alaska has increased by nearly 2 °C over the past 30 years. Warming of Alaskan waters will possibly have a detrimental effect on adult grayling, which grow best during cool and wet summers and which may actually lose weight during warm and dry summers (Deegan et al., 1999). Approximately 20 km from Toolik (Hobbie et al., 2003), permafrost temperatures at 20 m depth increased from -5.5 to -4.5 °C between 1991 and 2000. This warming of frozen soils probably accounts for recent increases in stream- and lake-water alkalinity.

Bacterial productivity and chlorophyll over the spring and summer of 2002 in Toolik Lake (averaged over depths of 3 to 12 m; adapted from Crump et al., 2003).

Climate has been shown to have a significant control on the vegetation of the site, which in turn has affected aquatic resources for productivity. Runoff from thawing soils within the catchment of Toolik Lake has affected lake productivity in a number of ways. Dissolved organic carbon from excretion, leaching, and decomposition of plants in the catchment, along with associated humic materials, has been found to reduce photosynthesis in the lake and absorb 99% of the UV-B radiation in the upper 20 cm (Morris et al., 1995). In spring, meltwater carries terrestrially derived DOC and abundant nutrients. Upon reaching the lake, meltwater flows cause a two-week high in bacterial productivity (~50% of the annual total) beneath the lake-ice cover (see figure). This peak in production, which takes place at 2 °C, illustrates that bacteria are carbon- and energy-limited, not temperature-limited, and as such will be indirectly affected by climate change. Phytoplankton biomass and primary production peak soon after the ice leaves the lake, and as solar radiation peaks. The lake stratifies so rapidly that no spring turnover occurs, causing oxygen-depleted bottom waters to persist over the summer. This effect is very likely to be amplified with higher temperatures, and will probably reduce the habitat available to fish species such as lake trout.

Future increases in average air temperature and precipitation are very likely to further affect freshwater systems at Toolik. Lakes will very probably experience early breakup and higher water temperatures. Stream waters are very likely to warm as well, and runoff is very likely to increase, although evapotranspiration could possibly offset increased precipitation. As waters warm, primary production in lakes and rivers at the site is very likely to increase, although most species of aquatic plants and animals are unlikely to change over the 21st century. Lake and river productivity are also very likely to increase in response to changes in the catchment, in particular, temperature increases in permafrost soils and increased weathering and release of nutrients. Increased precipitation will also affect nutrient supply to freshwater systems, and is likely to result in increased decomposition of organic matter in soils (Clein et al., 2000), formation of inorganic nitrogen compounds, and increased loss of nitrogen from land to water. The shift in terrestrial vegetation to predominantly shrubs is very likely to cause greater loading of DOC and humic materials in streams and lakes, and a reduction in UV-B radiation penetration. However, increases in organic matter are likely to have detrimental effects on the stream population of Arctic grayling at this site, resulting in their disappearance in response to high oxygen depletion. Lake trout, on the other hand, are likely to survive but their habitat will probably be slightly reduced by the combination of reduced deep-water oxygen and warmer surface waters.

permafrost landscape (see also section 6.6.1.3). Zepp et al. (2003) and Häder et al. (2003) provided comprehensive reviews of the projected interactive effects of changes in UV radiation levels and climate on DOC and DIC and related aquatic biogeochemical cycles.

Changes in freshwater catchments with climate change will affect not only loadings of nutrients, sediments, DOC, and DIC to freshwater systems but also the transport and transformation of contaminants. Contaminant transport from surrounding catchments to freshwaters is likely to increase as permafrost degrades and perennial snow melts (Blais et al., 1998, 2001; McNamara et al., 1999). The contaminants released from these frozen stores, and those originating from long-range transport and deposition in contributing basins, can then be stored in sediments or metabolized and biomagnified through the food web. Section 8.7 discusses this topic in more detail.

8.4.3. Effects on general hydro-ecology

8.4.3.1. Streams and rivers, deltas, and estuaries

A number of hydrologic shifts related to climate change will affect lakes and rivers, including seasonal flow patterns, ice-cover thickness and duration, and the frequency and severity of extreme flood events. In the present climate, most streams and rivers originating within the Arctic have a nival regime in which snowmelt produces high flows and negligible flow occurs in winter. In areas of significant glaciers, such as on some Canadian and Russian islands, Greenland, and Svalbard, ice melt from glaciers can sustain flow during the summer, whereas many other streams produce summer flow only from periodic rainstorm events unless they are fed by upstream storage in lakes and ponds.

The subarctic contains a much broader range of hydrologic regimes, which vary from cold interior continental (comparable to those of the Arctic) to maritime regimes fed moisture directly from open seas even during winter. Overall, a warmer climate is very likely to lead to a shift toward a more pluvial runoff regime as a greater proportion of the annual precipitation falls as rain rather than snow; the magnitude of the peak of spring snowmelt declines; thawing permafrost increases near-surface storage and reduces runoff peaks; and a more active groundwater system augments base flows.

Enhancement of winter flow will very probably lead to the development of a floating ice cover in some streams that currently freeze to the bed. This is very likely to be beneficial to the biological productivity of arctic streams and fish survival where winter freshwater habitat is limited to unfrozen pools (Craig, 1989; Prowse, 2001a,b). For other arctic streams and rivers, warming is very likely to result in a shortened ice season and thinner ice cover (section 6.7.3). Since river ice is such a major controller of the ecology of northern streams and rivers, there are likely to be numerous significant impacts.

Under conditions of overall annual temperature increases, a delay in the timing of freeze-up and an earlier breakup will very probably reduce the duration of river-ice cover. Data compiled over the last century or more indicate that changes in timing of these events are likely to be at a rate of approximately one day per 0.2 ºC increase in air temperature (Magnuson et al., 2000; see also sections 8.4.1 and 6.7.3). For freeze-up, higher water and air temperatures in the autumn combine to delay the time of first ice formation and eventual freeze-up. If there was also a reduction in the rate of autumn cooling, the interval between these two events would increase. Although all major ice types would continue to form, unless there were also significant changes in the flow regime, the frequency and magnitude of, for example, periods of major frazil ice growth will probably be reduced. This has implications for the types of ice that constitute the freeze-up cover and for the creation of unique under-ice habitats such as air cavities and those influenced by frazil concentrations (Brown et al., 1994; Cunjak et al., 1998; Prowse, 2001b).

Changes in the timing and duration of river ice formation will also alter the dissolved oxygen (DO) regimes of arctic lotic ecosystems. Following freeze-up and the elimination of direct water–atmosphere exchanges, DO concentrations steadily decline, sometimes to near-critical levels for river biota (e.g., Chambers et al., 1997; Power G. et al., 1993; Prowse, 2001a,b). Reductions in ice-cover duration and a related increase in the number of open-water re-aeration zones are very likely to reduce the potential for this biologically damaging oxygen depletion. Such benefits will possibly be offset by the projected enhanced input of DOC and its subsequent oxidation (e.g., Schreier et al., 1980; Whitfield and McNaughton, 1986), the rate and magnitude of which would also be increased as a result of the above-noted higher nutrient loading. Worst-case scenarios would develop on rivers where the flow is already comprised of poorly oxygenated groundwater, such as that supplied from extensive bogs and peatlands. Some rivers in the West Siberian Plain offer the best examples of this situation. Here, the River Irtysh drains large quantities of de-oxygenated water from vast peatlands into the River Ob, resulting in DO levels of only about 5% of saturation (Harper, 1981; Hynes, 1970).

The greatest ice-related ecological impacts of climate change on arctic lotic systems are likely to result from changes in breakup timing and intensity. As well as favoring earlier breakup, higher spring air temperatures can affect breakup severity (Prowse and Beltaos, 2002). While thinner ice produced during a warmer winter would tend to promote a less severe breakup, earlier timing of the event could counteract this to some degree. Breakup severity also depends on the size of the spring flood wave. While greater and more rapid snowmelt runoff would favor an increase in breakup severity, the reverse is true for smaller snowpacks and more protracted melt. Hence, changes in breakup severity will vary regionally according to the variations in winter precipitation and spring melt patterns.

For regions that experience a more "thermal" or less dynamic ice breakup (Gray and Prowse, 1993), the magnitude of the annual spring flood will very probably be reduced. For the many northern communities that historically located near river floodplains for ease of transportation access, reductions in spring ice-jam flooding would be a benefit. In contrast, however, reductions in the frequency and severity of ice-jam flooding would have a serious impact on river ecology since the physical disturbances associated with breakup scouring and flooding are very important to nutrient and organic matter dynamics, spring water chemistry, and the abundance and diversity of river biota (Cunjak et al., 1998; Prowse and Culp, 2003; Scrimgeour et al., 1994). Specifically, ice-induced flooding supplies the flux of sediment, nutrients, and water that is essential to the health of the riparian system; river deltas being particularly dependent on this process (e.g., Lesack et al., 1991; Marsh and Hey, 1989; Prowse and Conly, 2001). More generally, given that the magnitude and recurrence interval of water levels produced by ice jams often exceed those of open-water conditions, breakup is probably the main supplier of allochthonous organic material in cold-regions rivers (Prowse and Culp, 2003; Scrimgeour et al., 1994). In the same manner, breakup serves as an indirect driver of primary and secondary productivity through the supply of nutrients – a common limiting factor for productivity in cold-regions rivers. Even the mesoscale climate of delta ecosystems and spring plant growth depends on the timing and severity of breakup flooding (Gill, 1974; Hirst, 1984; Prowse, 2001a).

River ice is also a key agent of geomorphological change and is responsible for the creation of numerous erosional and depositional features within river channels and on channel floodplains (e.g., Prowse, 2001a; Prowse and Gridley, 1993). Since most geomorphological activity occurs during freeze-up and breakup, changes in the

timing of these events are very unlikely to have any significant effect. If, however, climatic conditions alter the severity of such events, this is likely to affect particular geomorphological processes. Furthermore, breakup events affect the general processes of channel enlargement, scour of substrate habitat, and the removal and/or succession of riparian vegetation. All such major river-modifying processes would be altered by any climate-induced shift in breakup intensity.

In summary, if climate change alters the long-term nature of breakup dynamics, the structure and function of rivers and related delta ecosystems are very likely to be significantly altered with direct effects on in-channel and riparian biological productivity. If, for example, significant reductions in dynamic breakups and the related level of disturbance occur, this will reduce overall biological diversity and productivity, with the most pronounced effects on floodplain and delta aquatic systems.

Owing to the reduced ice-cover season and increased air temperatures during the open-water period, summer water temperatures will very probably rise. Combined with greater DOC and nutrient loadings, higher water temperatures are likely to lead to a general increase in total stream productivity, although it is unclear whether temperature will have a significant direct effect on the processing rate of additional particulate detrital material. Irons et al. (1994), for example, found a comparable rate of litter processing by invertebrates in Michigan and Alaska and concluded that temperature was not a main factor. The effect of increased temperature on processing efficiency by "cold-climate" species of invertebrates, however, has not been evaluated. The effect of enhanced nutrient loading to arctic streams is more predictable. The current nutrient limitation of many arctic streams is such that even slight increases in available phosphorus, for example, will produce a significant increase in pri-

Table 8.1. A synthesis of the potential effects of climate change on arctic estuarine systems from both the bottom-up and top-down ecological perspectives (adapted from Carmack and Macdonald, 2002).

Bottom-up: nutrients/production/biota etc.	Top-down: humans/predators/biota etc.
• More open water, more wind mixing, upwelling and greater nutrient availability for primary producers (+) • More open water, more light penetration especially seasonally hence more primary production (+); potential for increased UV radiation levels (-/?) • Decreased ice cover, decreased ice-associated algal production, and subsequent impacts on pelagic and benthic food webs (-) • Increased basin rainfall, increased export of carbon to nearshore (+) • Increased storms and open water, increased coastal erosion (-), increased sediment loads, nutrients and mixing (+), possibly increased productivity especially in late season (?) but offset by decreased light penetration (-) • Potential positive feedback to climate change processes (e.g., permafrost thawing, release of methane, and increased radiative forcing) (-) • Contaminant inputs, mobilization, or increased fluxes driven by temperature changes will increase availability and biomagnification of contaminants in food chains (-)	• Shifting water masses and currents will affect biotic cues for habitat use and migrations of biota such as fish and marine mammals (?) • Redistribution of grazers will affect underlying trophic structure (-/?) • Climate-induced changes in freshwater, estuarine, and marine habitats seasonally used by anadromous fishes will affect distribution and suitability for use, with consequences for the prey communities and possibly fish availability for humans (-/?) • Physical absence or alteration of seasonality or characteristics of ice platforms will affect ice-associated biota (e.g., polar bears, seals, algae) (-), with cascading consequences for fish (+/-) • Increased open water will facilitate whale migrations (+) but increase predator risk to calves (-); shifts in whale populations may cascade through the trophic structure (e.g., shifted predation on fish by belugas; increased predation on plankton by bowhead whales) with unknown trophic consequences for anadromous and marine fish (?)

Cascading consequences from a human perspective as generally: positive (+); negative (-); neutral (0); or unknown (?).

mary productivity (Flanagan et al., 2003). Where productivity responses of stream biota are co-limited by phosphorus and nitrogen (e.g., as suggested by the experimental results of Peterson B. et al., 1993), increased loadings of both nutrients would be required to sustain high levels of enhanced productivity.

Table 8.1 summarizes the potential impacts of climate change on the dynamics of arctic estuaries (Carmack and Macdonald, 2002). The major factor affecting arctic estuarine systems given the degree of climate change projected by the ACIA-designated models will be the increase in freshwater discharge (section 6.8.3). In some arctic basins, such as the Chukchi Sea, there is presently very little freshwater runoff and consequently no estuarine zones. Increased river discharge could possibly create estuarine areas, providing new habitat opportunities for euryhaline species. In established estuarine systems, such as the Mackenzie River system and the Ob and Yenisey Rivers, increased freshwater input in summer (e.g., Peterson B. et al., 2002) is likely to increase stratification, making these habitats more suitable for freshwater species and less suitable for marine species. There are likely to be shifts in species composition to more euryhaline and anadromous species. In addition, increased freshwater input is likely to deposit more organic material, changing estuarine biogeochemistry and perhaps increasing primary productivity, the positive effects of which will possibly be offset in part by increased resuspension of contaminated sediments in these systems.

A secondary impact of increased freshwater discharge that is of serious concern, particularly for Siberian rivers that traverse large industrialized watersheds, is the potential for increased contaminant input. The Ob and Yenisey Rivers, for example, have high levels of organochlorine contamination compared to the Lena River (Zhulidov et al., 1998), which is considered relatively pristine (Guieu et al., 1996). Larsen et al. (1995) noted that arctic fishes have a life strategy that involves intensive feeding in spring and summer, allowing for the buildup of lipid stores and coping with food shortages in winter. The high body-lipid content of arctic fishes may make them more vulnerable to lipid-soluble pollutants such as polycyclic aromatic hydrocarbons (PAHs) or polychlorinated biphenyls (PCBs). In addition, reduced sea-ice coverage that leads to increased marine traffic is likely to have cascading negative consequences (e.g., pollution, risk of oil spills) for estuarine systems.

Arctic deltas provide overwintering habitat for many species that tolerate brackish waters. These areas are maintained as suitable habitat by a combination of continuous under-ice freshwater flow and the formation of the nearshore ice barrier in the stamukhi zone (area of grounded, nearshore ice pressure ridges). As temperatures rise, the seasonal ice zone of estuaries is likely to expand and the ice-free season lengthen (Carmack and Macdonald, 2002). Disruption of either the flow regime or the ice barrier could possibly have profound effects on the availability of suitable overwintering habitat for

desired fish species. Given that such habitat is probably limited and hence limits population abundance, the consequences for local fisheries will probably be significant. In addition, in early winter, subsistence and commercial fisheries target fish that overwinter in deltas. Thinning ice is likely to limit access to these fisheries.

Similar to freshwater systems, ecological control of marine systems can be viewed from bottom-up (i.e., nutrients–production–biota linkages) and/or top-down (i.e., human activities–predators–keystone biota) perspectives (Parsons, 1992). The special role of ice as both a habitat and a major physical force shaping the estuarine and nearshore arctic environment suggests that climate change will work in both modes to affect these systems (Carmack and Macdonald, 2002). One example is the loss of the largest epishelf lake (fresh and brackish water body contained behind the ice shelf) in the Northern Hemisphere with the deterioration and break up of the Ward Hunt ice shelf (Mueller et al., 2003). The loss of this nearshore water body has affected a unique community of marine and freshwater planktonic species, as well as communities of cold-tolerant microscopic algae and animals that inhabited the upper ice shelf.

8.4.3.2. Lakes, ponds, and wetlands

Lentic systems north of the Arctic Circle contain numerous small to medium lakes and a multitude of small ponds and wetland systems. Relatively deep lakes are primarily contained within alpine or foothill regions such as those of the Putorana Plateau in the lower basin of the Yenisey River. One very large and deep lake, Great Bear Lake (Northwest Territories, Canada), is found partly within the Arctic Circle. Variations in its water budget primarily depend on flows from its contributing catchment, comprised largely of interior plains lowlands and exposed bedrock north of 60º N. Its southern counterpart, Great Slave Lake, provides a strong hydrologic contrast to this system. Although also part of the main stem Mackenzie River basin and wholly located north of 60º N, its water budget is primarily determined by inflow that originates from Mackenzie River headwater rivers located much further to the south. Moreover, its seasonality in water levels reflects the effects of flow regulation and climatic variability in one of its major tributaries, the Peace River, located about 2000 km upstream in the Rocky Mountain headwaters of western Canada (Gibson J.J. et al., in press; Peters and Prowse, 2001). As such, the Mackenzie River system offers the best example of a northern lentic system that is unlikely to be significantly affected by changes in hydrologic processes operating within the north (e.g., direct lake evaporation and precipitation) but will be dependent principally on changes in water-balance processes operating well outside the Arctic.

The other major arctic landscape type that contains large, although primarily shallower, lakes is the coastal plains region found around the circumpolar north. As mentioned previously, these shallow systems depend

on snowmelt as their primary source of water, with rainfall gains often negated by evapotranspiration during the summer. Evaporation from these shallow water bodies is very likely to increase as the ice-free season lengthens. Hence, the water budget of most lake, pond, and wetland systems is likely to depend more heavily on the supply of spring meltwater to produce a positive annual water balance, and these systems are more likely to dry out during the summer. Another possible outcome of climate change is a shift in vegetation from non-transpiring lichens and mosses to vascular plants as temperatures rise and the growing season extends (Rouse et al., 1997), potentially exacerbating water losses. However, factors such as increasing cloud cover and summer precipitation will possibly mitigate these effects.

Loss of permafrost increases the potential for many northern shallow lotic systems to dry out from a warmer temperature regime. Ponds are likely to become coupled with the groundwater system and drain if losses due to downward percolation and evaporation are greater than resupply by spring snowmelt and summer precipitation. Patchy arctic wetlands are particularly sensitive to permafrost degradation that can link surficial waters to the supra-permafrost groundwater system. Those along the southern limit of permafrost, where increases in temperature are most likely to eliminate the relatively warm permafrost, are at the highest risk of drainage (Woo et al., 1992). Traditional ecological knowledge from Nunavut and eastern arctic Canada indicates that recently there has been enhanced drying of lakes and rivers, as well as swamps and bogs, enough to impair access to traditional hunting grounds and, in some instances, fish migration (Krupnik and Jolly, 2002; see section 3.4.5 for detailed discussion of a related case study).

Box 8.4. Lake-ice duration and water column stratification: Lake Saanajärvi, Finnish Lapland

Lake Saanajärvi (maximum depth 24 m, area 0.7 km^2; 69° N, 20° E) is the key Finnish site in the European research projects Mountain Lake Research and European Mountain Lake Ecosystems: Regionalisation, Diagnostics and Socio-economic Evaluation. Lake Saanajärvi has been intensively monitored since 1996. The data presented here have been published in several papers, including those by Korhola et al. (2002a), Rautio et al. (2000), Sorvari and Korhola (1998), and Sorvari et al. (2000, 2002). The mean annual temperature of the area is -2.6 °C, and annual precipitation is approximately 400 mm. The catchment area is mostly covered by bare rocks and alpine vegetation. Lake Saanajärvi is a dimictic, ultra-oligotrophic, clear-water lake. The lake is ice-free for nearly four months of the year, with highly oxygenated waters, and is strongly stratified for two months after spring overturn. Phytoplankton biomass and densities are low (Forsström, 2000; Forsström et al., in press; Rautio et al., 2000), consisting predominantly of chrysophytes and diatoms. Bacterial biomass is low as well, and zooplankton are not very abundant. Freshwater shrimp (*Gammarus lacustris*) are common and form an important food source for fish, which include Arctic char and brown trout (*Salmo trutta lacustris*).

Changes in water temperature and stratification of Lake Saanajärvi have been associated with climate changes in Finnish Lapland over the past 200 years (Alexandersson and Eriksson, 1989; Sorvari et al., 2002; Tuomenvirta and Heino, 1996). Mean annual air temperatures in Finnish Lapland, as in much of the Arctic, rose 1 to 2 °C following the Little Ice Age. During this period of warming, diatom communities changed from benthic–periphytic to pelagic, Cladocera increased in abundance, and chrysophytes became less numerous. These changes have been shown to be associated with increased rates of organic matter accumulation and increased concentrations of algal pigments during the climatic warming (Korhola et al., 2002a; Sorvari and Korhola, 1998; Sorvari et al., 2002; see figure). After a period of cooling from the 1950s to the 1970s, air temperatures in the Arctic continued to rise. More recently, interannual variability in temperatures has been shown to account for changes in the thermal gradient and mixing of Lake Saanajärvi surface waters. For example, Lake Saanajärvi normally stratifies in early July, two weeks after ice breakup, and retains a distinct, steep thermocline at a depth of 10 to 12 m throughout the summer. In 2001, this summer stratification was broken after a period of slight cooling in early August, after which the lake was only weakly stratified. In 2002, on the other hand, spring and summer temperatures were extremely warm. Spring ice breakup was early and waters warmed quickly, resulting in a very sharp thermocline that was stable during the entire summer stratification period.

Future temperature increases are therefore very likely to affect the thermal structure of lakes in Finnish Lapland and throughout the Arctic, which is likely to have dramatic consequences for lake biota. Rising mean annual temperatures are very likely to influence the duration of summer stratification and the stability and depth of the thermocline in Finnish lakes. As such, many of the presently isothermal lakes are likely to become dimictic as temperatures increase. In addition, the prolonged thermal stratification that is likely to accompany rising temperatures could possibly lead to lower oxygen concentrations and increased phosphorus concentrations in the hypolimnion, benefiting nutrient-limited primary production. As spring temperatures rise and the ice-free period extends, not only is thermal stratification likely to stabilize, but production in many high latitude lakes could possibly peak twice

Warming of surface permafrost, however, will very probably enhance the formation of thermokarst wetlands, ponds, and drainage networks, particularly in areas characterized by concentrations of massive ground ice. Thawing of such ice concentrations, however, is very likely to lead to dramatic increases in terrain slumping and subsequent sediment transport and deposition in rivers, lakes, deltas, and nearshore marine environments. This is likely to produce distinct changes in channel geomorphology in systems where sediment transport capacity is limited, and will probably have a significant impact on the aquatic ecology of the receiving water bodies. Catastrophic drainage of permafrost-based lakes that are now in a state of thermal instability, such as those found along the western arctic coast of Canada, is also very likely (Mackay J., 1992; Marsh and Neumann, 2001, 2003). Losses of thermokarst lakes within low-lying deltaic areas are also likely to result from rising sea

levels. Marine inundation resulting from continually rising sea level commonly drains lakes in the outer portion of the Mackenzie Delta (northern Richards Island: Dallimore et al., 2000). Moreover, Mackay J. (1992) estimated that one lake per year has drained in the Tuktoyaktuk coastlands of northern Canada over the last few thousand years. Future, more pronounced rises in sea level are likely to accelerate this process.

Changes in the water balance of northern wetlands are especially important because most wetlands in permafrost regions are peatlands, which can be sources or sinks of carbon and CH_4 depending on the depth of the water table (see also section 8.4.4.4). An analysis by Rouse et al. (1997) of subarctic sedge fens in a doubled-CO_2 climate suggested that increases in temperature (4 °C) would reduce water storage in northern peatlands even with a small and persistent increase in precipitation. While

rather than once during the open-water season (e.g., Catalan et al., 2002; Hinder et al., 1999; Lepistö, 1999; Lotter and Bigler, 2000; Medina-Sánchez et al., 1999; Rautio et. al., 2000). On a broader scale, changes in lake stratification and water mixing will probably affect species composition (e.g., diatoms; Agbeti et al., 1997).
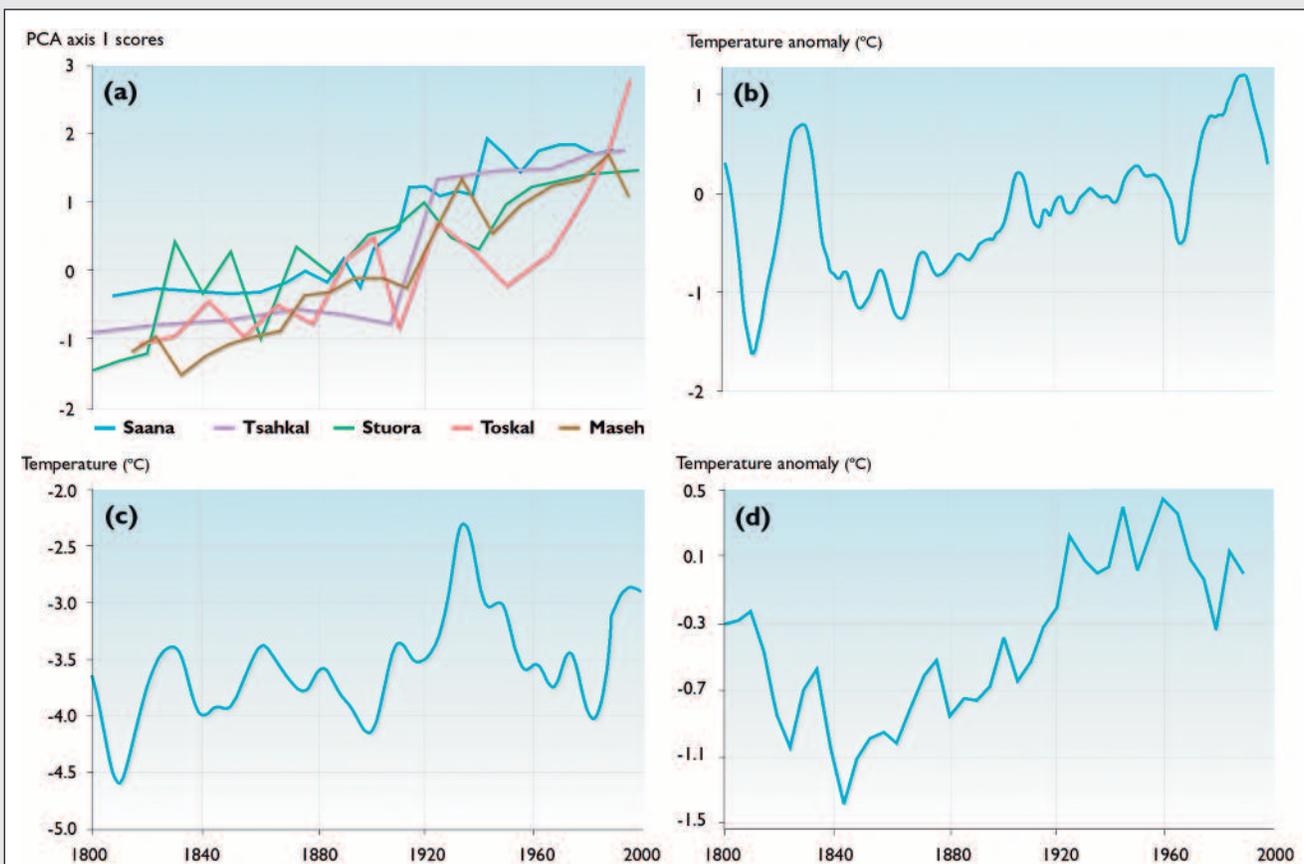
Comparison of diatom assemblage changes with regional and arctic-wide temperature anomalies, showing (a) principal components analysis (PCA) primary axis scores derived from the correlation matrices of the diatom percentage counts from the five study sites; (b) spring (March–May) temperature anomalies for northwestern Finnish Lapland, smoothed using a 10-year low-pass filter; (c) trend in mean annual air temperature in northwestern Finnish Lapland, smoothed using a 10-year low-pass filter; and (d) standardized proxy arctic-wide summer-weighted annual temperature, plotted as departure from the mean (panels a–c from Sorvari et al., 2000; panel d from Overpeck).

acknowledging that storage changes depend on variability in soil moisture and peat properties, projected declines in the water table were 10 to 20 cm over the summer.

As the ice cover of northern lakes and ponds becomes thinner, forms later, and breaks up earlier (section 6.7.3), concomitant limnological changes are very likely. Thinner ice covers with less snow cover will increase the under-ice receipt of solar radiation, thereby increasing under-ice algal production and oxygen (e.g., Prowse and Stephenson, 1986) and reducing the potential for winter anoxia and fish kills. Lower water levels, which reduce under-ice water volumes and increase the likelihood of winterkill, could possibly counteract this effect. Similarly, greater winter precipitation on a thinner ice cover is very likely to promote the formation of more highly reflective snow and white-ice layers. Such layers would reduce radiation penetration well into the spring because they also tend to delay breakup compared to covers comprised of only black ice. Notably, the ACIA-designated models project that incident radiation will decline. Reductions are likely to be relatively small (i.e., 10–12 W/m^2 in May-June between 1981–2000 and 2071–2090, section 4.4.4), however, compared to the major reductions that are likely to result from greater reflective loss from enhanced white-ice formation.

A longer ice-free season will also increase the length of the stratified season and generally increase the depth of mixing (Box 8.4), although the magnitude and duration of the effects will depend on factors such as basin depth and area. This is likely to lower oxygen concentrations in the hypolimnion and increase stress on cold-water organisms (Rouse et al., 1997). Furthermore, such an enhancement of mixing processes and reduction in ice cover will probably increase the potential for many northern lakes and ponds to become contaminant sinks (section 8.7).

With a longer and warmer ice-free season, total primary production is likely to increase in all arctic lakes and ponds, and especially in the oligotrophic high-arctic ponds that are currently frozen for a majority of the year (Douglas and Smol, 1999). Similar to the situation for arctic lotic systems, an enhanced supply of nutrients and organic matter from the more biologically productive contributing basins is likely to boost primary productivity (Hobbie et al., 1999). Again, however, there are likely to be offsetting effects because of reductions in light availability resulting from enhanced turbidity due to higher inputs of DOC and suspended sediment. Hecky and Guildford (1984) noted that analogous factors caused a switch from nutrient limitation, which is a common control of primary production in northern lakes, to light limitation.

8.4.4. Changes in aquatic biota and ecosystem structure and function

Climate change is very likely to have both direct and indirect consequences on the biota and the structure and function of arctic freshwater ecosystems. Changes in key physical and chemical parameters described previously are very likely to affect community and ecosystem attributes such as species richness, biodiversity, range, and distribution, and consequently alter corresponding food web structures and primary and secondary production levels. The magnitude and extent of the ecological consequences of climate change in arctic freshwater ecosystems will depend largely on the rate and magnitude of change in three primary environmental drivers: the timing, magnitude, and duration of the runoff regime; temperature; and alterations in water chemistry such as nutrient levels, DOC, and particulate organic matter loadings (Poff et al., 2002; Rouse et al., 1997; Vincent and Hobbie, 2000).

8.4.4.1. Effects on biological communities, biodiversity, and adaptive responses

Climate change will probably produce significant effects on the biodiversity of freshwater ecosystems throughout the Arctic and possibly initiate varying adaptive responses. The magnitude, extent, and duration of the impacts and responses will be system- and location-dependent, and difficult to separate from other environmental stressors. Biodiversity is related to, or affected by, factors including:

- the variability of regional and local climate;
- the availability of local resources (e.g., water, nutrients, trace elements, energy, substrate) affecting the productivity potential;
- the nature, timing, and duration of disturbance regimes in the area (e.g., floods, catastrophic water loss, fire);
- the original local and regional "stock" of species and their dispersal opportunities or barriers;
- the physiological capacity of individuals and populations to cope with new environmental conditions (e.g., physiological thresholds and tolerances);
- the levels of spatial heterogeneity (habitat fragmentation) and connections among aquatic systems;
- the intensity of biotic interactions such as competition, predation, disease, and parasitism;
- phenotypic and genotypic flexibility in reproductive and life-history strategies (e.g., facultative versus obligatory anadromy for certain fish; plasticity in sexual versus asexual reproductive strategies in aquatic invertebrate and plant species); and
- the overall genetic variability and adaptive capacity of the species (IPCC, 2001a; Pimm, 1991; UNEP, 2003).

Many arctic freshwater systems are exposed to multiple environmental stressors or perturbations including point- and/or nonpoint-source pollution (e.g., long-range aerial transport of contaminants; section 8.7); altered hydrologic regimes related to impoundments and diversions; water quality changes from landscape alterations (e.g., mining, oil and gas exploration); and biological resource exploitation (e.g., subsistence and commercial fisheries and harvesting of waterfowl and mammals;

section 8.5), to name a few. These stressors, along with climate variability, can synergistically contribute to the degradation of biological diversity at the species, genetic, and/or habitat–ecosystem levels (CAFF, 2001; IPCC, 2001a; Pimm et al., 1995; UNEP, 2003). There is little evidence to suggest that climate change will slow species loss. There is growing evidence, however, that climate change will contribute to accelerated species losses at regional and global levels (UNEP, 2003) and that the effects of alterations in the biodiversity of ecosystem structure and function are likely to be more dependent on given levels of functional diversity than on the total number of species (Chapin et al., 2000). Moreover, both the number and type of functional units present in a community largely affect ecosystem resilience and vulnerability to change (UNEP, 2003).

For these reasons, large uncertainties remain in projecting species- and system-specific responses and the impacts of changes in climate and UV radiation levels on biodiversity at local and regional spatial scales. However, several broad projections can be made.

First, locally adapted arctic species are likely to be extirpated from certain areas as environmental conditions begin to exceed their physiological tolerances and/or ecological optima. Hence, species with limited climatic ranges and/or restricted habitat requirements (related to particular physiological or phenological traits) are very likely to be vulnerable to climate change effects. Species with low population numbers and/or that reside in restricted, patchy, and highly specialized environments will be particularly at risk (UNEP, 2003). While wholesale extinctions of entire arctic species are unlikely, some highly valued species (e.g., certain fish species) may possibly become geographically or ecologically marginalized. For example, there are pronounced north–south gradients in the taxonomic composition of stream macroinvertebrate communities in the Arctic, with decreasing species diversity and an increasing importance of taxa such as dipterans with distance northward (Oswood, 1997). Moreover, many of the high-latitude filamentous algal species have temperature optima well above the low ambient water temperatures at which they reside, and are therefore likely to respond positively to moderate increases in temperature (Tang and Vincent, 1999; Tang et al., 1997). Hence, many high-latitude species are currently at their physiological limits and are likely to be very sensitive to future shifts in climate (Danks, 1992). Projected changes in regional runoff patterns and temperature regimes are very likely to affect river and stream environments, possibly reducing the severity of disturbance events that are an integral component of their current hydro-ecology (section 8.4.2). Specifically, Scrimgeour et al. (1994) suggested that if these disturbances play a role in maintaining habitat complexity and associated species richness and diversity, then climate-related changes in the severity of these events will affect macroinvertebrate and aquatic algal species distribution and associated biodiversity patterns (see also Prowse and Culp, 2003).

In estuarine habitats, there are likely to be shifts in species composition to more euryhaline and anadromous species (e.g., fourhorn sculpin – *Myoxocephalus quadricornis*, ninespine stickleback – *Pungitius pungitius*, threespine stickleback – *Gasterosteus aculeatus*, Arctic flounder – *Pleuronectes glacialis*, salmonines, and coregonines). Such shifts in species composition will possibly have cascading effects resulting from competition for food resources with marine species (e.g., Arctic cod – *Boreogadus saida*) that currently inhabit many estuarine zones. The subsequent effects on higher trophic levels (e.g., the impact of potentially decreased Arctic cod abundance on marine mammals and birds) remains unknown (see also section 9.3.4).

For other fish species (e.g., Arctic char), alterations in environmental conditions could possibly shift or reduce the availability of preferred habitats of certain morphs, leading, in the extreme case, to the extirpation of particular morphs from certain locations. For example, pelagic forms of Arctic char in Thingvallavatn, Iceland, occupy portions of the water column that experience summer heating. Should such heating ultimately exceed thermal preferences for this morph, its growth is likely to decrease, with a concomitant reduction in reproduction and productivity. Ultimately, exclusion from the habitat during critical times could possibly occur, permanently extirpating that morph from such areas.

Changes in habitat characteristics driven by climate change are also likely to differentially affect specific populations of fish. For example, some aspects of life-history variation in Dolly Varden on the Yukon north slope appear to be particularly associated with inter-river variation in groundwater thermal properties (e.g., egg size is larger and development time is shorter in rivers that have significant groundwater warming, and reproduction occurs annually in these warmer rivers because sea access allows for earlier feeding, compared to reproduction every two years or less often in colder rivers; Sandstrom, 1995). Thus, climate change effects that mimic this natural local inter-population variability are likely to result in similar shifts in populations presently occupying colder habitats.

A second major effect of climate change will probably be alterations in the geographic range of species, thereby affecting local and regional biodiversity. This is likely to occur through a combination of compression or loss of optimal habitat for "native" arctic species, and the northward expansion of "non-native" southern species. For instance, the large number of northward-flowing arctic rivers provides pathways for colonization of the mainland by freshwater species that, due to climatic limitations, are presently restricted to subarctic or temperate portions of the drainage basins. As climate change effects become more pronounced (e.g., degree-day boundaries or mean temperature isotherms shift northward), the more ecologically vagile species are likely to extend their geographic ranges northward (Oswood et al., 1992). In North America, for example, the distribution of yel-

low perch (*Perca flavescens*) is projected to expand northward beyond its current, primarily subarctic distribution. Traditional ecological knowledge from the western Canadian Arctic has identified new species of fish (Pacific salmon – *Oncorhynchus* spp. and least cisco – *Coregonus sardinella*) that were not previously present in some aquatic systems of the area (Krupnik and Jolly, 2002; see also Chapter 3, specifically Fig. 3.2). The complete consequences of such new colonizations are unknown, but could include the introduction of new diseases and/or parasites; population reduction or extirpation through competition for critical resources; increased predation; increased hybridization of closely related taxa; and others (see sections 8.5.1.1 and 8.5.2 for detailed discussions of climate-related range extensions in selected fish species and their potential ecological consequences).

Emergent aquatic plants are also expected to expand their distribution northward and thus alter the overall levels of primary production in ponds and small lakes in the Arctic. Alexander et al. (1980) reported total primary production of 300 to 400 g C/m^2/yr in ponds of emergent *Carex* (covering one-third of the pond) in Barrow, Alaska, compared to total primary production of 1 g C/m^2/yr for phytoplankton and 10 g C/m^2/yr for epilithic algae. Traditional ecological observations by trappers on the Peace-Athabasca Delta of the Mackenzie River system, Canada, suggest that muskrat abundance is likely to increase in high-latitude lakes, ponds, and wetlands as emergent aquatic vegetation becomes more prominent (Thorpe, 1986). While the potential northern limit for emergent aquatic macrophytes is not fully known, their projected increased presence will clearly influence the overall productivity and structural complexity of arctic pond and lake habitats.

An overarching issue affecting the responses of arctic aquatic biota and related biodiversity to rapid climate change is "adaptive capacity". The magnitude of change in arctic climate projected for the next 100 years does not exceed that experienced previously, at least at a geological timescale. The future rate of change however, is very likely to be unprecedented. To survive such a challenge, arctic aquatic biota, especially those that are truly arctic in nature, must have the inherent capacity to adapt (i.e., have sufficient genetic capacity at the population level to evolve at the required rate); acclimate (i.e., the phenotypic ability at the population and/or individual level to survive in the new conditions); and/or move (i.e., emigrate to more optimal situations). High levels of diversity that are present below the species level in many arctic organisms imply that some evolutionary compensation for rapid climate change is possible. Taxa with short generation times (e.g., zooplankton) will be able to evolve more rapidly than those with longer generation times (e.g., fish). Furthermore, assessment of genetic variability for some taxa (e.g., mitochondrial DNA in Arctic char; Wilson et al., 1996) suggests that previous events that reduced genetic diversity may have limited their capacity for such rapid evolution. This will probably further hamper responses by

such taxa and, with the projected rapid rate of climate change and other factors (e.g., competition from new colonizers), is likely to result in an increased risk of local extirpation and/or extinction.

Many arctic taxa may already be pre-adapted to acclimate successfully to rapid change. For example, many organisms already have enzymes with different thermal optima to allow them to cope with changing environmental conditions. Such capacity, which is presumed but not demonstrated to exist in most arctic taxa, could possibly counterbalance the increased risk of extinction noted above. Taxa that are capable of emigrating to new areas have additional options to cope with rapid climate change, although access issues are likely to preclude such movements to suitable conditions.

Clearly, significant changes in aquatic biodiversity are very likely to result from climate change, and biota have varying capacities to cope with the rate of this change. Ecologically speaking, any change will have significant ramifications in that adjustments in the ecosystem will follow (sections 8.4.4.2, 8.4.4.3, 8.4.4.4, and 8.5). However, from the human perspective, important questions surround the perceived significance of such changes from economic, cultural, and value perspectives (see Chapters 3, 11, and 12 for discussions of possible socioeconomic implications).

8.4.4.2. Effects on food web structure and dynamics

The impacts of climate change on the structure and dynamics of aquatic food webs remain poorly understood. To date, many of the insights as to how arctic food webs will respond (directly or indirectly) to climate change effects have been obtained from either descriptive studies or a select few manipulative/experimental studies where ecosystem-level or food web manipulations were conducted and response variables measured. Stream processes and biotic populations of the Kuparuk River and Oksrukuyik Creek, Alaska, have been shown to be controlled by the geomorphology of the systems (i.e., input from nutrient-rich springs; Craig and McCart, 1975); climate (i.e., precipitation affects discharge, which affects insect and fish production; Deegan et al., 1999; Hershey et al., 1997); resource fluxes from the surrounding catchments (Peterson B. et al., 1993); and corresponding biotic interactions. For example, nutrient enrichment of the streams resulted in greater primary and fish production, and a corresponding increase in the abundance of benthic macroinvertebrates (Harvey et al., 1998; Peterson B. et al., 1993). In addition, after seven years of artificial enrichment of the Kuparuk River, the dominant primary producers changed from diatoms to mosses (Bowden et al., 1994), which subsequently altered the abundance, distribution, and taxonomic composition of the macroinvertebrate community (Bowden et al., 1999).

Other recent studies of arctic systems have identified the structural and functional importance of the microbial

freshwater food web (Fig. 8.13). Work in this area has shown that the microbial food web can comprise a significant fraction of the total community biomass in arctic rivers and lakes, and that energy flow is routed through a diverse trophic network of microbial species displaying a wide array of nutritional modes (heterotrophic bacteria, phototrophic bacteria, phagotrophic protozoa, and mixotrophic flagellates; Vincent and Hobbie, 2000). How climate change will influence the response of the microbial food web is not entirely certain, but studies of temperate systems might help provide insight. Interestingly, research on microbial food webs of more temperate aquatic systems shows that in the absence of heavy grazing pressure on bacteria by macrozooplankton or benthic macroinvertebrates, the principal role of the microbial food web is the degradation (respiration) of organic matter (Kalff, 2002). Hence, the microbial food web is a significant source of energy to plankton, being largely responsible for recycling nutrients in the water column and thereby helping to sustain planktonic and benthic primary production and ultimately higher secondary and tertiary consumers in the food chain (Kalff, 2002). Projected increases in water temperature and inputs of DOC, particulate organic carbon (POC), and DIC arising from climate change are very likely to affect the structural and functional dynamics of the microbial food web, and are likely to increase rates of carbon processing. Pienitz et al. (1995) showed that the same abiotic parameters, along with lake morphometry, explain the greatest percentage of variance in diatom community composition in northwestern Canada. Furthermore, diatom community structure was highly correlated with DOC gradients in Siberian and subarctic Québec lakes (Fallu and Pienitz, 1999; Lotter et al., 1999). Hence, concomitant changes in the phytoplankton component of the food web probably will also cascade through the ecosystem.

Increasing temperature has the potential to alter the physiological rates (e.g., growth, respiration) of individuals, and the vital rates and resulting dynamics of populations (Beisner et al., 1997; McCauley and Murdoch, 1987). Mesocosm studies by Beisner et al. (1996, 1997), which investigated the influence of increasing temperature and food chain length on plankton predator–prey dynamics, showed that the predator–prey system is
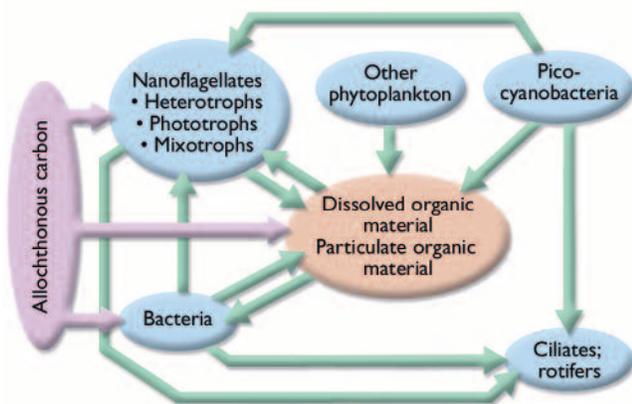
destabilized at higher temperatures (i.e., the macrozooplankton herbivore *Daphnia pulex* always became extinct), irrespective of the complexity of the food web (i.e., whether a two- or three-level food web was involved). Long-term studies of Toolik Lake, Alaska, project that rising temperatures are likely to eliminate lake trout (*Salvelinus namaycush*) populations in this lake, with concomitant impacts on the food web (see Box 8.3). The bioenergetics model used by McDonald M.E. et al. (1996) projects that a 3 ºC rise in July epilimnetic (surface mixed-layer) temperatures could cause young-of-the-year lake trout to require eight times more food than at present just to maintain adequate condition. This requirement greatly exceeds the current food availability in the lake, although it is probable that food availability will increase as temperatures rise. Furthermore, the oxygen concentrations projected by the lake model (Hobbie et al., 1999) show that a future combination of higher temperatures and increased loading of total phosphorus would greatly reduce the hypolimnetic (bottom-water) habitat available for lake trout.

An example of top-down control through size-selective predation was found in ponds and lakes in Barrow, Alaska: lakes with fish had small and transparent *Daphnia longiremis*, while lakes without fish and all ponds had large and pigmented *D. middendorffiana* and *D. pulex* as well as fairy shrimp and the copepod *Heterocope* spp. (Stross et al., 1980). Rouse et al. (1997) concluded that since top predators (fish) in arctic systems tend to be long-lived, population changes owing to recruitment failure may not be reflected in the adult populations for many years. However, the effects of the eventual loss of top predators from these systems are likely to cascade through the food web, affecting the structure and function of both benthic and planktonic communities (Carpenter et al., 1992; Goyke and Hershey, 1992; Hanson et al., 1992; Hershey, 1990; Jeppesen et al., 2003; O'Brien et al., 1992).

Given the information presented in this section, it is very probable that climate change will substantially affect biological interactions, including trophic structure and food chain composition. With top-down and bottom-up processes operating simultaneously in ecosystems (Golden and Deegan, 1998; Hansson, 1992; McQueen et al., 1989; and references therein), the degree to which each process influences producer biomass varies (McQueen et al., 1989). Consequently, the well-established relationship between phosphorus and algal biomass may differ between systems with different levels of productivity. For example, in a two-level trophic system (relatively unproductive), grazing zooplankton may control the algal biomass and the expected positive relationship between chlorophyll-a (Chl-a) and total phosphorus (P) would not be observed. Therefore, differences in productivity and trophic level interactions may explain the discrepancy in the Chl-a–total P relationship between temperate and arctic lakes (Fig. 8.14). The low productivity that has been observed in many arctic lakes may limit the presence of fish predators (i.e.,

Fig. 8.13. Microbial freshwater food web in arctic lakes (adapted from Vincent and Hobbie, 2000).

more closely represent a two-level trophic system) and may result in systems where algal biomass is controlled by extensive zooplankton grazing (Flanagan et al., 2003).

Top-down control of food web structure in arctic stream and river ecosystems is also important. Golden and Deegan (1998) found that young Arctic grayling (*Thymallus arcticus*) have the potential to produce top-down cascading trophic effects in arctic streams where nutrients are not limited. The grayling were found to affect trophic structure through consumption, nutrient excretion, and the modification of prey behavior. Epilithic Chl-a increased with increasing fish density in both reference P-limited) and fertilized (P-enriched) zones of the Kuparuk River, Alaska, while mayfly density decreased with increasing fish density in the fertilized zone only. These results further illustrate that projecting climate change impacts is not straightforward.

8.4.4.3. Effects on primary and secondary production

Primary and secondary productivity relationships in arctic aquatic ecosystems are highly susceptible to structural and functional alterations resulting from changes in cli-

mate, although the direction and absolute magnitude of the responses are likely to be difficult to project (Hobbie et al., 1999; Laurion et al., 1997; Rouse et al., 1997; Vincent and Hobbie, 2000). For example, while constituents of microbial food webs (e.g., the picocyanobacteria, heterotrophic bacteria, etc.; Fig. 8.13) are likely to respond positively to temperature increases, the photosynthesis rate in the picoplankton fraction (0.2–2 μm) is strongly stimulated by increased temperature to a greater extent than nanoplankton (2–20 μm) and microplankton (20–200 μm) fractions (Rae and Vincent, 1998b).

In general, lake primary productivity will probably increase because higher temperatures correlate with higher primary productivity (a longer ice-free season and more sunlight before the summer solstice are very likely to result in greater primary production by plankton; see Box 8.5). Brylinsky and Mann (1973) analyzed lake productivity in 55 lakes and reservoirs from the tropics to the Arctic, and found the best abiotic variables for estimating productivity to be latitude and air temperature. A closer examination of the relationship between total P, total nitrogen, latitude, and algal biomass (n=433 lake years) also revealed that average algal biomass during the ice-free season is significantly negatively related to the latitude of

Box 8.5. Productivity of northeastern Greenland lakes: species composition and abundance with rising temperatures

The Danish BioBasis monitoring program (part of Zackenberg Ecological Research Operations), initiated in 1995, includes two lakes located in the Zackenberg Valley, northeastern Greenland (74° N). The monitoring at Zackenberg is expected to continue for at least 50 years. The area is situated in a high-arctic permafrost area in North-East Greenland National Park. More information about the area and the monitoring program can be found in Meltofte and Thing (1997) and Christoffersen and Jeppesen (2000), as well as at http://biobasis.dmu.dk. The two lakes, Sommerfuglesø and Langemandssø, have areas of 1.7 and 1.1 ha and maximum depths of 1.8 m and 6.1 m, respectively. Lakes and ponds in the area are ice-covered for most of the year, except from the end of July to the beginning of September. Most water bodies probably freeze solid during the late winter and spring. Primary producers in these nutrient-poor lakes are dinophytes, chlorophytes, and diatoms. Zooplankton grazers are sparse, consisting of *Daphnia*, copepods, and protozoans. Benthic invertebrates include *Lepidurus*. There are no fish in Sommerfuglesø. Dwarf Arctic char in Langemandssø prey on *Daphnia*, therefore, copepods and rotifers dominate zooplankton populations in this lake.
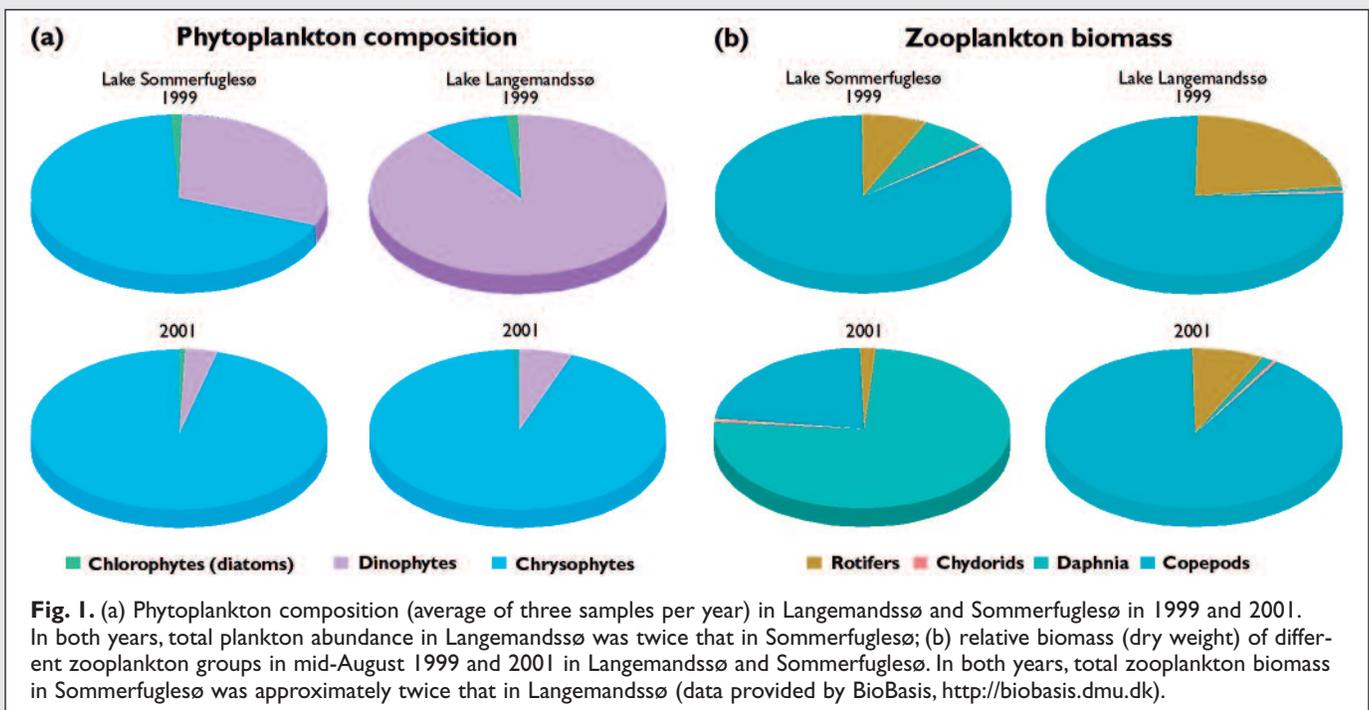
Plants and animals in Sommerfuglesø and Langemandssø are active prior to ice melt, thus phytoplankton biomass becomes substantial as incoming solar radiation increases (Rigler, 1978). However, primary productivity slows as nutrients are consumed, and phytoplankton density varies annually with nutrient abundance. For example, in warmer years, nutrient concentrations and thus productivity are higher due to increased loading of nutrients and humus from catchments as the active layer thaws.

Monitoring of plankton species in the two lakes during 1999 (a year of late ice melt and low water temperatures) and 2001 (a year of early ice melt and high water temperatures) has shown that not only do biomass and abundance change with temperature, but species composition changes as well. In 1999, when water temperatures were lower, chrysophytes and dinophytes represented 93% of total phytoplankton abundance in Sommerfuglesø, while dinophytes dominated phytoplankton (89% of total abundance) in the deeper and colder Langemandssø. In 2001, when ice broke early and water temperatures were higher, chrysophytes completely dominated phytoplankton in both lakes (94–95% of total phytoplankton abundance). Compared to 1999, total phytoplankton abundance was approximately twice as great in 2001, when nutrient levels were higher as well. Zooplankton abundance, in turn, was 2.5 times greater in 2001 than in 1999 in both lakes, likely in response to greater phytoplankton abundance. *Daphnia* and copepods were more abundant in 2001, while rotifers were less abundant than in 1999, perhaps in response to competition for food resources.

the system, independent of the nutrient concentration (Flanagan et al., 2003). This strong latitudinal effect on algal biomass yield suggests that arctic lakes are likely to show a significant increase in productivity if temperature and nutrient loadings in these systems increase as scenarios of future climate change project. While Shortreed and Stockner (1986) found that arctic lakes have lower primary productivity than temperate lakes, Flanagan et al. (2003) showed that at a given level of phosphorus, the productivity of arctic lakes is significantly less than lakes in the temperate zone, with the biomass of lower (trophic level) producers not accounted for simply by lower nutrient concentrations in the Arctic. Further examination of detailed observations of phytoplankton community structure from arctic Long-Term Ecological Research sites indicates that there is no fundamental shift in taxonomic group composition between temperate and arctic phytoplankton communities. This suggests that the difference in the Chl-a–total P relationship between temperate (Watson et al., 1997) and arctic lakes is not an artifact of changes in the Chl-a–biomass ratio resulting from a taxonomic shift in algal communities (Flanagan et al., 2003). Hence, the observed difference in the Chl-a–total P relationship for temperate and arctic lakes may provide insight about the future effects of climate change (Fig. 8.14).

Primary productivity is likely to increase if climate conditions at high latitudes become more suitable for industrial development, and if the associated pollution of currently nutrient-poor aquatic systems increases. For example, mountain lakes in the Kola Peninsula (e.g., Imandra Lake) and lakes and ponds in the Bolshezemelskaya tundra are currently stressed by heavy loadings of anthropogenic organic matter, heavy metals, and crude oil and drilling fluid, as well as thermal pollution. Phytoplankton structure (e.g., species) in these systems has changed, and primary as well as secondary productivity and biomass have increased significantly.

Arctic lakes, although relatively unproductive at present, will probably experience a significant increase in productivity as climate changes. If temperature and nutrient loads increase as projected, it is likely that phytoplankton will no longer experience temperature-induced photosynthetic rate inhibition, and growth rates will probably become more similar to those in the temperate zone, thus allowing for a greater accumulation of algae. If algae are heavily grazed by herbivores at present because of a lack of predation, higher-level predators are likely to invade as the productivity of the system increases. Subsequent increased predation of the grazer community

Fig. 1. (a) Phytoplankton composition (average of three samples per year) in Langemandssø and Sommerfuglesø in 1999 and 2001. In both years, total plankton abundance in Langemandssø was twice that in Sommerfuglesø; (b) relative biomass (dry weight) of different zooplankton groups in mid-August 1999 and 2001 in Langemandssø and Sommerfuglesø. In both years, total zooplankton biomass in Sommerfuglesø was approximately twice that in Langemandssø (data provided by BioBasis, http://biobasis.dmu.dk).

The climate of northeastern Greenland is projected to become more maritime in the future. Based on the five years of monitoring at Zackenberg thus far, increasing temperature and precipitation are projected to have major impacts on physicochemical and biological variables in the lakes. If snowfall increases, ice-cover duration is likely to be prolonged, shortening the growing season and reducing productivity, and possibly reducing food availability to the top predator in arctic lakes, the Arctic char. Greater runoff will probably increase nutrient loading and primary productivity, which could possibly result in oxygen depletion and winter fish kill. Thus, one probable outcome of climate change will be the extirpation of local fish populations in shallow lakes in similar ecological situations. Increased particulate loading is likely to limit light penetration for photosynthesis. Increased humus input with snowmelt is also likely to limit light penetration, reducing UV radiation damage to biota.
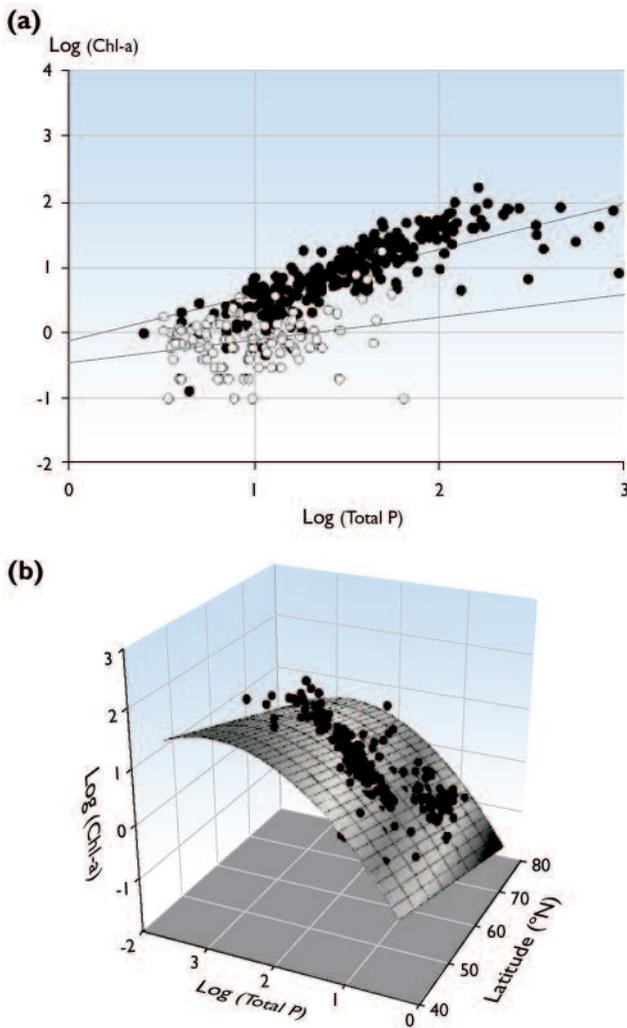
Fig. 8.14. (a) Comparison of the relationship between chlorophyll-a (Chl-a) and total phosphorus (P) in temperate and arctic freshwater systems. The difference between the slopes of the regression lines is statistically significant ($p<0.05$). Solid circles represent temperate lakes ($r^2=0.28$, $n=316$, $p<0.05$) and open circles represent arctic lakes ($r^2=0.07$, $n=113$, $p<0.05$). (b) The observed non-linear response of Chl-a to log total P and latitude (from Flanagan et al., 2003).

would permit an increase in algal biomass. In addition, the projected increase in nutrient concentration would augment these changes, making the increase in productivity even more dramatic.

Several empirical studies support this hypothesis. One study compared Swedish lakes (three-level trophic system) to unproductive antarctic lakes (two-level trophic system). The slope of the Chl-a–total P relationship for the antarctic lakes was significantly less than the Swedish lakes. This was hypothesized to be a consequence of the different trophic structures of the lakes, since productive (three-level) Swedish lakes showed a Chl-a–total P relationship similar to temperate lakes, suggesting that climate-related abiotic factors were not causing the differences between the Swedish and unproductive antarctic lakes (Hansson, 1992). Other empirical evidence supporting this hypothesis comes from subarctic lakes in the Yukon, which showed higher levels of zooplankton biomass relative to P concentrations than in temperate

regions, suggesting a two-level trophic system. Shortreed and Stockner (1986) attributed the high abundance of zooplankton to the low abundance of planktivorous fish, which led to an over-consumption of algae.

However, a significant factor further complicating the possible productivity response in arctic systems is the interaction of productivity with DOC. High DOC levels can differentially affect measured primary productivity by influencing light penetration (more DOC leads to darker water), affecting turbidity, and adding carbon for processing. For example, benthic diatoms and total diatom concentrations increased significantly during conditions of high DOC concentrations and low water transparency, whereas planktonic forms decreased (Pienitz and Vincent, 2000). In Southern Indian Lake, northern Manitoba, Hecky and Guildford (1984) found that high DOC concentrations decreased light penetration sufficiently to cause a switch from nutrient to light limitation of primary production. In shallow tundra ponds, over 90% of algal primary production was by benthic algae (Stanley D., 1976), although this level of productivity is very likely to decline if there is appreciable DOC-related light reduction. By contrast, increased DOC is likely to reduce harmful UV-B radiation levels, and thereby have a possible countervailing effect on productivity (Vincent and Hobbie, 2000).

Changes in primary productivity resulting from climate change, whether attributed to increased water temperatures or increased DOC loading, are likely to affect secondary production in arctic freshwaters. Productivity of lake zooplankton is very likely to rise in response to increases in primary production. At Toolik Lake, a 12-fold increase in primary production yielded a less than 2-fold increase in secondary production (O'Brien et al., 1992). This enhanced production is very likely to result in an increase in the abundance of secondary producers, as observed in Alaska, where the abundance of microplankton (rotifers, protozoans) rose with increased primary production (Rublee, 1992). Although larger zooplankton showed little species change with increasing productivity, microzooplankton increased both in number of species (i.e., biodiversity) and trophic levels (i.e., productivity). Observations by Kling et al. (1992a) indicated that zooplankton abundance and diversity are more sensitive to changes in primary productivity with latitude, with species number and types declining to the north, than to changes in lake primary productivity at any given latitude. Therefore, lake productivity and species abundance and diversity will probably shift in favor of zooplankton as primary production increases in a progressively northward direction with climate change.

Climate change is unlikely to affect bacterial species assemblages. Bahr et al. (1996) found that the species of plankton in Toolik Lake, Alaska, were identical to species found in other lakes in temperate regions. The overall productivity of the lake did not appear to be related to the species of bacteria involved, instead, the total bacterial biomass in the plankton was affected by overall primary
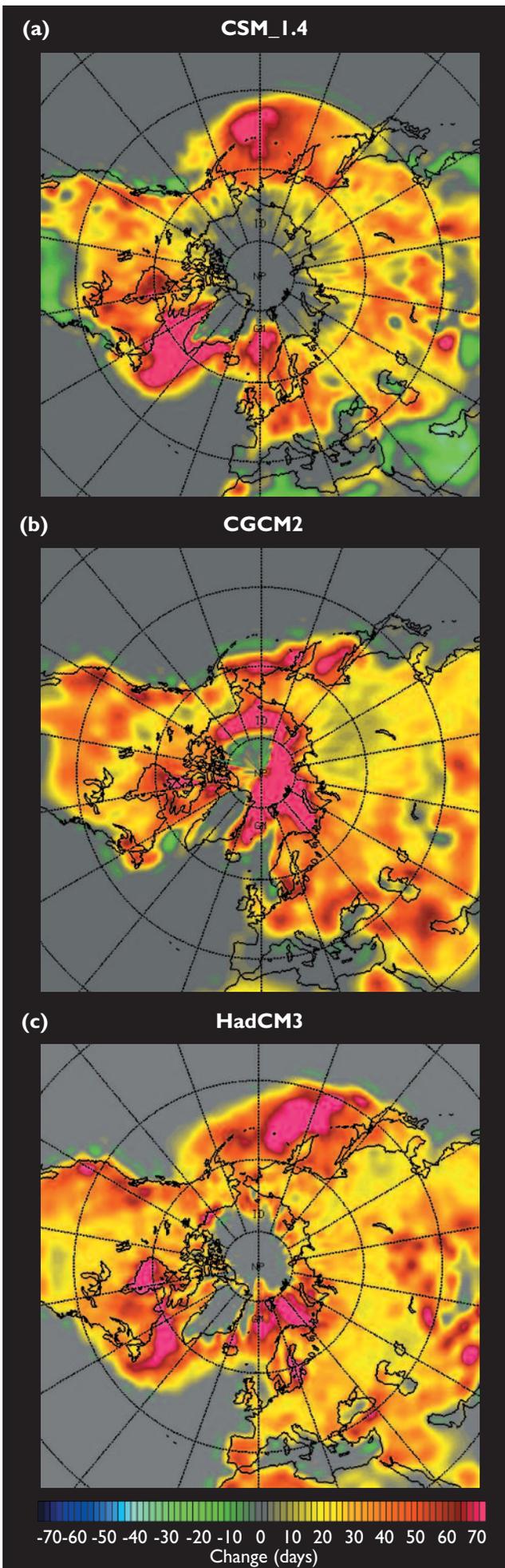
production and by the amount of allochthonous organic matter entering the lake from the drainage basin. Crump et al. (2003) and O'Brien et al. (1997) reported that over half of the bacterial productivity in Toolik Lake was based on terrestrial DOC. As a result, the bacterial numbers, biomass, and productivity in this lake are many times higher than they would be if it contained a plankton-based microbial food web. In contrast, protozoa and rotifer communities are likely to change with the increasing primary productivity that will probably result from climate change. For example, major changes occurred in protozoan, algal, and rotifer assemblages and production owing to significant artificial nutrient additions (four times ambient loading rates; Bettez et al., 2002).

8.4.4.4. Effects on carbon dynamics

The ACIA-designated models project that by 2080, the majority of the Arctic will experience increases in air temperature (section 4.4.2), precipitation (section 4.4.3), evaporation (section 6.2.3), available degree-days for biological growth, and major changes in the extent and nature of permafrost (section 6.6.1.3). Although there are variations between model projections, permafrost degradation is projected to occur most extensively at more southerly latitudes of the circumpolar Arctic, with regional west-to-east gradients across North America and Eurasia (for distribution among ACIA regions see Figs. 6.23 and 8.2). Overall (based on a "median" model projection; section 6.6.1.3), total permafrost area is projected to decrease by 11, 18, and 23% by 2030, 2050, and 2080, respectively. The loss of permafrost and deepening of the active layer is projected to be greatest in the western and southern areas of arctic and subarctic North America and Eurasia because initial permafrost temperatures are closer to 0 °C than in more easterly and northern areas, and these areas are more likely to become snow-free earlier in the spring, permitting enhanced soil warming (e.g., Groisman et al., 1994; section 6.4.4). Growing degree-days are projected to increase across the Arctic (Fig. 8.15), with the greatest increase in Regions 1 and 4, with the exception of Greenland where growing degree-days are projected to remain the same or decrease. On average, a 20- to 30-day increase in growing-season length is projected for areas north of 60° N by the end of the 21st century. As the number of degree-days increases in the Arctic, carbon cycling in arctic wetlands is very likely to not only be affected by changes in the rates and magnitudes of primary and microbial productivity, but also in the quantity and quality of organic material that accumulates in these systems. This in turn will affect carbon loading to, and processing within, arctic lakes and rivers.

Fig. 8.15. Projected changes in the length of the growing season defined as the number of days where the minimum temperature is greater than 0 °C, derived from the ACIA-designated models: (a) CSM_1.4 projected change between 1980–1999 and 2080–2099; (b) CGCM2 projected change between 1976–1994 and 2071–2090; and (c) HadCM3 projected change between 1971–1990 and 2071–2090 (see section 4.2.7 for model descriptions).

Wetlands are a very prominent feature of the Arctic, and are particularly sensitive to climate change. The structure of these systems, and their function as net sources or sinks of carbon, is likely to respond dramatically to changes in permafrost thawing, peatland distribution, and air temperatures and water budgets.

Thawing of perennially frozen wetland soil and ice is likely to result initially in a substantial efflux of carbon, as perennial stores of CO_2 and CH_4 are released to the atmosphere. Such an effect accounted for an estimated 1.6- to 3-fold increase in carbon emissions from degrading permafrost along the 0 °C isotherm in Canada (Turetsky et al., 2002). Permafrost thaw and warming has also accounted for a 100-fold increase in the rate of CO_2 and CH_4 formation in the Ob River basin (Panikov and Dedysh, 2000), and is responsible for drastically increased effluxes of these two gases from a high-latitude mire in Sweden (Friborg et al., 1997; Svensson et al., 1999). This initial increase in CO_2 and CH_4 emissions with permafrost thaw has potential positive climate feedbacks. The effect is likely to decline over time as gas stores are depleted, and as wetland vegetation, hydrology, and carbon sink/source function progressively change with climate.

Permafrost thaw and a greater number of growing degree-days are very likely to result in increased distribution and biomass of wetland vegetation at more northerly latitudes, increasing carbon storage in arctic and subarctic landscapes. Projections based on doubled atmospheric CO_2 concentrations (Gignac and Vitt, 1994; Nicholson and Gignac, 1995) indicate a probable 200 to 300 km northward migration of the southern boundary of peatlands in western Canada, and a significant change in their structure and vegetation all the way to the coast of the Arctic Ocean. Increases in carbon accumulation have been associated with peatland expansion, along with northward movement of the treeline, during Holocene warming, a process that slowed and eventually reversed with the onset of the Little Ice Age (section 8.3.2; Gajewski et al., 2000; Vardy et al., 1997). Similar expansion of peatlands and enhanced biomass accumulation have been recorded in North America in more recent times (Robinson and Moore, 2000; Turetsky et al., 2000; Vitt et al., 2000). Hence, as temperatures rise, wetland/peatland distribution is likely to increase at high latitudes, and arctic landscapes are likely to become greater carbon sinks. Carbon accumulation at high latitudes is likely to be limited by loss due to disturbance (e.g., increased occurrence of fire as temperatures and evapotranspiration increase in some areas; Robinson and Moore, 2000; Turetsky et al., 2002), which will possibly result in greater carbon loading to lakes and rivers (Laing et al., 1999).

Changes in available growing degree-days, along with changes in the energy and water balances of high-latitude wetlands, will have varying effects on the rates and magnitudes of photosynthetic assimilation of CO_2, and anaer-

obic and aerobic production of CO_2 and CH_4 in existing arctic and subarctic wetlands:

- Rates and magnitudes of primary productivity, and hence carbon sequestration, are very likely to increase in arctic wetlands as air and soil temperatures rise, growing season lengthens (e.g., Greenland: Christensen et al., 2000; Finland: Laurila et al., 2001), and as vegetation changes (as discussed above in the context of permafrost degradation). Carbon fixation in arctic and subarctic wetlands will, however, possibly be limited by UV radiation effects on vegetation (Niemi et al., 2002; see also sections 7.4.2 and 8.6).
- Carbon dioxide accumulation in high-latitude wetlands is likely to be limited by warming and drying of wetland soils, and the associated production and loss of CO_2 through decomposition (e.g., Alaska: three-fold increase, Funk et al., 1994; Finland: Aurela et al., 2001). This effect is likely to lead to substantial losses of CO_2 and potential climate feedbacks.
- Methane production and emissions are likely to decline as high-latitude wetland soils dry with rising temperatures and increased evapotranspiration, and with regional declines in precipitation (e.g., Finland: Minkkinen et al., 2002; Greenland: Joabsson and Christensen, 2001). Moore T. and Roulet (1993) have suggested that only a 10 cm deepening of the water table in northern forested peatlands results in their conversion from a source to a sink of atmospheric CH_4. Methanotrophy is likely to be most pronounced in drier wetlands that tend toward aerobic conditions. The projected shift in vegetation toward woody species will possibly also limit CH_4 release to the atmosphere (section 7.5.3.2; Liblik et al., 1997).
- Methane production in some wetlands is likely to increase as temperatures and rates of methanogenesis increase, and as water tables rise in response to regional increases in water availability (e.g., Finland – projected 84% increase in CH_4 release from wet fen with 4.4 °C temperature increase, Hargreaves et al., 2001; Alaska – 8 to 33-fold increase in CH_4 emissions with high water table, Funk et al., 1994). Methane production will probably increase in those wetlands that have highly saturated soils and standing water, and those that may become wetter with future climate change, with potential climate feedbacks.

Overall, arctic and subarctic wetlands are likely to become greater sources of CO_2 (and in some instances CH_4) initially, as permafrost melts, and over the long term, as wetland soils dry (Gorham, 1991; Moore T. et al., 1998). Although many high-latitude wetlands are likely to experience a net loss of carbon to the atmosphere under future climate change, the expansion of wetland (e.g., peatland) distribution in the Arctic, and the increase in carbon accumulation with permafrost

degradation, is likely to offset this loss (see section 7.5 for further treatment of this topic).

In addition to wetlands, wholly aquatic systems (rivers, lakes, and ponds) are also important to carbon cycling in the Arctic. Kling et al. (2000) showed that high-latitude lakes in Alaska were net producers of DOC, whereas streams were typically net consumers. Many arctic lakes and rivers are supersaturated with CO_2 and CH_4, often emitting these gases to the atmosphere via diffusion; increases in productivity (e.g., primary and secondary) deplete carbon in surface waters, resulting in diffusion of CO_2 into the water (see Fig. 8.7; Kling et al., 1992b; Schindler D.E. et al., 1997). Kling et al. (1992b) found that coastal freshwater systems release carbon in amounts equivalent to between 20 and 50% of the net rates of carbon accumulation in tundra environments. Enhanced loadings of carbon to arctic lakes and rivers as permafrost degrades (surface and groundwater flows contribute dissolved CO_2 and CH_4, as well as POC) will affect carbon cycling in these systems in a number of ways.

Dissolved organic carbon loading of lakes and rivers is likely to result in increased primary productivity and associated carbon fixation. This increase in photosynthetic CO_2 consumption by aquatic vegetation (e.g., algae, macrophytes) will possibly reduce emissions of this gas from lake waters to the atmosphere. This effect has been noted in experimental fertilization of both temperate and arctic lakes (Kling et al., 1992b; Schindler D.E. et al., 1997). Nutrient loading of high-latitude rivers, however, is unlikely to have a similar effect, as these waters have a rapid rate of renewal.

Although DOC loading of surface waters will possibly cause a decline in CO_2 emissions from some lakes, increased inputs of DOC and POC will possibly offset this effect and, in some cases, increase CO_2 production. Enhanced DOC and POC loads increase turbidity in some lakes, reducing photosynthesis (section 8.4.4.3). This rise in the availability of organic matter will probably result in a concomitant increase in benthic microbial respiration, which produces CO_2 (Ramlal et al., 1994). These effects are likely to be less pronounced or absent in flowing-water systems.

Increased nutrient loading and water temperature in high-latitude freshwater bodies are also likely to enhance methanogenesis in sediments. Slumping of ice-rich Pleistocene soils has been identified as a major source of CH_4 release from thermokarst lakes, such as in extensive areas of north Siberian lakes (e.g., Zimov et al., 1997), and may explain high winter concentrations of atmospheric CH_4 between 65° and 70° N (Semiletov, 2001; Zimov et al., 2001). Methane produced in such systems is often released to the atmosphere via ebullition, a process that will probably increase as the open-water season lengthens. Emission of CH_4 to the atmosphere is also likely to be enhanced in lakes, ponds, and streams that experience an increase in macrophytic growth, and an associated increase in vascular CH_4 transport.

8.5. Climate change effects on arctic fish, fisheries, and aquatic wildlife

Fish and wildlife intimately associated with arctic freshwater and estuarine systems are of great significance to local human populations (Chapter 3) as well as significant keystone components of the ecosystems (see e.g., section 8.2). Accordingly, interest in understanding the impacts of climate change on these components is very high. However, in addition to the problems outlined in section 8.1.1, detailed understanding of climate change impacts on higher-order biota is complicated by a number of factors:

- Fish and wildlife will experience first-order effects (e.g., increased growth in arctic taxa due to warmer conditions and higher productivity) of climate change as well as large numbers of second-order effects (e.g., increased competition with species extending their distribution northward). The responses of such biota will integrate these sources in complex and not readily discernible ways; further, responses to climate change will be embedded within those resulting from other impacts such as exploitation and habitat alteration, and it may be impossible to differentiate these. These multiple impacts are likely to act cumulatively or synergistically to affect arctic taxa.
- Higher-level ecosystem components affect lower levels in the ecosystem (i.e., top-down control) and in turn are affected by changes in those levels (i.e., bottom-up control). The balance between such controlling influences may shift in indiscernible ways in response to climate change.
- Higher-level ecosystem components typically migrate seasonally between habitats or areas key to their life histories – arctic freshwater fishes and aquatic mammals may do so locally, and aquatic birds tend to do so globally between arctic and non-arctic areas. Thus, the effects of climate change on such organisms will represent the integrated impacts across numerous habitats that indirectly affect the species of interest.

These biotic circumstances increase the uncertainty associated with developing understanding of species-specific responses to climate change, particularly for key fish and other aquatic species that are of economic and ecological importance to arctic freshwater ecosystems and the communities of northern residents that depend on them.

8.5.1. Information required to project responses of arctic fish

Implicit in much of the previous text is the linkage between atmospheric climate parameters and habitat parameters present in aquatic ecosystems, and the linkage of these to effects manifested in organisms and populations. It follows from this logic that changes in climate regimes, however they may manifest, will only indirectly

affect aquatic organisms of interest. That is, the aquatic environment itself will be directly affected by changes in climate, but will modify and then transmit the influences in some fashion. Thus, for example, substantive shifts in atmospheric temperature regimes will affect water temperatures, but given the density differences between water and air and the influence of hydrodynamic factors, the effects on aquatic systems will be modified to some degree. In turn, changes in atmospheric parameters will have indirect effects on biota present in aquatic systems and thus may be ameliorated or partially buffered (e.g., thermal extremes or seasonal timing shifted). In some instances, however, climate change effects may be magnified or exacerbated, increasing the multiplicity of possible outcomes resulting from these changes. For example, stream networks amplify many environmental signals that occur at the watershed level, and that are concentrated in the stream channel (Dahm and Molles, 1992). This added level of complexity and uncertainty in the magnitude and direction of climate change manifestations in arctic freshwater ecosystems is not as acute for terrestrial environments. It results in greater uncertainty in projecting potential impacts on aquatic organisms. Figure 8.16 provides an example of the logical associations and direct and indirect effects of climate parameters on anadromous fish and the various aquatic environments used.

8.5.1.1. Fish and climate parameters

The Arctic as defined in this chapter (Fig. 8.2) includes high-, low-, and subarctic areas defined by climate, geography, and physical characteristics. In addition, many areas included in this assessment (e.g., southern

Alaska, the southern Northwest Territories, northern Scandinavia, and Russia) are significantly influenced by nearby southern maritime environments and/or large northward-flowing rivers. This proximity ameliorates local climatic regimes, resulting in more northerly distributions of aquatic taxa than would otherwise occur based strictly on latitudinal position. Moreover, the Arctic includes many different climatological zones. Given that the distribution of many freshwater and anadromous fish species is controlled or significantly influenced either directly or indirectly by climate variables (particularly temperature), it follows that primary associations of fish distribution with climate variables will be important.

Fish are ectotherms, thus, for the most part, their body temperature is governed by that of the surrounding waters. In addition, individual fish species can behaviorally choose specific thermal preferenda (preferred optimal temperatures; Beitinger and Fitzpatrick, 1979) at which physiological processes are optimal (i.e., greatest net benefit is achieved for the individual). This is typically a thermal range that may be fairly narrow; temperatures outside this are suboptimal (i.e., net benefit is still attained but it is not the greatest possible), grading to detrimental (i.e., non-lethal but net energy is expended while in such conditions) and ultimately to lethal conditions (i.e., death ensues after some level of exposure). Furthermore, within a species, local northern populations often have such preferenda set lower than do southern representatives, which presumably represents differential adaptation to local conditions. In addition, individual life stages (e.g., egg, alevin, juve-
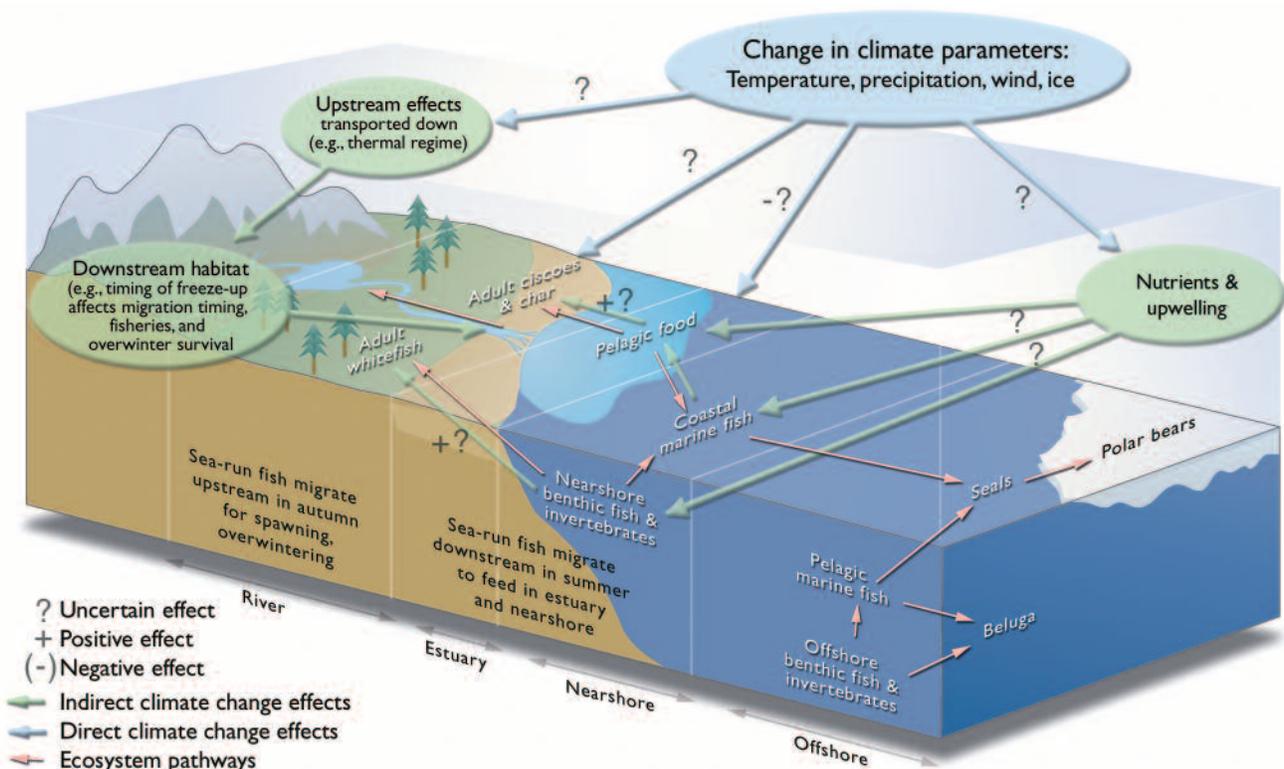

Fig. 8.16. A stylized portrayal of some potential direct effects of climate parameters on arctic aquatic environments and some potential indirect effects on aquatic organisms such as anadromous fish.

nile, adult) differ in their thermal preferenda linked to optimizing criteria specific to their developmental stage. For most species, only limited understanding of such thermal optima is available, and typically only for some life stages of southern species. Fish control body temperatures behaviorally, sensing and moving into appropriate, or from inappropriate, zones (Coutant, 1987). Aquatic thermal regimes are spatially and temporally heterogeneous and availability of water at the preferred temperature may be limited, making it an important resource for which competition may ensue. This may be particularly important in species found in Alaskan and Yukon North Slope rivers (e.g., Dolly Varden and Arctic grayling) during winter, when physical habitat is limited due to rivers freezing to the bottom over long reaches (Craig, 1989). Thus, the thermal niche of individual fish species can be defined.

Magnuson et al. (1979) grouped temperate species into three thermal guilds defined by thermal niches: Warmwater (preferred summer temperatures centered upon 27–31 ℃), Coolwater (21–25 ℃), and Coldwater (11–15 ℃). Following this approach, Reist (1994) defined an Arctic Guild as fish distributed wholly or primarily in northern areas and adapted to relatively colder waters (<10 ℃) and related aspects of the habitat such as short growing seasons, extensive ice presence, and long periods of darkness. Freshwater fishes occurring within the geographic definition of the Arctic as used here represent all of these guilds (Box 8.6), however, those of the Warmwater Guild tend to be present only along the southern margins of arctic waters, often associated with local climatic amelioration resulting from inputs from nearby maritime areas or northward-flowing rivers. Some of these guilds can be further subdivided based upon the nature of the fish distribution. Within the generalities discussed below, the impacts of climate change will be species- and ecosystem-specific, thus the following should be viewed as a range of possibilities only. In addition, although thermal regimes are emphasized in this discussion, the influence of other climate parameters may be equally or more important to specific species in particular areas or at particular times during life.

Species of the Arctic Guild have their center of distribution in the Arctic with the southern limits defined by, for example, high temperatures and associated ecological factors including competition from southern fish species. Fish such as broad whitefish (*Coregonus nasus*), Arctic cisco, and many char taxa are examples of Arctic Guild species. The pervasive and ultimate impacts of climate change upon such species are likely to be negative. These impacts generally will appear as range contractions northward driven by thermal warming that exceeds preferences or tolerances; related habitat changes; and/or increased competition, predation, or disease resulting from southern taxa extending their range northward, possibly preceded by local reductions in growth, productivity, and perhaps abundance. Many of these effects will possibly be driven or exacerbated by shifts in the life history of some species (e.g., from

anadromy to freshwater only). Other than conceptual summaries, no detailed research has been conducted to outline such impacts for most fish species of this guild.

Fish that have distributions in the southern arctic are northern members of the Coldwater Guild. This group includes species such as the lake/European/Siberian whitefish complex and lake trout, which have narrow thermal tolerances but usually are widely distributed due to the availability of colder habitats in water bodies (e.g., deeper layers in lakes; higher-elevation reaches in streams; Schelsinger and Regier, 1983). Two distributional subtypes can be differentiated: those exhibiting a wide thermal tolerance (eurythermal) as implied, for example, by a wide latitudinal distribution often extending well outside the Arctic (e.g., lake whitefish – *Coregonus clupeaformis*); and those exhibiting a narrow thermal tolerance (stenothermal) implied by occupation of very narrow microhabitats (e.g., lake trout occupy deep lakes below thermoclines in the south but a much wider variety of coldwater habitats in the north) and/or narrow latitudinal distribution centered in northern areas (e.g., pond smelt – *Hypomesus olidus*). The overall impacts of arctic climate change on these two distributional subtypes are likely to be quite different. Thus, eurythermal species are likely to have the capacity for reasonably quick adaptation to changing climate and, all other things being equal, are likely to exhibit increases in growth, reproduction, and overall productivity. Such species are also likely to extend the northern edge of their distribution further northward where this is at present thermally limited, but this is likely to be a secondary, relatively small response. Conversely, stenothermal coldwater species are likely to experience generally negative impacts. Lake trout in northern lakes, for example, will possibly be forced into smaller volumes of suitable summer habitat below deeper lake thermoclines and will possibly have to enter such areas earlier in the season than at present. Subsequent impacts on such species are very likely to be negative as well. To some degree, northern members of the Coldwater Guild are likely to experience the same general impacts as described for arctic-guild species in the previous paragraph (i.e., reductions in productivity characteristics, increased stress, local extirpation, and/or range contractions). Similar to the arctic-guild species, little or no detailed research assessing impacts on northern coldwater-guild fishes has been conducted to date.

Coolwater Guild species (such as perches) have southern, temperate centers of distribution but range northward to the southern areas of the Arctic as defined herein; these include northern pike (*Esox lucius*), walleye (*Sander vitreus*), and yellow perch (Schlesinger and Regier, 1983). Like those of the Coldwater Guild, these species can also be differentiated into eurythermal and stenothermal species. For example, the perches have a wide latitudinal range and occupy a number of ecological situations extending outside temperate regions, and hence can be described as eurythermal. Northward range extensions of approximately two to eight degrees

of latitude are projected for yellow perch in North America under a climate change scenario where annual mean temperatures increase by 4 °C (Fig. 8.17; Shuter and Post, 1990). Shuter and Post (1990) found that the linkage between perch distribution and climate was indirect; that is, the first-order linkage was the direct dependency of overwinter survival (and related size at the end of the first summer of life) on food supply, which limited growth. The food supply, in turn, was dependent upon climate parameters. Alternatively, many northern minnows (e.g., northern redbelly dace – *Chrosomus eos* – in North America) and some coregonines (e.g., vendace – *Coregonus albula* – in Europe) are proba-

bly stenothermal, as implied by their limited latitudinal range and habitat associations. Range contraction along southern boundaries is likely for these species, initially manifested as contraction of distribution within the local landscapes, followed by northward retraction of the southern range limit. Because of their stenothermal tolerances, however, their northward extension is not likely to be as dramatic as that described for perch. To some degree, the presence of many of these species in the large northward-flowing arctic rivers such as the Lena, Mackenzie, Ob, and Yenisey is very likely to promote their northward penetration. The associated effects of heat transfer by such river systems will facilitate north-

Box 8.6. Freshwater and diadromous fishes of the Arctic

There are approximately 99 species in 48 genera of freshwater and diadromous (i.e., anadromous or catadromous forms moving between fresh and marine waters) fish present in the Arctic as defined in this chapter (Fig. 8.2). These represent 17 families (see table). Ninety-nine species is a conservative estimate because some groups (e.g., chars and whitefishes) in fact contain complexes of incompletely resolved species. Many species are also represented by local polymorphic forms that biologically act as species (e.g., four morphs of Arctic char in Thingvallavatn, Iceland). The most species-rich family is the Salmonidae with more than 33 species present, most of which are important in fisheries. The next most species-rich family is the Cyprinidae with 23 species, few of which are fished generally, although some may be fished locally. All remaining families have six or fewer species, and five families are represented in the Arctic by a single species. These generalities hold true for the individual ACIA regions as well. All of the families represented in the Arctic are also present in lower-latitude temperate and subtemperate regions. Most have a southern center of distribution, as do many of their associated species (Berra, 2001). Individual species may be confined to the Arctic, or may penetrate northward from subarctic areas to varying degrees.

Freshwater and diadromous fish present in the Arctic.

Family name	Number of arctic forms in ACIA area		Number of species in ACIA regions				Thermal guild[a]	Exploitation in ACIA regions	Comments
	Genera	Species	1	2	3	4			
Petromyzontidae (lampreys)	2	5	4	2	2	1	Cool	Some in Region 1	
Acipenseridae (sturgeons)	1	5	2	2	1	1	Warm/Cool	Region 1, some in Region 4	
Hiodontidae (goldeyes)	1	1	0	0	1	0	Warm	Region 3 where they occur and are abundant	Goldeye (*Hiodon alosoides*), in North America only
Anguillidae (freshwater eels)	1	2	1	0	0	1	Warm	Region 1, eastern Region 4	Mostly in southern areas only
Clupeidae (shads[b])	1	3	2	0	1	0	Warm/Cool	Region 1, limited in Region 3	Southern areas in interior; also in northern coastal areas influenced by warm currents
Cyprinidae (minnows)	14	23	11	4	13	1	Warm	Some species in Regions 1 and 2; not exploited or limited elsewhere	Most species only occur in southern ACIA area
Catostomidae (suckers)	2	3	0	1	2	3	Warm/Cool/ Cold	Limited in Region 2 and western Region 4	
Cobitidae (loaches)	1	1	1	0	0	0	Warm	Not fished	Stone loach (*Noemacheilus barbatulus*) only. Subarctic only; very southern edge of Region 1
Esocidae (pikes)	1	1	1	1	1	1	Cool/Cold	Extensively fished in all four Regions	Northern pike (*Esox lucius*) only, and widely distributed

ward colonization by these species as well as eurythermal species also present in the systems. Knowledge of the association of ecological processes with climate parameters and research quantifying the potential impacts of climate change on coolwater-guild species, although inadequate overall, generally tends to be more comprehensive than for the previous two guilds, but is often focused upon southern populations. Hence, its applicability to arctic populations of the species may be limited.

Warmwater Guild species have their center of distribution well south of the Arctic. Those present in the Arctic as defined in this chapter are few in number (Box 8.6)

and with few exceptions (some cyprinid species) are generally distributed only in the extreme southern portions of the ACIA regions. In many areas of the Arctic, a number of species of this guild are present in southerly areas immediately outside the boundary of the Arctic. Presumably, their northward limit is in most cases determined by present thermal and ecological regimes, especially in the large northward-flowing rivers of Siberia and the western Northwest Territories. As the effects of climate change increasingly ameliorate local limiting factors, species of this guild are very likely to extend their geographic ranges into the Arctic or, if already there, to more northerly locales.

Substantive differences in the number of species present are apparent between the ACIA regions. Region 3 (unglaciated Beringia and the western Canadian Arctic) contains 58 named taxa, followed by Region 1 (Arctic Europe and Russia) with 38, while Regions 2 (Siberia) and 4 (eastern North America) are about equal at 29 and 32, respectively. This probably represents a combination of historical effects (e.g., glacial events, postglacial recolonization routes and access) as well as present-day influences such as local climate, habitat diversity, and ecological processes (e.g., competition and predation). Arctic char is the only species that is truly holarctic, being present on all landmasses in all ACIA regions, occurring the farthest north to the extremes of land distribution (~84° N), and also exhibiting the widest latitudinal range (about 40 degrees) of all true arctic species (i.e., south in suitable lakes to ~45° N). A few additional species are distributed almost completely across the Holarctic but are absent from one or more areas within an ACIA region (e.g., burbot with ~75% of a complete circumpolar distribution; northern pike with ~85%; lake whitefish, European whitefish, and Siberian whitefish (*Coregonus pidschian*) with ~85%; and ninespine stickleback with ~90%). With the exception of the stickleback, all are fished extensively where they occur, representing the mainstays of food fisheries for northern peoples and supporting significant commercial fisheries in most areas. These species are often the only ones present in extremely remote areas, inland areas, and higher-latitude areas, and thus are vital for local fisheries. Where they are regionally present, many other species are exploited to a greater or lesser degree.

Family name	Number of arctic forms in ACIA area		Number of species in ACIA regions				Thermal guild[a]	Exploitation in ACIA regions	Comments
	Genera	Species	1	2	3	4			
Umbridae (blackfish[c])	1	2	0	0	2	0	Cold/Arctic	Limited at most, where they occur	Blackfishes (*Dallia* spp.) only
Osmeridae (smelts)	2	3	0	0	2	0	Cool/Cold	Limited at most, where they occur	
Salmonidae (salmon, char, whitefishes, ciscoes)	10	33+	9	14	22	14	Cool/Cold/Arctic	Most species extensively fished in all four Regions	Salmonids are the most widely distributed and abundant arctic group and fisheries mainstay
Percopsidae (trout-perches)	1	1	0	0	1	1	Cool/Cold	Not fished	Trout perch (*Percopsis omiscomaycus*) only
Gadidae (cods)	1	1	1	1	1	1	Cool/Cold	Extensively fished in all four Regions	Burbot (*Lota lota*) only, and widely distributed
Gasterosteidae (sticklebacks)	3	3	2	1	3	2	Warm/Cool/Cold	Not fished	
Cottidae (sculpins)	2	6	2	2	4	3	Cool/Cold	Not fished	
Percidae (perches)	4	6	2	1	3	3	Warm/Cool	Fished where they occur, especially Region 1	Mostly temperate species, but enter the Arctic via warmer northward-flowing rivers
Totals	48	99	38	29	58	32			
Total families	17	--	12	10	14	12			

[a]Magnuson et al. (1979) and Reist (1994); see section 8.5.1.1 for definitions; [b]only Alosinae (shads) are arctic representatives; [c]only *Dallia* (blackfish) are arctic representatives.

Fig. 8.17. Present and projected future distributional limits of yellow perch in North America. Northward displacements (shown by arrows) are based on overwinter survival assuming a 4 °C increase in mean annual temperature (adapted from Shuter and Post, 1990).

Thermal preferenda presumably optimize all internal physiological processes (i.e., benefits outweigh costs) in individual fish associated with digestion, growth, muscle (hence swimming) efficiency, gas exchange across gills, cellular respiration, reproduction, and so on. The relationship of temperature to such processes is perhaps most easily seen with respect to growth (e.g., increase in size or weight over time; Fig. 8.18). In addition to exhibiting higher growth rates at lower temperatures, arctic fish species also exhibit narrower ranges of temperature preference and tolerance (i.e., stenothermic; Fig. 8.18), which has profound effects on productivity. Stenothermic tolerances also imply that the species may have little capacity to accommodate thermal impacts of climate change. Conversely, species exhibiting eurythermic or wide thermal tolerances or responses are likely to have a much wider capacity to accommodate climate changes (see above and Box 8.6).

Population-level influences of thermal regimes are also apparent. Effects on individuals, such as temperature effects on mortality, feeding, parasitism, and predation, are integrated into consequences for fish populations through the various processes that connect fish populations to their ecosystems (Fig. 8.19). As noted previously, environmental parameters such as temperature may affect various life stages differently and thus can be modeled separately, but it is important to remember that the ultimate effects of all these influences are integrated throughout the fish population of interest. Similarly, environmental changes also have specific effects on other organisms relevant to fish, such as predators, parasites, and food organisms. Therefore, a single environmental parameter may exert both indirect and direct effects at many levels that influence the fish population, but the actual effect of this may be indiscernible from the effects of other natural and anthropogenic influences. Figure 8.19 provides examples of linkages between environmental parameters that affect key processes at the fish population level. Migratory aspects of life history are not shown in the figure, but will also (especially in anadromous fish) be significantly affected by abiotic processes.

Salinity will also be a factor for sea-run phases of adult life history. Climate change and increased variability in climate parameters will drive changes in aquatic abiotic parameters. Such changes will affect the fish directly as well as indirectly via impacts on their prey, predators, and parasites. This cascade of effects, and synergies and antagonisms among effects, greatly complicates the projection of climate change impacts on valued northern fish populations. In addition, other parameters not shown in Fig. 8.19, such as groundwater inflows to spawning beds, will affect the survival of various life-history stages. The ultimate effects of all these interacting factors will in turn affect sustainability of the populations and human uses in a fishery context.

Temperature effects on individual fish and fish populations are perhaps the most easily understood ones, however, other climate parameters such as precipitation (amount and type) will directly affect particular aquatic environmental parameters such as productivity (e.g., see Box 8.7) and flow regimes (amounts and timing). For example, flattening hydrographs and shifts in water sources (sections 8.4.2 and 8.4.3) are very likely to alter the availability of arctic rivers as migratory routes for anadromous fish. Increased and earlier vernal flows are very likely to enhance fish survival during out-migration and lengthen the potential summer feeding period at sea (both positive effects at the levels of the individual fish and the population). However, autumnal flows are required in many smaller rivers to provide access to returning fish (Jonsson, 1991); reduction in amounts and shifts in timing of these flows are very likely to have negative effects. Svenning and Gullestad (2002) examined environmental influences on migrations of Arctic char, particularly local temperature
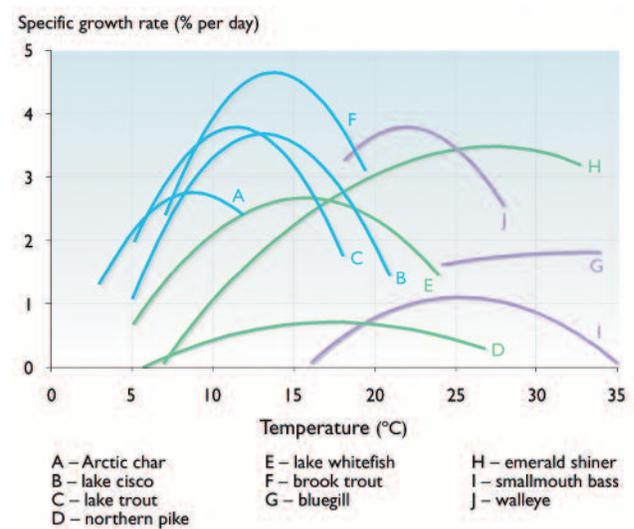

Fig. 8.18. Growth rates of fish species at varying temperatures determined from laboratory studies. Stenothermic northern species (e.g., A, B, C, and F) are grouped towards the lower temperatures on the left, whereas mesothermic southern species (e.g., G, I, and J) are grouped towards the right. Stenothermic species tend to have a more peaked curve indicating only narrow and typically low temperature ranges over which optimal growth is achieved. Wide-ranging eurythermic species (e.g., D, E, and H) probably exhibit the greatest possibilities for adapting rapidly to shifting thermal regimes driven by climate change.
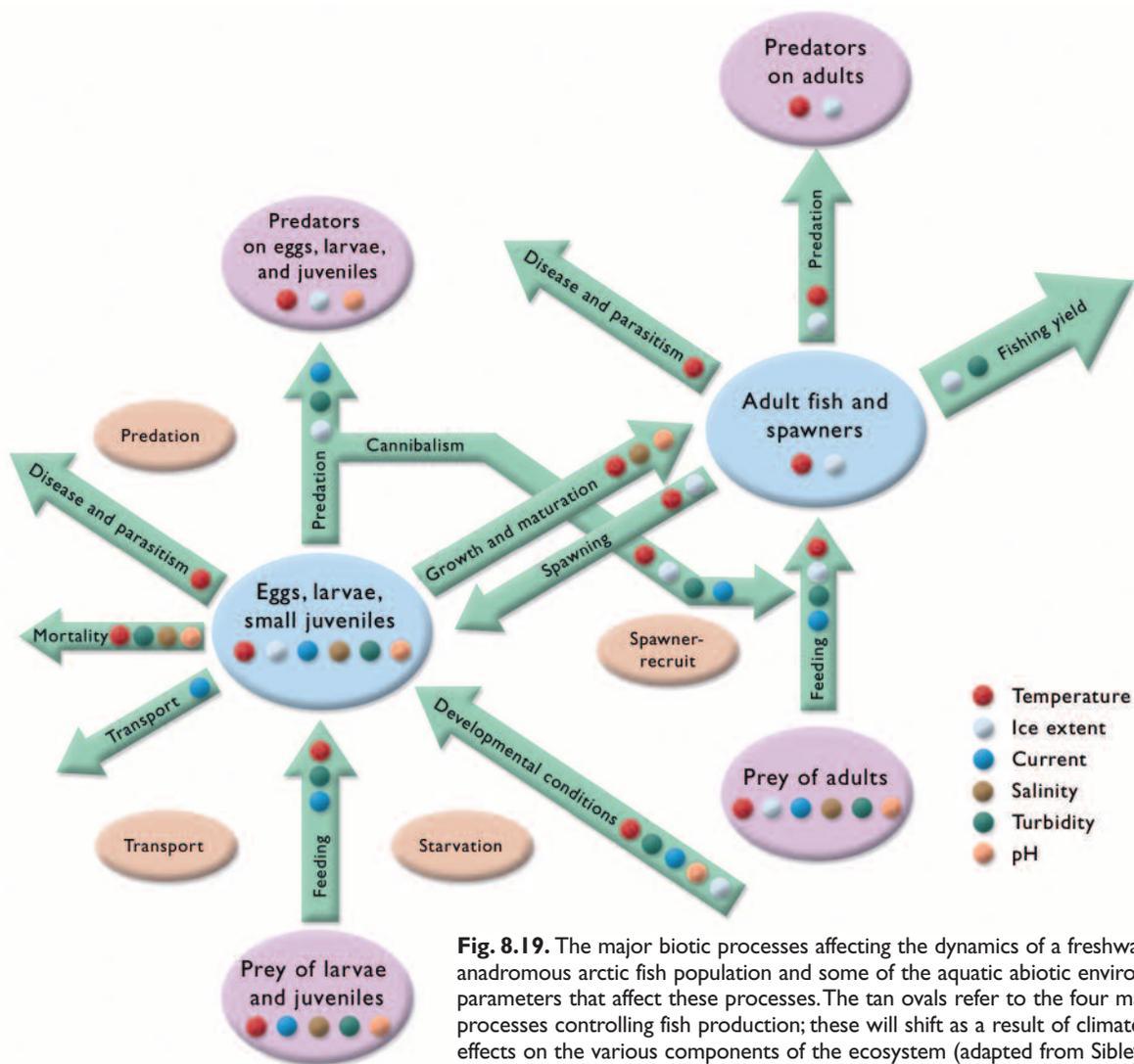
Fig. 8.19. The major biotic processes affecting the dynamics of a freshwater or anadromous arctic fish population and some of the aquatic abiotic environmental parameters that affect these processes. The tan ovals refer to the four major processes controlling fish production; these will shift as a result of climate change effects on the various components of the ecosystem (adapted from Sibley and Strickland, 1985).

effects on flow regimes and the consequences for fish population abundance and structure.

Additional secondary environmental factors that may change in response to direct changes in basic climate parameters will also have important effects on aquatic biota. These include the nature and duration of freeze-up, ice types, ice-cover periods, and breakup, and the nature and penetration of incident radiation into aquatic systems. Similarly, terrestrial impacts of climate change may influence aquatic habitat and indirectly affect its biota (e.g., permafrost alteration and runoff influences on sediment loads, pH and related water chemistry, etc.). Another potential class of indirect effects of climate change includes those affecting the behavior of aquatic biota. For example, fish use thermal regimes and spatiotemporal shifts in these regimes, at least in part, as behavioral cues or thresholds to trigger critical life history functions. Water mass boundaries defined by temperature act as barriers to movement and may define feeding areas (Coutant, 1987). Final gametic maturation in autumn-spawning species is probably triggered by decreasing water temperatures and perhaps also photoperiod in arctic whitefishes. There is anecdotal evidence that decreased sediment loads resulting from freezing of riverbanks trigger final

upstream movements by broad whitefish from holding areas to spawning sites (Reist and Chang-Kue, 1997), an adaptation to ensure eggs are not smothered. Water temperature integrated over time (e.g., as degree-days) affects the rate of egg development. Thus, aquatic thermal regimes affect ectotherms such as fish in two basic ways: by influencing physiology and as cues for behavioral changes. Although typically less understood, similar effects probably result from other physical (e.g., currents, flows, turbidity, ice dynamics) and chemical (e.g., pH, oxygen) parameters in the aquatic habitat (e.g., Sibley and Strickland, 1985). Climate-induced alteration of these habitat characteristics is very likely to significantly affect arctic fish populations, although substantive research is required to quantify such effects.

Freshwater and diadromous fishes of the Arctic exhibit high diversity in the way that climate parameters affect their distributions, physiology, and ecology. These factors, together with the more complex indirect effects that climate may have upon their habitats, implies a wide range of possible responses to climate change. Other than logical extrapolations, most responses to climate change are impossible to quantify due to the absence of basic biological information for most arctic

Box 8.7. Effects of environmental change on life-history and population characteristics of Labrador Arctic char

Present-day relationships between environmental and biological parameters must be understood to provide the foundation for assessing future climate change effects on fish populations. The general lack of such understanding for most arctic fishes currently precludes in-depth development of comprehensive and accurate qualitative scenarios of impacts, and limits quantification of effects under those scenarios. Development of such understanding requires substantive long-term data that are relatively sparse for most arctic fish; a circumstance that demands redressing. A notable exception is the availability of data for Arctic char. The distribution and life-history patterns of Arctic char are complex, and few attempts have been made to relate fluctuations in abundance, catch rates, and stock characteristics to environmental variables such as temperature and precipitation. The table lists associations between biology and variability in environmental parameters for Arctic char from northern Labrador, Canada.

Environmental associations for Nain Arctic char.

Timing	Significant environmental parameters	Probable environmental effect	Observed biological effect on individual fish	Observed biological effect on fish population
Within year	Summer air temperature	Increased marine productivity within limits	Increased weight	Better condition
			Increased length	
	Sea-surface temperature		Increased growth	
First summer of life	Winter precipitation	Increased snowpack	Increased overwinter survival	More fish
		Decreased seasonal freezing		
		More overwintering habitat	Decreased energetic costs for maintenance (increased growth)	Earlier recruitment to the fishery (i.e., lower age-at-catch)
Fourth year of life (first year at sea)	Summer air temperature	Increased nutrient loading to nearshore habitat	Increased growth	Increased weight at catch
	Summer precipitation	Increased nearshore productivity	Increased survival	Decreased age-at-catch

Long-term (1977–1997) monitoring of the char fishery at Nain, Labrador (56° 32' N, 61° 41' W) has produced data on both anadromous fish and environmental variables that have been applied in assessing long-term variability in catch biometrics (Power M. et al., 2000). Climate variability, particularly annual and seasonal, was found to have effects at critical life-history stages, and to affect average stock age, weight, and length characteristics, thus determining the dynamics of exploited Arctic char populations several years later and their eventual spawning success (Power M. et al., 2000). The table also summarizes aspects of climate variability and the probable effects on the population.

Mean age-at-catch and weight of Arctic char from the Nain fishery declined significantly, with a lag of four years, in response to high summer precipitation. This precipitation-related change is probably due to fluctuations in river flow and nutrient dynamics during the initial migration of Arctic char to nearshore marine areas. First-time migrants tend to stay in the nearshore areas (Berg, 1995; Bouillon and Dempson, 1989) and are most likely to be immedi-

fish species and the incomplete understanding of the overall associations of ecological processes with present-day climate parameters.

8.5.1.2. Ecosystems, habitat, and fish: climate change in the context of multiple stressors

Aquatic ecosystems are highly structured and complex entities consisting of both abiotic and biotic elements, and functional relationships within and between those elements. Similarly, individual components of ecosystems, such as a single fish species, exhibit a unique but complex structure. From the perspective of an individual or even a population, climate parameters and change in them may be experienced as either a stressor (i.e., that which perturbs homeostatic systems; Adams S., 1990), or as a promoter (i.e., that which promotes homeostasis). Stressors and promoters directly and indirectly influence underlying physiological processes and their outcomes at both the level of the individual and that of the population. Points of action within individuals range from the molecular to the organismal level; those affecting whole individuals overlap with effects on populations and communities (Adams S., 1990). Events occurring at other levels of the hierarchy also influence the various organizational levels. Levels within the individual tend to have short-term responses and limited overall ecological relevance, whereas those at the population/community/ecosystem level tend to be longer-term responses with higher ecological relevance (Adams S., 1990). Given the structured complexity inherent in a fish population, the effect of any particular

ately affected by changes in nutrient inputs resulting from variability in river flow. High-precipitation years increase nutrient and POC exports from river and lake catchments (Allan, 1995; Meyer and Likens, 1979), which increase nutrient inputs to nearshore marine feeding areas and probably increases productivity at all trophic levels.

The significance of increased winter precipitation is related to events occurring in the first critical winter of life for char. Heavier, more frequent snowfalls in Labrador maintain ice cover in an isothermal state and limit ice thickness (Gerard, 1990). Deeper snowpack maintains taliks, or unfrozen areas, in lake and river beds (Allan, 1995; Prowse, 1990), improving winter refugia conducive to fish survival (Allan, 1995; Power G. and Barton, 1987; Power G. et al., 1999).

The possible effects of temperature on Arctic char are complex. Mean fish length increased with rising summer temperatures and the persistence of optimal growth temperatures (12–16 °C) over a longer period of time (Baker, 1983; Johnson, 1980). High spring temperatures and accelerated ice breakup, however, can have negative effects on populations migrating with ice breakup (Nilssen et al., 1997). In the Fraser River (Labrador), breakup typically occurs in late April or early May (Dempson and Green, 1985) and would be well advanced, as would seaward migration, in years experiencing above-normal May temperatures. Although temperature increases can advance preparatory adaptations for marine residency (i.e., smoltification), they also result in a more rapid loss of salinity tolerances and a shortening of the period for successful downstream migration (McCormick et al., 1997). Rapid increases in temperatures are likely to impinge on the development of hypo-osmoregulatory capabilities in migrants and decrease growth due to the increased energetic costs of osmoregulatory stress, increase the probability of death during migrations to the sea, and decrease average growth by reducing the average duration of marine residence.

Several conclusions arise from this study:

- Long-term, comprehensive biological and environmental datasets are critical to assess and monitor climate change impacts on fish populations.
- Climate variables are very important in understanding year-to-year variability in stock characteristics.
- Causative relationships appear to exist between life history and environment but precise roles played, timing of the effect, and limits to the effect need more thorough investigation.
- For long-lived arctic fish, the effects of particular environmental conditions are often lagged by many years, with cascading effects on fishery production and management.
- Environmental effects are manifested in the fish population in the same way that other effects such as exploitation are (e.g., in terms of individual growth that translates into survival, fitness, reproduction, and ultimately into population-dynamic parameters such as abundance), thus distinguishing specific effects of climate change from other proximate drivers may be problematic.
- Particular environmental effects tended to reinforce each other with respect to their effect on the fish; although generally positive in this study, effects from several environmental parameters could presumably act antagonistically resulting in no net effect, or could synergistically act in a negative fashion to substantially impact the population.

stressor or promoter can be manifested at many levels simultaneously; can interact with others in an additive or cumulative fashion; and can typically be observed (if at all) in wild populations only at the more general population or community level.

For example, the effect of a temperature change may induce a short-term physiological response in an individual (e.g., processes occurring outside of the zone of optimal enzyme performance), a medium-term acclimatization response such as expression of new enzyme alleles optimal for the new temperature, and a somewhat longer-term response of changed biological condition. Concomitant expressions at the population level might be a shift in age structure, lower overall abundance, and ultimately local extirpation or adaptation to new conditions.

Another important point is that at least locally, the impacts of climate change on fish populations will be but one of several stressors. Other stressors affecting arctic fish both now and in the future include exploitation, local habitat change due to industrial development or river regulation, contaminant loadings, and changes in incident UV radiation levels. These stressors will result in effects similar to those described for climate change at individual and population levels. However, all these stressors will also interact additively and multiplicatively on individual fish and fish populations; hence, the effects are likely to be cumulative (Reist, 1997b). Perhaps the greatest future challenge associated with climate change will be to effectively recognize and manage in an integrated fashion all potential and realized impacts on arctic fish populations to ensure their conservation and sustainability.

8.5.1.3. Effects of climate-induced changes on physical habitat

Physical changes in aquatic habitats will very probably affect arctic fishes as climate changes in the north. This section provides some examples to illustrate the linkages and various potential effects on biota, but the underlying absence of data precludes quantification of causal linkages in most cases. Rectifying these and similar knowledge gaps is a major future challenge.

Groundwater and fish

Groundwater flows sustain fish habitat and are extremely important during periods of low flow in many arctic rivers (Power G. et al., 1999) and perhaps some lakes (sections 8.2 and 8.4). For stream-dwelling salmonids, inflows along stream bottoms clear fine-grained sediments from spawning areas, supply thermally regulated and oxygenated water to developing eggs and larval fish, and in many cases provide physical living space for juvenile and adult fish. In highly channeled shallow arctic rivers that characterize many areas of the North American Arctic and Chukotka, groundwater inputs are critical to fish migrations and stranding prevention (Power G. et al., 1999). In winter, many Alaskan and western Canadian North Slope rivers cease flowing and freeze to the bottom over large stretches, and groundwater provides refugia that support entire populations of Arctic grayling and Dolly Varden as well as any co-occurring species (Craig, 1989). Overwintering mortality, especially of adults weakened from spawning activities, is suspected as a primary regulator of the populations of Dolly Varden in this area and a major factor in such mortality is the quality and amount of winter habitat maintained by groundwater. Possible increases in groundwater flows resulting from climate change are likely to positively affect overwinter survival, especially if coupled with shorter duration and thinner ice cover. However, increased nutrient loadings in groundwater will possibly have more complex impacts (e.g., increases in in-stream primary and secondary productivity are likely to promote growth and survival of larval fish, but increases in winter oxygen demand associated with vegetation decomposition will possibly decrease overwinter survival of larger fish). How these various effects will balance in specific situations to result in an overall net effect on particular fish populations is unknown.

In summer, ground and surface water inflows ameliorate summer temperatures and provide thermal refugia, especially along southern distributional margins (Power G. et al., 1999). This is probably especially relevant for fish belonging to the arctic and coldwater thermal guilds. However, even the small increases in water temperatures (2 to 4 ℃) that are likely to result from climate change (e.g., warmer surface flows) will possibly preclude some species from specific aquatic habitats (e.g., temperature in higher-elevation cold-water stream reaches determines habitat occupancy of bull trout – *Salvelinus confluentus*; Paul and Post, 2001). Increased

ambient conditions above physiological thermal optima are very likely to further stress populations and, combined with other possible effects such as competition from colonizing southern taxa, such impacts are likely to exacerbate range contractions for arctic species.

Ice and fish

The influence of ice on arctic fish and fish habitat is significant, especially in smaller lotic systems important to salmonids (Craig, 1989; Cunjak et al., 1998; Power G. et al., 1999; Prowse, 2001a,b). Effects include possible physical damage (e.g., from frazil ice), limitation of access to habitat (e.g., decreasing water volumes in winter due to ice growth), and annual recharge of habitat structure during dynamic breakup (e.g., cleansing of interstitial spaces in gravel). Shifts in the timing and duration of ice-related events are very likely to affect the survival and success of fish, with some effects being advantageous and others disadvantageous. In the north, these effects will be superimposed upon a poorly known but complex biological and environmental situation. Limited knowledge precludes accurate forecasting of many of these potential effects, and novel approaches are required to redress this (Cunjak et al., 1998).

Decoupling of environmental cues due to differential effects of climate change

A speculative issue, which may present surprises and unanticipated effects, is the potential for decoupling of various types of environmental drivers due to climate change affecting some differentially. Fish and other organisms use progressive and/or cusp-like changes in environmental parameters as cues to trigger key life-history functions such as migration, reproduction, and development. For example, although quantitative linkages are lacking, change in photoperiod (e.g., declining light period) is probably coupled with declining water temperatures in the autumn and together these trigger final gonadal maturation and reproductive activities in many northern fishes (especially salmonids). Environmental cues that drive major life-history events are especially critical for migratory species, and in the Arctic, particularly for anadromous species. This coupling is probably especially strong in the north where both parameters change rapidly on a seasonal basis. Although not explored to date in the context of climate change, as seasonal photoperiod shifts remain unchanged but coincident cues such as declining temperatures occur later in the autumn, such decoupling will possibly have profound impacts on population processes. The initial impact of such decoupling may be quite subtle (e.g., lowered fecundity, fertilization success, and/or egg survival in the previous example), not readily discernible, and almost certainly not directly attributable to climate change. However, a critical threshold is likely to be reached when impacts become significant (e.g., total reproductive failure in one year resulting in a failed year class, ultimately leading to population extirpation if it occurs over successive years

approaching the generation time of the population). Investigation of coupling between cues, their influence upon population processes in fish and other aquatic organisms, and their potential for decoupling due to climate change in the Arctic should be a priority.

These are but a few examples of likely influences of physical habitat on fish populations and the potential effects of climate-induced change on them that will have cascading effects on the integrity, sustainability, and future productivity of northern fishes. These serve to illustrate the general lack of knowledge that exists regarding associations between physical habitat and biology in northern aquatic biota, and thus how the impacts of climate change impacts will manifest. Redress of this knowledge gap is required on a community- and/or species-specific basis to account for local and historical influences and filters, which greatly affect the present-day structure and function of these aquatic ecosystems (Tonn, 1990).

8.5.1.4. Issues at the level of fish populations

As implied previously, projecting climate change impacts at the population level for most species is complex and fraught with uncertainty, especially for arctic species for which there is a dearth of fundamental biological information. A variety of approaches to address this problem are available (section 8.5.2) and most have been applied in one way or another to develop some understanding of climate change impacts on northern fish populations.

In North America, much of the research focus on climate change effects on freshwater fish populations and communities has been in the south, for example, in the Great Lakes region and associated fisheries (e.g., Assel, 1991; Hill and Magnuson, 1990; Magnuson et al., 1990; Meisner et al., 1987; Minns and Moore, 1992; Regier et al., 1990, 1996; Shuter and Post, 1990; Smith J., 1991). In that region, climate change is projected to result in effects similar to those projected for the Arctic (e.g., significant reductions in the duration and extent of ice cover, an earlier seasonal disappearance of the 4 °C depth isotherm, measurable declines in DO, and slight hypolimnetic anoxia in shallower basins; Blumberg and Di Toro, 1990; Schertzer and Sawchuk, 1990). Loss of suitable cool-water habitat associated with lake warming is also projected, which will very probably differentially affect species within lacustrine fish communities (e.g., promote growth and survival in lake whitefish but negatively affect these in lake trout; Magnuson et al., 1990). Preliminary consideration of northern areas has occurred for European systems (e.g., Lehtonen, 1996). Relatively less attention has been paid to the possible effects of climate change on resident fish communities in other ecosystems, particularly those in the Arctic. With respect to freshwater fish populations, the IPCC (Arnell et al., 1996) concluded that fish populations in streams and rivers on the margins of their geographic distributions (e.g., arctic and

subarctic species) will be the first to respond to the effects of climate change because these systems have a high rate of heat transfer from the air. Some of these effects include:

- Nutrient level and mean summer discharge explained 56% of the variation in adult Arctic grayling growth over a 12-year period in two Alaskan rivers (Deegan et al., 1999). Summer temperature added to these variables explained 66% of variation in young-of-the-year growth. Correlation with discharge was positive for adults and negative for young, thus grayling life history appears able to respond to variability in the arctic environment by balancing adult growth with year-class strength. How this balance will shift under climate change is uncertain at present.
- Temperature effects on growth appear to be greatest at the extremes of the geographic range of the species (Power M. and van den Heuvel, 1999), and local effects will be species-specific (King et al., 1999). Generally, young-of-the-year fish appear to grow better in warmer summers and reach relatively larger sizes, predisposing them to higher overwinter survival, which determines year-class strength and population abundance (Shuter et al., 1980); potentially a positive result of climate change assuming food is not a limiting factor.
- Northern lake cisco (*Coregonus artedi*) populations along the coast of Hudson Bay exhibited reduced growth and later maturity due to lower temperatures and shorter growing seasons (Morin et al., 1982). Individual fecundity did not change, but the most northerly populations skipped reproduction more frequently (hence overall population productivity was lower). This latitudinal gradient represents responses to temperature stresses whereby further trade-offs in energy allocation between reproduction and growth currently are not possible (Morin et al., 1982); a common circumstance for most arctic fish populations and one that will probably be ameliorated under scenarios of increased temperature, potentially resulting in increased population abundances.
- Counter-gradient variation (Levins, 1969), whereby genetic influences on growth in species such as brown trout (*Salmo trutta*) vary inversely with mean annual water temperatures (Jensen et al., 2000), suggest that trout in the coldest rivers are specifically adapted to low temperatures and short growing seasons. Thus, increased temperatures are likely to negatively affect growth rates, age/size structure, and abundances of northern populations.

8.5.2. Approaches to projecting climate change effects on arctic fish populations.

Uncertainty in projections of future temperature, hydrology, and precipitation, and their associated consequences for vegetation and nutrient patterns in arctic aquatic

ecosystems, makes projecting the specific effects of climate change on a fish species difficult. To date, fisheries literature has suggested three approaches to this problem:

1. the use of regionally specific climate projections that can be coupled directly to knowledge of the physiological limits of the species;
2. the use of empirical relationships relating local climate (weather) to measurements of species or stock dynamics (e.g., abundance, size, growth rate, fecundity) and comparison of population success temporally (e.g., from a period of climatically variable years) or spatially (e.g., locales representing the extremes of variation in weather conditions such as latitudinal clines); and
3. the use of current distributional data and known or inferred thermal preferences to shift ecological residency zones into geographic positions that reflect probable future climate regimes.

8.5.2.1. Physiological approaches

Temperature is typically regarded as a factor affecting individual physiological and behavioral processes, but it is also a key characteristic of the habitat of an organism. Hutchinson (1957) defined the niche of an animal as the complete range of environmental variables to which it must be adapted for survival. At the fringes of the distributional range, abiotic parameters associated with particular niche axes are likely to exert a greater influence over the physiological responses (e.g., growth) of the species to its environment than elsewhere. Growth rates and population dynamics of fish living at the limits of their distribution usually differ from those of the same species living in the optimum temperature range (Elliott, 1994). For example, in studies of northern populations of yellow perch, Power M. and van den Heuvel (1999) noted that although heterogeneous thermal environments allow fish opportunities to compensate for temperature fluctuations by selecting for preferred temperatures, such opportunities are limited in the portion of the geographic range where temperatures do not typically exceed those that define the optimum scope for growth. Accordingly, unless future temperatures increase above the point where the maximum scope for growth is realized, northern fish will be limited in their abilities to select for optimal growth temperatures and, consequently, are very likely to more strongly reflect the influence of temperature on growth than southern populations. This also suggests that analogues derived from lower-latitude populations will not be accurate guides to the probable impacts of temperature increases on subarctic and arctic fishes. Nevertheless, the effects of climate change in the north are very likely to include faster, temperature-driven growth and maturation rates, reductions in winter mortality, and expanded habitat availability for many species (Regier et al., 1996). However, somatic gains will possibly be offset by increased maintenance-ration demands to support temperature-induced increases in metabolism. Ration demands for lacustrine fish are likely to be met as tem-

peratures increase, since warm-water lakes are generally more productive than cold-water lakes (Regier et al., 1996). Basic knowledge of temperature–growth relationships and temperature-dependent energy demands is lacking for many key arctic fish species, particularly those exhibiting primarily riverine life histories, thus accurate physiologically based projections of climate change impacts cannot be made.

8.5.2.2. Empirical approaches

Empirical approaches to projecting the possible effects of climate change on fish populations can be subdivided into two groups. The first group examines the integrated responses of a population measured by yield or production over time. The second group examines the population characteristics spatially and uses inherent latitudinal variability to make inferences about how they will change under climate change scenarios.

Temporal Yield/Production Projections: There are numerous models for projecting freshwater fish production in lakes (see Leach et al., 1987). However disagreement exists among researchers as to which lake characteristics most significantly influence productivity. Comparative studies based on lakes covering a wide range of geographic areas and trophic status have suggested that fish production in oligotrophic to hypereutrophic lakes of moderate depth is better correlated with primary production than the morphoedaphic index (Downing et al., 1990). Limitations surrounding such modeling center on the deficiencies in fish distribution data and knowledge of the interactive effects of climate-induced changes in key environmental variables (Minns and Moore, 1992). Together with limited fishery databases of sufficient length, these limitations in most cases preclude this approach for projecting productivity changes in arctic populations.

Latitudinal Projections: Organism life-history characteristics often vary with latitude because of predictable changes in important environmental factors (e.g., Fleming and Gross, 1990; L'Abée-Lund et al., 1989; Leggett and Carscadden, 1978; Rutherford et al., 1999). Among the most important environmental factors which may vary with latitude is temperature, which is known to influence growth rate in fish populations (Elliott, 1994; Wootton, 1990) and thereby indirectly affect life-history attributes that determine population dynamics (e.g., longevity, age-at-maturity, and fecundity). In salmonids, temperature has been shown to influence movement and migration (Jonsson, 1991), habitat occupancy (Paul and Post, 2001), migration timing (Berg and Berg, 1989), smolting (McCormick et al., 1998; Power G., 1981), growth rate (Brett et al., 1969; Jensen et al., 2000), age-at-maturity (L'Abée-Lund et al., 1989; Power G., 1981; Scarnecchia, 1984), fecundity (Fleming and Gross, 1990), and the proportion of repeat spawners (Leggett and Carscadden, 1978). Many studies have demonstrated latitudinally separated disparate populations of the same species with distinctive

metabolic rates, thermal tolerances, egg development rates, and spawning temperature requirements consistent with a compensatory adaptation to maximize growth rates at a given temperature (Levinton, 1983). Fish living in low-temperature, high-latitude locales would therefore be expected to compensate by increasing metabolic and growth rates at a given temperature relative to fish in high-temperature, low-latitude locales. There are two generalizations that may be made from studies on latitudinal variation in growth rates: high-latitude fish populations often attain larger maximum body size than conspecifics at lower latitudes; and, although lower temperatures often reduce activity and constrain individuals to grow more slowly, they compensate by accelerating growth rate or larval development time relative to low-latitude conspecifics when raised at identical temperatures. Although adaptation to low temperature probably entails a form of compensation involving relative growth acceleration of high-latitude forms at low temperature, the shift in metabolism increases metabolic costs at higher temperatures, leaving cold-adapted forms with an energetic disadvantage in the higher-temperature environments (Levinton, 1983) that are likely to result from climate change. Accordingly, fish populations are likely to be locally adapted for maximum growth rate and sacrifice metabolic efficiency at rarely experienced temperatures to maximize growth efficiency at commonly experienced temperatures. This suggests that the effects of temperature increases on northern fish will possibly include decreased growth efficiency and associated declines in size-dependent reproductive success. Therefore, particular responses to temperature increases are likely to be population-specific rather than species-specific, which greatly complicates the ability to project future situations for particular species over large areas of the Arctic.

8.5.2.3. Distributional approaches

Many attempts to project biological responses to climate change rely on the climate-envelope approach, whereby present-day species distributions are mapped with respect to key climate variables (e.g., temperature, precipitation) and the distributions shifted in accordance with climate change projections (e.g., Minns and Moore, 1992). For example, Shuter and Post (1990) have argued that weight-specific basal metabolism increases as size decreases with no associated increase in energy storage capacity, resulting in smaller fish being less tolerant of the starvation conditions typically associated with overwintering. Size-dependent starvation endurance requires that young-of-the-year fish complete a minimum amount of growth during their first season of life. Growth opportunity, however, is increasingly restricted on a south–north gradient and the constraint has been demonstrated to effectively explain the northern distributional limit of yellow perch in central and western North America (Fig. 8.17), European perch (*Perca fluviatilis*) in Eurasia, and the smallmouth bass in central North America. If winter starvation does form the basis for the geographic distributions of many fishes (e.g., 11 families and 25 genera of fish within Canadian waters; Shuter and Post, 1990), climate-induced changes in growing-season length, and consequent reductions in the period of winter starvation, are very likely to be associated with significant range extensions of many species. Species already well established within low-arctic watersheds are likely to show the greatest potential for range extensions. Associated changes in species assemblages are likely to shift patterns of energy flow in many aquatic systems. For example, increasing the number of cyprinids that consume plankton (e.g., emerald shiner – *Notropis atherinoides*, lake chub – *Couesius plumbeus*) in northern waters will possibly divert energy from existing planktivores (e.g., ciscoes) and reduce their population abundances. In turn, top predators (e.g., lake trout) are likely to have altered diets and changes in the ratio of pelagic and benthic sources of carbon in piscivore diets are likely, in turn, to alter tissue mercury concentrations (Power M. et al., 2002; section 8.7), thus linking general climate change impacts with local contaminant loadings.

The dominant result of simulations used to project the impact of climate change on the distribution and thermal habitat of fish in north temperate lakes is an increase in available warmer habitat. Temperature influences on thermal habitat use are strong enough that Christie and Regier (1988) were able to develop measures of thermal habitat volume during the summer period by weighting the amount of lake-bottom area and pelagic volume with water temperatures within species' optimal thermal niches. Thermal habitat volume explained variations in total sustained yield of four commercially important species: lake trout, lake whitefish, walleye, and northern pike.

Although distributional changes provide a convenient and easy means of assessing possible range extensions, the flaw in the approach is that species distribution often reflects the influence of interactions with other species (Davis et al., 1998; Paine, 1966) or historical effects (Tonn, 1990). Projections based on changes in single-species climate envelopes will therefore be misleading if interactions between species are not considered when projections are made. Microcosm experiments on simple assemblages showed that as the spatial distribution of interdependent populations changed as a result of temperature increases, the pattern and intensity of dispersal also changed. Thus, climate change will possibly produce unexpected changes in range and abundance in situations incorporating dispersal and species interaction (e.g., competition and predator–prey dynamics). Feedbacks between species are likely to be even more complex than simple experiments allow (Davis et al., 1998); for example, distributions of stream-resident salmonids are not simple functions of either temperature or altitude (Fausch, 1989). Accordingly, whenever dispersal and interactions operate in natural populations, climate change is likely to provoke similar phenomena and projections based on extrapolation of the climate envelope may lead to serious errors (Davis et al., 1998).

In theory, the temperature signal should be strong enough to project long-term changes in the availability of fish thermal habitat and to use available empirical relationships to project sustainable yields. However, until the results of such research are available for arctic fishes, interannual variability and latitudinal differences in climate will provide the best tests for hypotheses about the importance and effects of climate change on arctic fish species (Magnuson and DeStasio, 1997).

8.5.3. Climate change effects on arctic freshwater fish populations

The ability of fish to adapt to changing environments is species-specific. In the case of rapid temperature increases associated with climate change, there are three possible outcomes for any species: local extinction due to thermal stress, a northward shift in geographic range where dispersive pathways and other biotic and abiotic conditions allow, and genetic change within the limits of heredity through rapid natural selection. All three are likely to occur, depending on the species (Lehtonen, 1996). Local extinctions are typically difficult to project without detailed knowledge of critical population parameters (e.g., fecundity, growth, mortality, population age structure, etc.). Dispersal and subsequent colonization are very likely to occur, but will very probably be constrained by watershed drainage characteristics and ecological and historical filters (Tonn, 1990). In watershed systems draining to the north, increases in temperature are very likely to allow some species to shift their geographic distribution northward (see section 8.5.1.1). In watershed systems draining to the east or west, increases in temperature will possibly be compensated for by altitudinal shifts in riverine populations where barriers to movements into headwaters do not exist. Lake populations needing to avoid temperature extremes are very likely to be confined to the hypolimnion during the warmest months provided anoxic conditions do not develop. Patterns of seasonal occurrence in shallower littoral zones are very likely to change, with consequent effects on trophic dynamics. Changes in species dominance will very probably also occur because species are adapted to specific spatial, thermal, and temporal characteristics that are very likely to alter as a result of climate-induced shifts in precipitation and temperature.

Before successful range extensions can occur, habitat suitability, food supply, predators, and pathogens must be within the limits of the niche boundaries of the species. In addition, routes to dispersal must exist. Physiological barriers to movement such as salinity tolerances or velocity barriers (i.e., currents) will possibly restrict range extensions where physical barriers to migration (e.g., waterfalls, non-connected drainage basins) do not exist. Against this background of dynamic physical and biotic changes in the environment, some regional and species-specific climate change projections have been made.

8.5.3.1. Region 1: European percids

Under scenarios of climate change, spawning and hatching of spring and summer spawning populations are likely to occur earlier in the year. For example, European perch are very likely to advance spring spawning by as much as a month (Lehtonen, 1996) and juveniles will very probably experience longer growth periods and reach larger sizes at the end of the first summer. However, this species may not realize the potential benefits of increased size if higher egg incubation temperatures are associated with smaller larvae having smaller yolk sacs and increased metabolic rates (e.g., Blaxter, 1992; Peterson R. et al., 1977). Small larvae are more susceptible to predation, have higher mortality rates, and have a shorter period during which they must adapt to external feeding to survive (Blaxter, 1992). In addition, increased overwinter survival is very likely to be associated with increased demand for prey resources and will possibly lead directly to population stunting (i.e., smaller fish sizes).

The zander (*Sander lucioperca*) is a eurythermal species distributed widely in Europe whose growth and recruitment success correlates with temperature (Colby and Lehtonen, 1994). The present northern distribution coincides with the July 15 °C isotherm and is likely to shift northward with climate change. Successive year-class strengths and growth rates in northern environments are also likely to increase as temperatures increase. Increases in both abundance and size are very likely to have consequences for the competitiveness of resident coldwater-guild fishes if concomitant increases in lake productivity fail to yield sufficient ration to meet the needs of expanding populations of zander and other percids. Evidence that northward colonization is already occurring comes from the Russian portion of Region 1. Over the last 10 to 15 years, northern pike, ide (*Leuciscus idus*), and roach (*Rutilus rutilus lacustris*) have become much more numerous in the Pechora River Delta and the estuary Sredinnaya Guba (~68° N) of the Barents Sea (A. Kasyanov, Institute of Inland Waters, Russian Academy of Sciences, pers. comm., 2004).

8.5.3.2. Region 2: Fishes in Siberian rivers

Many species of fish in the large northward flowing rivers of Siberia have the potential for significant northward range extensions and/or responses to climate change. Several species in the Yenisey and Lena Rivers that prefer warmer boreal-plain habitats (e.g., roach, ide, common dace – *Leuciscus leuciscus baicalensis*, European perch, and ruffe – *Gymnocephalus cernuus*) are likely to move into the northern mouth areas of these rivers that are currently dominated by whitefishes and chars. Overall, fish species diversity is likely to increase, but this probably will be at the expense of the coldwater salmonids. The speed at which this process might occur is uncertain, however, it may already be occurring and is likely to be within approximately the next ten years. In addition, as environments change, intentional stocking of other species (e.g.,

carp bream – *Abramis brama* and zander) is likely to occur in the area, which is likely to result in additional pressures upon native arctic fish populations.

8.5.3.3. Region 3: Alaskan game fish

Nutrient availability often determines food availability and lotic productivity, which are believed to be major controlling factors in riverine fish production. Several studies have found that fish density and growth correlate with nutrient status and food availability in streams, with larger standing crops in nutrient-rich streams (Bowlby and Roff, 1986; McFadden and Cooper, 1962; Murphy et al., 1981). In particular, salmonid biomass in nutrient-poor environments varies with nutrient levels, habitat type, and discharge (Gibson R.J. and Haedrich, 1988). The bottom-up propagation of nutrients through algal and invertebrate production to fish has been projected to be a possible result of climate-induced increases in nutrient additions associated with permafrost degradation. However, this premise has rarely been tested, and the relationship between nutrient loading and fish production is poorly understood (Peterson B. et al., 1983). Shifts in stable carbon and nitrogen isotope distributions have demonstrated a coupling between the stimulation of benthic algal photosynthesis and accelerated growth in stream-resident insect and fish populations (Peterson B. et al., 1993). In addition, experimental fertilization of Alaskan tundra rivers has demonstrated increased growth rates for adult and young-of-the-year Arctic grayling, with the strongest response observed in the latter (Deegan and Peterson, 1992).

Temperature increases associated with climate change are also likely to be associated with lower flows, with which growth of adult Arctic grayling is also highly correlated. At low flows, adult growth is low, whereas young-of-the-year continue to grow well (Deegan and Peterson, 1992). As Arctic grayling in many Alaskan systems are already food-limited, the associated increases in metabolic costs are likely to be associated with decreased survival unless nutrient loading associated with permafrost degradation offsets the increased metabolic costs of low-flow conditions (Rouse et al., 1997).

Lake trout are a keystone predator in many Alaskan lakes. Low food supply and temperatures, however, keep the species near physiological limits for survival with the result that lake trout will possibly be particularly sensitive to changes in either temperature or food supply initiated by climate change (McDonald M.E. et al., 1996). Increases in temperature are very likely to increase metabolic demands, which will very probably lead to lower realized growth rates unless met by sufficient increases in ration.

Many populations are already food-limited, which suggests that further increases in temperature are very likely to have significant effects on population abundance. Bio-energetic modeling of juvenile populations of lake trout in the epilimnion of Toolik Lake suggests that they will not survive a 3 °C increase in mean July epilimnetic temperatures given existing ration, and would require a greater than eight-fold increase in food to achieve historical end-of-year sizes (McDonald M.E. et al., 1996). Documented increases in epilimnetic temperatures, however, have not been associated with increased food availability. If recent changes in the lake foreshadow long-term trends, these modeling results suggest that young lake trout will not overwinter successfully, and the associated changes in mortality patterns may lead to local extinction and the disruption of lake-trout control of the trophic structure in many arctic lakes (McDonald M.E. et al., 1996).

8.5.3.4. Region 4: Northern Québec and Labrador salmonid and pike populations

Among the salmonids of northern Québec and Labrador, the response to temperature changes is very likely to track physiological preferences for warmer waters. Several species, such as native Atlantic salmon and brook trout (*Salvelinus fontinalis*) and introduced brown trout and rainbow trout (*Oncorhynchus mykiss*), are very likely to extend their ranges northward. While the warmer-water percid and cyprinid species are restricted to the southwest and unlikely to extend their range to the north (unless moved by humans) because of dispersal barriers (Power G., 1990b), the euryhaline salmonids are able to move from estuary to estuary as conditions allow. For example, Dumont et al. (1988) documented the successful movement of rainbow and brown trout and exotic salmon species in the estuary of the Gulf of St. Lawrence, and there is some indication that brown trout dispersal in Newfoundland has been temperature-limited (Crossman, 1984). As a result of probable range extensions, Arctic char are very likely to be reduced or replaced by anadromous Atlantic salmon and/or anadromous brook trout throughout much of the southern portion of the region and brook trout are very likely to become a more important component of native subsistence fisheries in rivers now lying within the tundra zone (Power G., 1990b). Lake trout are likely to disappear from rivers and the shallow margins of many northern lakes and behave as currently observed in temperate regions (Martin and Olver, 1980).

Northern pike habitats in much of subarctic North America and Europe are projected to sustain some of the most severe consequences of global climate change. Adult northern pike actively avoid surface temperatures in excess of 25 °C, which are very likely to become more frequent as air temperatures increase throughout much of the distributional range. In shallower lakes, changes in lake chemistry associated with temperature increases will possibly result in cooler bottom waters becoming anoxic and a restriction of suitable habitat (e.g., Schindler D.W. et al., 1990). Studies in Ohio impoundments have shown that although northern pike show summer growth, there is an associated weight loss during the periods of habitat restriction (Headrick and Carline, 1993). Accordingly, northern pike throughout much of their current range

are expected to be restricted in both numbers and size as a result of climate change.

Attempts to relate fish yields and mean annual air temperatures have been coupled with geographic information techniques to project shifts in both distribution and yields of important freshwater fishes in this region (Minns and Moore, 1992). In general throughout subarctic Québec, yields for lake whitefish are projected to increase by 0.30 to >1.0 kg/ha/yr. Northern pike yields in southern portions of the Hudson Bay drainage are projected to increase by 0.03 to 0.10 kg/ha/yr, and those in northern portions to increase marginally (0.01–0.03 kg/ha/yr). Walleye yields in the southern drainage basin of Hudson Bay are projected to increase by 0.01 to 0.10 kg/ha/yr. These changes are projected to result from occupancy of new, presently unsuitable areas in the north, and increased overall productivity throughout the entire area. Declining production in southern areas that become unsuitable due to suboptimal thermal regimes for these species or local population extirpation may possibly offset the overall productivity gains.

8.5.4. Effects of climate change on arctic anadromous fish

About 30 species within the arctic regions belonging to the families Petromyzontidae, Acipenseridae, Anguillidae, Clupeidae, Osmeridae, Salmonidae, and Gasterosteidae (Box 8.6) exhibit diadromous behavior (i.e., spend part of their lives in the marine environment and migrate to freshwater to spawn, or the converse). Most arctic diadromous species are actually anadromous (i.e., use estuarine and/or marine environments for feeding and rearing; and freshwater environments for spawning, early life history, and, in the case of most arctic species, overwintering); only freshwater eels (Anguillidae) and some lampreys (Petromyzontidae) are catadromous (i.e., breed at sea and rear in freshwater). Most anadromous species in the Arctic are facultatively anadromous (Craig, 1989) in that many individuals in a population do not necessarily migrate to sea even though it is accessible. Typically, anadromous behavior is most prevalent at northern latitudes (McDowall, 1987) because the ocean is more productive than adjacent freshwater habitats in

Box 8.8. Projecting stock-specific effects of climate change on Atlantic salmon

Differences in stock characteristics, local geography, and interannual variations in spawning escapement of Atlantic salmon confound attempts to apply the results of specific field studies (e.g., Buck and Hay, 1984; Chadwick, 1987; Egglishaw and Shackley, 1977, 1985) in projecting the effects of climate change (Power M. and Power, 1994). Further complications arise from the ongoing debate regarding whether environmental variation and population effects are greatest in fresh or marine waters (Friedland, 1998), and how these act to determine survival of various life stages and population abundance. Knowledge of Atlantic salmon biology, however, is sufficient to describe the range of temperature conditions required for optimal growth and reproductive success, and thus to allow inferences of climate change effects. Atlantic salmon life-history stages all occur within optimal temperature ranges (Dwyer and Piper, 1987; Peterson R. and Martin-Robichaud, 1989; Power G., 1990a; Wankowski and Thorpe, 1979). However, variation in the required range of optimal temperatures for salmon at different life stages makes projecting the effects of climate change difficult. To date, three approaches to tackling the problem have been proposed in the scientific literature (see section 8.5.2).

Results of modeling experiments projecting the possible effects of climate change on different populations of Atlantic salmon (Power M. and Power, 1994).

Population location	Temperature increase		Temperature decrease	
	Smolt production	Parr density	Smolt production	Parr density
47° 01' N, 65° 27' W	decrease	increase	no change	no change
50° 11' N, 61° 49' W	increase	decrease	decrease	increase
53° 42' N, 57° 02' W	increase	decrease	decrease	increase

In the first approach, regional climate scenarios and projections are coupled directly to knowledge of the physiological limits within which salmon operate. For example, winter discharges and associated overwintering habitat will respond to precipitation changes (Power G., 1981). Low summer discharge on the east coast of Newfoundland and in southern Québec, which limits parr (young salmonid with parr-marks before migration to the sea) territory and hampers upstream adult migration, is also very likely to change, affecting population abundances in many rivers (Power G., 1981). Problems with this approach include uncertainty in precipitation and extreme events forecasts, and coupling of regional climate models with ocean circulation models.

A second approach to understanding the possible impacts of climate change on Atlantic salmon is to apply what is known about relationships between weather and salmon population dynamics. For example, historical records from the salmon fisheries in the Ungava region of northern Québec show a correlation between ice conditions, the late arrival of salmon, and poor catches. This relationship suggests that an improvement in salmon abundances will possibly occur in the future associated with a climate-induced reduction in the extent and duration of sea-ice cover (Power G., 1976; Power G. et al., 1987). The correlation between stock characteristics and latitude (Power

temperate and arctic zones (Gross et al., 1988). For a number of facultative anadromous species (e.g., Arctic char, Dolly Varden, brook trout, brown trout, and three-spine stickleback), anadromous behavior declines in frequency or ceases toward the southern portion of the distributional range of the species (several references in McDowall, 1987). Anadromy in Arctic char also declines or ceases towards the extreme northern geographic limits, probably because access to and time at sea, hence benefits, are limited. Facultative anadromous species exhibit anadromy in polar regions to take advantage of marine coastal productivity and escape extreme oligotrophic conditions that typify arctic lake systems. Generally, individuals of a population that exhibit anadromous behavior have a larger maximum size and higher maximum age, indicating some benefit to seaward migration and feeding.

Diadromous fishes will integrate climate change effects on freshwater, estuarine, and marine areas, hence the total impact on these fishes is very likely to be significant (e.g., see Fleming and Jensen, 2002; Friedland, 1998).

This will have major resulting impacts since these fishes support important fisheries in all arctic regions (section 8.5.5; Chapter 3). The following paragraphs discuss the consequences of climate change for diadromous fishes.

The projected impacts of climate change on arctic lakes suggest that, overall, productivity of these limited systems will very probably increase due to a longer ice-free growing season and higher nutrient loads. Anadromous fish populations will probably benefit initially with increases in survival, abundance, and size of young freshwater life-history stages, which will possibly cascade to older, normally anadromous stages. Thus, facultatively anadromous species will possibly exhibit progressively less anadromous behavior if the benefits of remaining in freshwater systems outweigh the benefits of migrating to coastal areas for summer feeding over time. Nordeng (1983) reported that when the freshwater food supply was experimentally increased, the incidence of anadromous migration by Arctic char decreased. However, the increased estuarine production discussed previously will possibly offset any tendency to reduce facultative

G., 1981) suggests that mean smolt (young salmonid which has developed silvery coloring on its sides, obscuring the parr marks, and which is about to migrate or has just migrated into the sea) ages are likely to decrease in association with increases in average temperatures and growing-season length. The modeling results of Power M. and Power (1994) projected that temperature increases and decreases will have varying effects on populations at different latitudes (see table). Where present-day temperatures are at the upper end of the optimal temperature range for growth, increases in temperature reduced growth, increased average riverine residency and associated riverine mortalities, decreased smolt production, and increased parr densities. The reverse (increased smolt production and decreased parr densities) occurred when temperatures at the lower end of the temperature range optimal for growth were raised. Modest changes in precipitation, and thus available habitat, had no significant direct effect or interactive effect with changes in temperature on either smolt production or parr density under any of the considered temperature scenarios. Thus, depending upon the exact location and characteristics of the salmon population, the precise impact of a given environmental change under a future climate scenario may be positive or negative relative to present conditions. This makes regional differences in fish biology, present-day local climate, and climate change scenarios extremely important in projecting future situations.

A third approach to projecting the effects of climate change involves attempting to shift ecological zones into more appropriate geographic locations to reflect probable future climate regimes and the known physiology of potentially affected species. The present distribution of many fish is limited by the position of the summer isotherms that limit the fish either directly due to thermal relationships or indirectly through effects on critical resources such as food (Shuter and Post, 1990). Use of this approach suggests that Atlantic salmon will possibly disappear from much of their traditional southern range in both Europe and North America as temperatures rise, and find more suitable habitat in cold rivers that experience warming. In the eastern Atlantic, the overall area occupied by salmon is likely to shrink due to a lack of landmasses to the north with potentially suitable environments. In the western Atlantic, rivers in the Ungava Bay area will possibly become more productive and are likely to experience increases in the numbers of salmon (e.g., the Koroc and Arnaux Rivers). Rivers that currently have large salmon runs are also likely to become more productive (e.g., the George, Koksoak, and Whale Rivers) and experience associated increases in salmon abundances (Power G., 1990a). There are also rivers on Baffin Island and Greenland that will possibly become warm enough for Atlantic salmon to colonize. Such colonization, however, is likely to come at the expense of Arctic char populations that currently inhabit the rivers because of competition between the two species. Constraints on redistribution northward with climate change include reductions in the availability of spawning substrate with increased sediment loading of rivers, changes in stream and river hydrology, and delay in the establishment of more diverse and abundant terrestrial vegetation and trees known to be important for the allochthonous inputs that provide important sources of carbon for salmon (Doucett, 1999).

the relevant impacts of climate change on these species in marine waters.

Arctic freshwater fisheries generally involve mostly local indigenous peoples, although some may also involve non-indigenous local people as well as visitors to the Arctic. (See Chapter 3 for indigenous accounts of changes in fishes and fishing in recent years.) Although details vary locally, at least three types of freshwater fisheries can be distinguished:

- commercial fisheries, where the product is sold commercially either locally or often in markets far removed from the sources;
- recreational fisheries in which non-indigenous people participate primarily for the experience rather than for economic, cultural, or nutritional reasons; and
- domestic or subsistence fisheries conducted by indigenous or local peoples primarily for cultural and sustenance reasons (see also Chapter 12).

Arctic freshwater fisheries can be substantial but generally never achieve the same economic significance that marine fisheries do, in part due to abundances and in part due to the lack of fishery infrastructure (e.g., absence of processing plants in many areas such as the lower Lena River, extremely long distances to markets). For the nine arctic countries, reported commercial catches for northern fishes in 2000 (8 to 350000 tonnes) represented 0.002 to 32% of total commercial catches for all species within those countries (FAO, 2002), although about 10% or less of this catch was truly "arctic" as defined herein. Rather, arctic fisheries are diverse, locally widely dispersed, and target a variety of species that are locally abundant. Such fisheries are extremely important in meeting the needs of the local peoples and contribute significantly to the economy and society of northern peoples (see also Chapter 12), thus their value must be measured in more than simple economic terms and understood in the context of climate impacts.

8.5.5.2. Impacts on quantity and availability of fish

Over the short term, projected productivity increases in arctic freshwater ecosystems, increased summer survival and growth of young fish, and increased overwinter survival of fish will probably result in increased biomass and yields of many fished species. Production shifts will depend upon local conditions such as faunal composition of the fishes and food species, tolerances and reactions of individual species to climate change, and general productivity shifts in aquatic ecosystems (Lehtonen, 1996). However, there will be much regional and local variation and responses are likely to be primarily species- or ecosystem-specific (Tonn, 1990). Thus, for wholly freshwater species, shifts in productivity are more likely to occur in lakes along the southern fringe of the Arctic, and less likely to be observed in flowing-water ecosystems. For anadromous species, increased summer nearshore productivity will possibly enhance

growth rates, hence biomass and potential fishery yields. Furthermore, recent work conducted on Atlantic salmon while in marine waters suggests that warmer sea-surface temperatures (i.e., of 8–10 ºC) enhance survival in both winter (Friedland et al., 1993) and early summer (Friedland et al., 2003). Increased growth and survival are very likely to enhance fish returns to freshwaters. Shifts in river flow regimes critical to upstream migrations of anadromous fish, especially in the late summer, will possibly have a negative effect, counterbalancing any positive effects to some degree. Arctic freshwater fisheries production will probably show some increases over the next decade or two. The greatest manifestation of this increase is likely to occur at the southern boundary of the Arctic, and is very likely to involve species that are primarily subarctic (i.e., occurring throughout northern temperate regions and extending into the Arctic). Fisheries yields for such subarctic fish species (i.e., northern pike, lake whitefish, and walleye in eastern North America, and northern pike, European whitefish – *Coregonus lavaretus*, and percids in northern Europe) have been linked with species-specific (and perhaps region-specific) habitat optima (e.g., Christie and Regier, 1988; Lehtonen, 1996; Schlesinger and Regier, 1983). Such yield relationships have been further examined in the context of GCM projections of temperature increase for some areas (e.g., Québec and subarctic Canada; Minns and Moore, 1992; Shuter and Post, 1990). This regional approach suggests that, at least for deeper lakes and perhaps larger rivers, substantial redistribution of fishery potential driven by population productivity as well as by redistribution of species is very likely.

As thermal optima are exceeded locally, and perhaps as ecosystems re-equilibrate and nutrient limitations occur, reductions in biomass and yields are possible. For example, climate change will affect species individually owing to differential colonization, extinction, and productivity rates (Tonn, 1990). This will possibly lead to substantive ecological reorganization (Peterson G. et al., 1997). These effects are likely to be most severe for true arctic species such as broad whitefish and Arctic char, which will possibly also be affected by increased competition from more southerly species extending their geographic distributions northward. Thus, in the longer term, the effects of climate change on the yields of arctic fisheries are likely to be negative for true arctic fish species but positive for subarctic and northern temperate species.

As freshwater productivity increases, the frequency of anadromy will possibly decrease within populations that exhibit facultative anadromy (e.g., Arctic char, Dolly Varden, and broad whitefish). Given that anadromy and feeding at sea results in greater size at a given age and larger populations (Gross et al., 1988), a switch away from anadromy is likely to result in decreased productivity. To ensure sustainability, this may necessitate lower harvests of native anadromous species; shifts in harvesting of alternate species, if available; and/or a change in location or timing of fisheries. The consequences of these changes

in fisheries of local indigenous people who rely on the autumn upstream runs of anadromous fish are very likely to be substantial from economic (i.e., protein replacement and increased costs to travel to new fishing areas for smaller catches), social, and cultural perspectives.

As noted previously, one of the hallmarks of climate change in the Arctic is likely to be increased interannual variability in climate parameters. Although it may be partially lost in the background noise of typically high inherent variability in arctic climate, this in turn will possibly increase the variability of good and poor year-classes in arctic fish. The consequence of this for fisheries will probably be increased variability in fishing success and unstable yields of targeted species. Such increased variability is very likely to exacerbate problems discussed previously that affect the biomass and yields of fisheries. Consequences include those associated with domestic sustenance if the local people rely heavily on the fished species, as well as difficulties with developing stable commercial or recreational fisheries that are economically viable and sustainable. As climate change becomes more pronounced, southern fish species are very likely to colonize newly available areas, enhancing the possibility of negative impacts on arctic fish species from competition. However, they may also represent opportunities for new fisheries. Hence, flexible, adaptive management will be key to the success of future fisheries (Peterson G. et al., 1997), particularly in responding to uncertainties associated with available data; an attribute not currently present in many fishery management regimes in the Arctic (e.g., Reist, 1997a; Reist and Treble, 1998).

Availability of fish species to fisheries will probably change as a result of several factors. For example, most fished arctic species are salmonids that tend to prefer cool or cold thermal regimes especially as adults (e.g., lake trout), thus they seek summer refuge in colder waters below thermoclines in lakes. As thermocline depths deepen, the availability of these species to fisheries will possibly change because deeper waters are more difficult to fish. This is very likely to occur in larger, deeper arctic lakes (e.g., Great Slave Lake in Canada) and will possibly necessitate gear changes for fisheries and/or retraining of fishers in new techniques. Questions as to how this might occur and how costs can be covered are currently not being addressed. In addition, the optimal temperature habitats of salmonids (e.g., European whitefish and brown trout) are very likely to change in northern Europe and summer temperatures in shallow arctic lakes will possibly become too high for these species (Lappalainen and Lehtonen, 1997), with consequent effects on local fisheries.

8.5.5.3. Impacts on quality of fish

Quality of fish captured in a fishery refers to its suitability for marketing (e.g., locally or distantly by trade, cultural exchange, and/or sale) and for consumption by humans. This suitability is affected by factors inherent in the fish resulting from environmental conditions experi-

enced prior to capture, as well as factors that affect the fish product after capture. Factors influencing fish quality before capture include "fish condition" (typically an index of weight and length that measures fatness or nutritional state or "well being"; Busacker et al., 1990); flesh firmness, which is typically influenced by water temperatures immediately prior to capture (i.e., warmer waters generally result in poorer-quality flesh); general appearance (e.g., color and lack of imperfections) of both the fish itself and key consumed organs such as livers; parasite loads and disease; and contaminant burdens. Factors influencing fish quality after capture include preservation (e.g., cooling or freezing), and the ease, conditions, and time associated with transport to the consumption site, market, or processing facility. As for all other impacts of change in climate parameters or UV radiation levels, both direct and indirect impacts will influence fish quality.

Indirect and direct impacts on quality of fish before capture are primarily those considered in previous sections. For example, impacts on ecosystem structure and trophic pathways are very likely to affect food availability (both amount and quality) to the fish, influencing fat levels and condition; impacts on migratory patterns or access are very likely to influence growth and condition; and impacts such as higher late-season water temperatures will possibly decrease flesh firmness of cold- and cool-water fishes such as salmonids, reducing either perceived or real quality. There is evidence that the color, size, and firmness of livers and flesh in some species is affected by nutritional state, for example, burbot (*Lota lota*) livers appear to be affected by fat content and presumably nutritional state (Lockhart et al., 1989). This appears to relate in part to seasonal variance in nutrition rather than specifically to environmental impacts such as contamination. Thus, climate change impacts that affect nutrition of fished species are very likely to have consequent effects on fish quality, but these may be difficult to distinguish from ongoing typical seasonal effects.

Some additional potential impacts are worth noting or emphasizing. In general, climate change is very likely to result in increased contaminant burdens in fish flesh, with a concomitant decrease in fish quality and acceptability for human consumption; these contaminant burdens will possibly exceed safe consumption limits. This will possibly be particularly acute for some contaminants such as heavy metals (e.g., mercury) and in some areas of the Arctic. Thus, cautions and caveats associated with arctic contaminants as discussed in the Arctic Monitoring Assessment Programme report (AMAP, 1998) will possibly become more relevant as climate change occurs (see also section 8.7).

Furthermore, the potential impacts of climate change on fish parasites and hence on fish quality have been poorly addressed but appear to represent major higher-order impacts (Marcogliese, 2001). Potential direct impacts on aquatic parasites include many of the same ones noted for fish species, for example, both biological challenges

and opportunities associated with parasite physiology either as a direct effect of the environment on the parasite (e.g., higher temperatures and/or shorter durations of low temperatures accelerating development) or as mediated through the host fish (e.g., shifts in fish feeding affecting parasite development). Higher parasite developmental rates suggest increased burdens upon fish hosts, which are very likely to result in decreased productivity of the population and/or poorer condition of individuals (Marcogliese, 2001). A further potential impact of parasites on arctic freshwater fishes is the introduction of new parasites to new host species or new areas (i.e., those not presently colonized) via host colonization of such areas through range extension. This will be complicated by a tendency toward higher levels of eutrophication in arctic water bodies associated with a general increase in temperature, resulting in changes in the species composition of both parasite and fish communities. In addition, disruption of normal developmental synchronicities between parasites and host fish, such as seasonal migrations within a water body, will possibly result in shifts in transmission rates to various hosts necessary to the life cycle of the parasite, but will possibly also result in switching to different hosts. Thus, parasites typically found in temperate fishes will possibly switch to arctic fishes, affecting the latter both biologically and from the perspective of quality. Shifts in thermal regimes that result in increased local densities of hosts, especially intermediate ones such as planktonic or benthic invertebrates, are also very likely to increase parasite species diversity (Marcogliese, 2001 and references therein). Conversely, activities such as fishing (which reduce the density of larger and older fish in relatively pristine fish populations, increasing the density of younger and smaller fish) can result in the "repackaging" of parasites and a net overall increase in parasite density within individual fish (T. Dick, University of Manitoba, Winnipeg, pers. comm., 2001). This reduces fish quality and marketability. The nature and timing of water delivery and potential shifts in overall amounts of precipitation may also affect parasite levels: a general increase in parasites and associated problems is likely to accompany a general decrease in water levels. Although poorly studied at present, the potential impact of fish diseases must also be addressed. Climate change is likely to result in increased incidence and spread of diseases, and perhaps increased intensity locally as fish populations are stressed. Furthermore, effects such as those associated with parasites, disease, and contaminants are part of the cumulative effects on local populations and must be considered when addressing issues of impacts on fish quality.

Many of these effects are most likely to occur, and present major problems for fish quality, in areas of the southern Arctic that presently have both reasonably high levels of exploitation and large southern catchments that flow north to the Arctic Ocean (section 8.2.3). Thus, problems that may be small at present and confined marginally to the southern Arctic will possibly increase in intensity and spatial distribution as climate change becomes more pronounced throughout the Arctic.

The impacts of increased UV radiation levels on some fish parasites will possibly be beneficial for fish by slowing infection rates and/or inhibiting the spread of some parasites (Marcogliese, 2001). However, immunosuppression resulting from increased UV radiation exposure will possibly exacerbate the effects of parasitism, disease, and contaminant loading on individual fish. This will possibly lower population productivity by decreasing survival. In addition, any obvious physical damage such as lesions or growths resulting from increased UV radiation exposure is very likely to decrease fish condition and quality.

8.5.5.4. Impacts on access to and success of fisheries

From the perspective of the fishers, climate change is very likely to have substantive impacts on how, when, and where fisheries may be conducted. Climate change will very probably affect access to and from fishing sites, and local knowledge associated with fish presence, migratory timing, and species composition. The success of the fisheries, especially as measured by transportation of high-quality product to market or point of consumption, is very likely to be similarly affected. Section 16.3 addresses some aspects of the latter impacts, such as transportation and infrastructure issues. Most arctic freshwater fisheries are small in scale, conducted locally and seasonally, and often use limited and relatively simple gear. Climate change impacts that fishers will very probably have to accommodate include increased frequency of extreme events such as high-intensity storms, and increased winter precipitation and stronger water flows that will possibly imperil the fishers, restrict their access to fishing sites, or result in the loss of fishing gear (hence economic burden). Generally, arctic freshwaters have long winter periods during which ice provides a stable platform for transportation across lakes and rivers and for deploying some types of fishing gear such as gill nets. Decreased length of the ice season, concomitant increases in the duration of freeze-up and breakup, and increased ice roughness from storms are very likely to result in substantive changes in timing, duration, and methods by which fisheries are conducted in the future. Chapter 3 documents indigenous observations of changes in ice, including declines in ice duration, thickness, stability, and predictability, which not only alter the timing and safety of ice travel, but also limit and reduce the success of traditional and subsistence activities such as ice fishing (e.g., sections 3.4.1 and 3.4.9).

Success of fisheries often depends upon the experience of the fishers, and for domestic fisheries is intimately connected with traditional knowledge of where and when to fish for particular species. The predictability associated with this will possibly decrease as climate change impacts occur. The timing of migratory runs, the typical keystone event in many northern domestic fisheries, is very likely to exhibit increased variability and decrease the ability of the fishers to know when best to begin fishing. Such circumstances will possibly result in decreased success of fisheries. Furthermore, such variability is likely to become the norm as ecosystems

undergo shifts, at least until new equilibriums are established. Because the changes wrought by climate change are likely to be protracted and depend in large part upon local ecological circumstances and the nature of the biota present, new equilibriums are unlikely to be quickly established. Thus, fishers will possibly have to tolerate highly variable and unstable conditions in freshwater and coastal ecosystems. This is very likely to result in highly variable successes in freshwater and anadromous fisheries, at least over longer timeframes.

Table 8.2. Summary of possible, likely, and very likely effects of changes in climate or UV radiation levels on *quantity* of fish in arctic freshwater and anadromous fisheries.

Climate change or UV radiation effect	Potential impact on fisheries	Consequences/comments
Increased productivity at lower trophic levels is very likely to result in increased growth, recruitment, and survival of freshwater species	Biomass and yields increased	Short-term management for increased fishery yields, especially for temperate species in the southern Arctic
Increased productivity at lower trophic levels is likely to result in increased growth in early years for facultatively anadromous species that promotes a shift to wholly freshwater life histories	Shifts in balance of anadromy versus non-anadromy decreases yields overall (i.e., smaller fish and perhaps more fish)	Long-term management for change in type and location of fisheries, and for decreased fishery yields
Local water temperature increases will at some point exceed thermal optima for individuals, possibly decreasing growth	Biomass and yields decreased	Especially true for arctic species and for cool-water species in the southern Arctic; population declines and local extirpation; synergistic effects from other factors such as competition from southern taxa; management issues associated with declining fishery yields
Reduced ice-cover duration on arctic lakes especially in northern arctic areas, increased and more rapid stratification, earlier and increased primary production, and decreased oxygenation at depth will possibly result in a reduction in the quality and quantity of habitat for species such as lake trout	Survival, biomass, and ultimately yields of preferred species generally decreased	Management for decreased fishery yields; potential management for declining fisheries and loss of populations
Improved quality of winter habitat will possibly result in increased survival (but this would also be affected by summer conditions, stratification, and overturns)	Biomass and yields increased	Short-term management for increased fishery yields; long-term implications unknown
Increased water temperatures generally and seasonally, but ultimately a decrease in summer habitat (e.g., deeper thermoclines in lakes, shrunken hypolimnia in lakes, reduced colder waters in rivers) are likely to reduce available habitat and decrease fish productivity, resulting in fish movements to deeper areas and/or fatal stresses on some fish species (e.g., Arctic grayling)	Short-term increase in biomass and yields (several to tens of years) Long-term decrease in biomass and yields (greater than tens of years) Decreased availability of traditionally targeted species and/or loss of key populations	Short-term management for increased fishery yields (e.g., limit growth of fishery) Long-term decrease in traditional fisheries, switch to alternative fisheries if available Long-term relocation of fisheries to new areas such as deeper portions of lakes, possible cost issues to support this relocation
Southern arctic and subarctic fish species very likely to extend distribution ranges northward, which is likely to result in some significant negative effects on native species	Decreased availability or local loss of native species; increased opportunity to fish new species (especially in southern arctic areas)	Management issues for emerging fisheries, i.e., manage to allow increase in populations and successful colonization of arctic areas; retooling and education in new ways of fishing if needed
Northern (wholly arctic) species are very likely to experience range contraction and/or local extirpation	Decreased availability of arctic species to local fisheries, potential for replacement by other species low or uncertain	Management issues for declining fisheries, and ultimately addressing rare or endangered species; in Canada this also has implications under land claim legislation for basic needs provisions
Decreased water flow in summer is likely to decrease habitat availability and possibly deny or shift access for migrating fish	Decreased biomass and yields Decreased availability due to changes in migratory runs	Management issues for declining fisheries Replacement of protein and potential social issues for peoples that heavily rely on traditional fishing; switch to other wildlife
Increased UV radiation levels in surface waters are likely to disrupt development and/or cause damage to young fish consequently decreasing survival, or forcing fish deeper thus slowing growth	Decreased biomass and yields	Management for declining fishery yields
Increased interannual variability in climate, aquatic habitats, productivity, and fish growth and production characteristics are very likely	Unknown: some arctic species are relatively long-lived indicating an ability to withstand prolonged periods of poor year-class success Increased frequency of good and poor year classes	Variability in fishing success; conservative management for median (at best) or low-yield year classes to ensure sustainability; management for highly unpredictable fisheries Instability in yields of targeted species results in uncertainty of product for fisheries
Increased water flows in winter, increased runoff in winter, and decreased spring floods	Changes in migratory runs; possible decreased biomass and yields	Revised management needs for relocated or declining fisheries

Another aspect that deserves consideration is shifts in species composition as new species colonize an area. If the new colonizer is similar to existing species (e.g., Pacific salmon as another salmonid present in an area), the existing experience and interest of fishers is likely to be applicable. Alternatively, if the new species represents an unfamiliar taxon, fishers will possibly have to build the experience base for capture and marketing, assuming the species is desirable. Undesirable species (defined by local needs and wants such as, for example, spiny-rayed species) will possibly prove to be pests by clogging nets and reducing capture efficiency. Such species may also be considered substandard for local use based upon either tradition or physical characteristics. Although highly adaptable, northern peoples will still require time and experience to modify existing practices and develop necessary adaptations for continuing successful fisheries.

Fishing as an industry carries relatively high inherent risks associated with the environment and with the tools employed. These include loss of equipment (i.e., fishing gear and boats) and injury and death of the fishers. Along with the projected changes and increased variability in climate systems, and thus decreased predictability associated with forecasts and environmental conditions, the incidence and severity of catastrophic climatic events such as severe storms are very likely to increase. Such circumstances will imperil fishers exposed to the elements. For example, protracted breakup or freeze-up periods will make ice conditions more unpredictable. Travel over ice is essential to arctic life and especially to early winter fisheries conducted through the ice; the choice facing fishers will be increased risk or decreased fishing time, hence decreased catch.

This general summary of the impacts of changes in climate and UV radiation levels on arctic freshwater and anadromous fisheries is by no means comprehensive. Tables 8.2, 8.3, and 8.4 summarize numerous additional potential impacts.

Detailed regional and local analyses of particular types of fisheries (e.g., commercial, recreational, or domestic) and of specific arctic freshwater and anadromous fisheries are required to more fully elucidate all impacts, understand their consequences for local fisheries, and stimulate the development of appropriate short- and long-term adaptive responses by fishery managers and related constituents of the fishery infrastructure. Failure to address these issues in a timely fashion will undermine coherent and comprehensive preparedness to meet challenges that changes in climate and UV radiation levels present for arctic freshwater and anadromous fisheries.

Table 8.3. Summary of possible, likely, and very likely effects of changes in climate or UV radiation levels on *quality* of fish in arctic freshwater and anadromous fisheries.

Climate change or UV radiation effect	Potential impact on fisheries	Consequences/comments
If water temperatures increase, thermal optima for individual growth are likely to be exceeded, resulting in negative effects on individuals	Individual fish condition reduced, thus quality is lower Biomass and yields are reduced	Especially true for arctic species and arctic-adapted cool-water species requiring thermal refugia; value of individual fish and total amount landed are reduced
If water temperatures increase, flesh firmness will possibly decrease due to capture in warmer waters	Flesh quality reduced	Value is reduced; preservation compromised
If air temperatures increase, fisheries may occur under warmer conditions, which is very likely to increase problems of preserving and transporting the product	Problems with immediate preservation increased (e.g., on-board refrigerators required) Transportation costs increased (i.e., faster method or more return trips to fish plants) or impossible Quality of product decreased Costs of production increased	Low-value marginal fisheries will not be economically viable; northern fishery development compromised; and some fisheries may be abandoned if transportation is not possible Consumption of lower-quality or poorly preserved product may increase human health risks
Changes in climate and/or UV radiation levels will possibly result in physical disfiguration of fish (e.g., discolorations, lesions, growths, etc.)	Perceived and real quality and value of fish decreased	Increased concern voiced by local peoples requiring appropriate investigation and response from management agencies, e.g., ruling out potential proximate causes other than changes in climate or UV radiation levels Increased inspection and addressing of real and perceived health concerns required
Changes in climate and/or UV radiation levels will possibly result in increased parasitism, and new parasites and/or diseases in traditionally fished arctic species	Decreased interest in fisheries especially those based upon high-quality fish (e.g., recreational fisheries)	Economic development compromised
Persistent contaminants mobilized from natural sources (e.g., mercury liberated by permafrost thawing or flooding), or fluxes from anthropogenic sources to arctic ecosystems increase, which is likely to result in higher body burdens in arctic fish and cascade effects on other higher trophic levels	Real and perceived quality of fish decreased Compromised fish health reduces growth, decreases biomass and fishery yields	Increased inspection and monitoring required Health concerns about fish consumption, especially for domestic fisheries that typically are not routinely monitored

Table 8.4. Summary of possible, likely, and very likely effects of changes in climate or UV radiation levels on the *success* of arctic freshwater and anadromous fisheries.

Climate change or UV radiation effect	Potential impact on fisheries	Consequences/comments
Increased climate variability and frequency of extreme events (e.g., storms affecting fishing, catastrophic winter fish kills) will possibly result in biological consequences for fish populations, consequent synergistic effects on biotic systems (e.g., parasites), and synergistic effects from other impacts (e.g., local industrialization)	Increased unpredictability in places, times, and amounts of fish present in an area, and amounts captured and transported to processing, distribution, or consumption points Increased risk of gear and boat loss Increased personal risk to fishers	Extreme unpredictability in fish volumes has significant consequences for local peoples relying on fish for sustenance, for infrastructure development to support fisheries (e.g., fishing supplies, fish processing plants, transportation), and for development of markets for products from commercial and sport fisheries Loss of gear decreases success, economic viability, and persistence of fishery Need for search and rescue increased; fishing as an occupation falls from favor with a societal cost
Shifted environmental regimes are likely to affect time and difficulty of transportation to fishing sites and of product from sites to distribution or consumption points	Decreased economic value (or increased cost) of many arctic fisheries remote from communities or without permanent access Costs associated with fishing are increased	Marginal fisheries not economically viable, fishery development compromised; increased reliance on local easily accessible domestic fisheries raises the probability of over-exploitation with consequent sustainability and management issues As/if domestic fisheries fail, issues with protein replacement from other sources increase
Changes in the distribution and abundance of traditionally harvested fishes will cause traditional fishing sites to have fewer fish available	Decreased harvests and fewer fish available for communities	Indigenous fishers are tied to location and particular species by tradition and adaptation may be difficult

8.5.5.5. Impacts on specific fishery sectors

In addition to the general impacts discussed previously, climate change will have impacts specific to the various types of fisheries conducted in the Arctic.

Commercial fisheries

Perhaps the most significant challenge facing commercial fisheries will be development of appropriate adaptive management strategies that deal with the complex, synergistic, and cumulative effects of climate change on fish populations and their environment, particularly in the context of sustainable use and long-term conservation.

For example, the conundrums of how to manage both declining and increasing populations of two fishable species in a particular location, how to understand and integrate climate change impacts through functional ecosystem pathways to project future states, and how to balance the needs of local peoples and competing demands all represent real problems for northern fishery management. Clearly, some sort of adaptive or heuristic approach that incorporates elements of both fishery and ecosystem management is required (Reist and Treble, 1998). Generally this is either unavailable or not being applied at present, a situation that must be rectified in order to adapt to climate change as it unfolds in the north.

Furthermore, the research necessary to both underpin management approaches and to elucidate ecosystem linkages to fisheries must be undertaken in the north to fill gaps in understanding. The best approach would be to leave sufficient resilience and compensatory capacity within fished populations and their supporting ecosystems to account for all impacts, and to provide sufficient

buffers for increased variability and surprises associated with climate change. Current management practices incorporate such buffers in a limited way, especially in the Arctic. The development and application of such buffers (e.g., through risk analysis or other techniques) need to be extended. This presents a significant challenge in terms of developing or modifying appropriate tools for use in arctic fisheries.

Domestic fisheries

The subsistence sector in the arctic portion of the Canadian northern economy is estimated to be approximately CAN$ 15000 per year per household (Fast and Berkes, 1998). This represents one-quarter to one-half of the total local economy, and this proportion may be growing. Similar values are likely for domestic fisheries in other arctic countries, especially in more remote regions where the proportion of the total economy, hence value, may be even higher. Furthermore, replacement of this sector by wage or industrial economies is generally unlikely. Fisheries, which in the Canadian Arctic include marine mammals in coastal areas, comprise as much as 20% of the overall subsistence harvest in some areas (Fast and Berkes, 1998). Thus, climate-mediated impacts on fish habitat, individual fish, and fish populations are very likely to have significant effects on the availability, use, and sustainability of domestic fisheries. In addition to those discussed previously, the following effects are likely to occur within domestic fisheries.

Climate change will possibly compromise traditional ecological knowledge developed over hundreds or thousands of years of direct environmental contact (Fast and Berkes, 1998), with more pronounced impacts in particular areas where climate change effects are acute. Extreme events, which are unpredictable, are likely to exacerbate these

impacts. Thus, increased climate variability and concomitant unpredictability of environmental conditions will possibly be more significant than will change in the trends of such conditions. As noted previously, this will possibly alter access to traditional fishing areas, increase risk associated with travel on the land or ice, and change fishery success. Loss of a significant portion of fish from the household economy is very likely to require replacement with some other means – perhaps increased reliance on food transported from the south and/or on other local northern foods (e.g., terrestrial mammals), further stressing those populations. The former solution (i.e., a dietary shift to southern transported foods) will possibly contribute to dietary problems and increased health costs (Fast and Berkes, 1998). Increased transportation costs for such foods are likely to be covered in some manner by subsidies from southern portions of the national economies, but this feedback from the north would increase the economic impact of climate change in southern areas. The availability of new fish species in some areas will possibly mitigate these problems but may not provide immediate solutions.

Recreational fisheries

Impacts similar to those outlined previously will also affect sport or recreational fisheries. In addition, management demands and economics associated with such fisheries will possibly alter. For example, recreational fishing for Atlantic salmon in eastern North America is regulated in part through river closures driven by higher temperatures and low water levels. The rationale is that such conditions stress fish, and catch-and-release angling (the norm for the area) would further stress individuals and affect populations (Dempson et al., 2001). Between 1975 and 1999, about 28% of 158 rivers on average were closed annually, with up to 70% affected in some years. This resulted in a 35 to 65% loss of potential fishing days with the warmest period (1995–1999) most affected. In part, this stress was the result of increased upstream migratory energy demands associated with lower water levels and higher water temperatures. Although this study was conducted in Newfoundland, it represents a possible future situation for arctic sport fisheries based upon riverine migrating fishes such as Atlantic salmon and Arctic char. Such fishes support significant local tourist economies in many areas of the Arctic, hence climate change impacts on recreational fisheries will possibly result in substantive economic impacts by increasing the frequency and duration of closures (Dempson et al., 2001).

8.5.5.6. Impacts on aquaculture

Aquaculture of fish in northern areas of arctic countries tends to focus upon cold-water species with high economic value such as Atlantic salmon and Arctic char. In general, such culture is presently located in areas south of the Arctic as defined herein, but this is likely to change as demand and opportunity increase. Aquaculture can be conducted wholly in freshwater using locally available or exotic species either indoors or out, or in protected nearshore marine areas primarily using anadromous species (see also Chapter 13). Climate change is very likely to result in a number of possible shifts in this industry, however, similar to those described previously for fisheries dependent upon wild populations, these will possibly be complex and interactive with both positive and negative consequences. The details will be specific to the local situations. Possible changes include production increases, especially in northern locations, due to temperature-driven increased growth rates of cultured fish and also decreased times necessary for culture to marketable sizes (Lehtonen, 1996), but this is likely to increase food requirements. Increased production will depend upon other factors not becoming limiting, especially available volumes of freshwater needed for inland operations. Knowledge of projected shifts in precipitation and evaporation with concomitant impacts on groundwater levels will be important to the viability of such endeavors. Production increases will possibly be offset by increased costs associated with oxygenating warmer waters, especially those for summer use, and increased loss to disease or costs associated with prevention (Lehtonen, 1996).

As warmer conditions extend northward, the areas in which aquaculture is economically viable (i.e., revenue exceeds costs) will possibly increase, opening new areas for this activity. However, increased climate variability and frequency of extreme events will possibly also increase engineering costs. New aquaculture efforts will present economic opportunities, but also have potential negative impacts on local native species, especially if the cultured species is exotic (e.g., a non-native southern species). As climate change effects are realized, the suite of southern species potentially viable for aquaculture will probably increase and present new economic opportunities. This will increase the need for regulatory scrutiny of such development, especially if the risk of escape and naturalization of such species is high. A related issue is very likely to be an increased risk of intentional but unauthorized introductions of exotic species into natural systems already affected to some degree by climate change. Escape and naturalization of Atlantic salmon along the Pacific Coast of North America (Volpe et al., 2000) serves as a valuable model of potential negative effects. Appropriate management and control of such activities will be required; such activities will possibly add significant additional stress to native fish populations already highly stressed by climate change. Strategies to deal with such possibilities are presently lacking or extremely limited, especially for potential transfers within countries.

8.5.6. Impacts on aquatic birds and mammals

Given the increasing understanding of the critical role of climate in driving the population dynamics of waterfowl and aquatic wildlife, it is very likely that progressive, rapid change in climate will trigger substantial fluctuations in endemic fauna and flora. Population- and

community-level responses of aquatic birds and mammals will probably result from combinations of direct and indirect impacts. These include changes in winter severity; seasonal snow and ice distribution and depths; timing and peaks of lake, pond, and wetland productivity; predator–prey dynamics; parasite–host interactions; habitat quality and distribution; and fire frequency, intensity, and distribution.

As discussed in section 8.4.1, projections from the five ACIA-designated models suggest that coastal land areas (and associated estuarine and freshwater habitats) are likely to experience dramatic temperature increases and changes in their hydrologic regimes. Such changes are likely to produce significant alterations in the quantity and quality of existing coastal estuarine and delta habitats, thereby affecting associated communities of birds and aquatic mammals.

It is therefore probable that changes in freshwater and estuarine habitat will result in altered routes and timing of migration. Emigration of aquatic mammals and waterfowl is likely to extend northward as more temperate ecosystems and habitats develop at higher latitudes (section 7.3.5). Migration will possibly occur earlier in the spring with the onset of high temperatures, and later in the autumn if high temperatures persist. Breeding-ground suitability and access to food resources are likely to be the primary driving forces in changes in migration patterns. However, many species living in these areas are adapted to, even dependent on, extreme natural fluctuations in climate and associated impacts on water resources. Hence, their responses to such changes are likely to be species-specific and quite varied.

A number of direct and indirect effects are likely to occur in shallow arctic lakes and ponds that lack a thermocline. Summer maximum temperatures are likely to climb above physiological preferences or thresholds of algae, plankton, and benthic invertebrates, which would produce substantial shifts through time in diversity and/or abundance at these lower trophic levels. Such shifts will probably result in earlier or reduced seasonal peaks in abundance of key foods, thereby creating mismatches between resource availability and timing of breeding. This will possibly lead to a lowering of reproductive success in higher-level consumers such as waterfowl.

Changes in water regimes are very likely to dramatically alter the quantity and quality of aquatic and riparian habitat, leading to local changes in the distribution of birds and mammals, and at larger scales, are likely to affect overall habitat availability, carrying capacity, and reproductive success. Aquatic mammals and waterfowl are highly dependent on the availability and quality of aquatic habitats for successful breeding, and in the case of waterfowl, nesting. Northern species will possibly have diminished reproductive success as suitable habitat either shifts northward or declines in availability and access. Northward colonization of southern species will

possibly result in competitive exclusion of "northern" species for habitat and resources. Many of the projected responses are likely to result from changes in temperature and precipitation. For example, Boyce and Miller (1985) showed that water depths have a significant positive effect on the annual production of juvenile whooping cranes (*Grus americana*), and suggested that increased summer temperatures are likely to create drier conditions in whooping crane nesting marshes over the long term, decreasing production of young and slowing the annual population growth rate.

Many shorebirds (e.g., sandpipers, plovers, snipe, godwits, curlews) are also dependent on water levels and the persistence of shallow wetlands. For instance, most North American species of shorebirds breed in the Arctic, with ten species common to the outer Mackenzie Delta (Gratto-Trevor, 1994, 1997). These species are dependent on invertebrate prey during reproduction, and hatchlings are highly dependent on mosquitoes and chironomids, the preferred foods of developing young. Any changes in timing and availability of food at staging sites in the Arctic, let alone the availability of wetland habitat, are likely to have detrimental effects on the success of hatchlings. Therefore, most species are very likely to be adversely affected by loss of shallow wetland habitat as ponded areas dry in response to rising temperatures, a potential decline in precipitation, and permafrost degradation. Conversely, thawing permafrost and precipitation increases are very likely to increase the occurrence and distribution of shallow wetlands, and probably the success of shorebirds in the Arctic.

Long-term survey data are available for a limited number of wetland-dependent migratory birds in Canada that demonstrate some of the possible effects of climate-related change. These data clearly indicate dramatic declines in the abundance of several waterfowl species (e.g., scoters – *Melanitta* spp., lesser scaup – *Aythya affinis*) with core breeding areas located in the northwestern boreal forest of Canada. Several hypotheses have been proposed to explain these patterns, including changes in wetland systems (e.g., food resources for breeding birds or their offspring). It is difficult to identify causes of decline because changes have also occurred simultaneously in the wintering, migration, and breeding areas of each species; however, breeding-ground changes are the probable cause because indices of productivity have decreased during the past 20 years (Afton and Anderson, 2001; Austin et al., 2000).

The dynamics and stability of aquatic mammal populations have also been linked to observed variability and extremes in hydrologic conditions. Thorpe (1986) found that in the Peace-Athabasca Delta, Canada, years with observed spring ice-jam flooding (and associated re-flooding of perched basins) had high success in local trapping of muskrats. A decade with low water levels in the delta resulted in dryer perched basins and fewer muskrats, followed by a decade of higher water levels

and high muskrat harvesting. In this case, perched-basin water levels and the extent of emergent vegetation development seemed to be the controlling factors in muskrat occurrence and abundance. Independent traditional ecological knowledge studies of the area also provided corroborative evidence of this trend (Crozier, 1996). Hence, projected decreases in the frequency and intensity of ice-jam flooding under future climate scenarios would probably cause decreases in the re-flooding of perched basins, negatively affecting muskrat populations in years with low water levels.

It is also possible that projected climate change in the Arctic will produce an increased incidence of mortality from disease and/or parasites in bird and aquatic mammal populations. As temperatures rise, southern species of mammals and waterfowl are likely to shift northward. These species will probably carry with them new diseases and/or parasites to which northern species are not adapted.

8.6. Ultraviolet radiation effects on freshwater ecosystems

Ultraviolet radiation is the most photochemically reactive wavelength of solar energy reaching the surface of the earth, and has a broad range of effects on aquatic biogeochemistry, biota, and ecosystems. As a result of anthropogenic impacts on the atmosphere of the earth, UV radiation exposure in arctic environments is changing substantially. Although anthropogenic emissions of ozone-depleting substances have declined since the ratification of the Montreal Protocol and its amendments, future levels of ozone and UV radiation in the Arctic are uncertain, depending not only on continued compliance with the Protocol and changes in legislation, but also on climate change effects on temperatures and trace gases (e.g., sections 5.6.2, 7.5, and 8.4.4.4). This section provides an overview of how underwater UV radiation exposure is linked to climate, followed by a discussion of general principles concerning UV radiation impacts in aquatic ecosystems (including natural protection mechanisms) and a systematic analysis of potential UV radiation impacts on arctic freshwater habitats.

8.6.1. Climate effects on underwater ultraviolet radiation exposure

To understand the overall impact of changes in UV radiation levels, the synergistic and antagonistic processes resulting from climate change have to be considered since they have the potential to modify the underwater UV radiation regime and consequently the stress on aquatic organisms. Climate change is very likely to be accompanied by shifts in biological UV radiation exposure in arctic river, lake, and wetland environments via three mechanisms (Vincent and Belzile, 2003): changes in stratospheric ozone levels, changes in snow- and ice-cover duration, and changes in the colored materials dissolved in natural waters that act as sunscreens against UV radiation.

Although it is projected that the downward trends in ozone levels are likely to reverse in the near future as a consequence of reduced anthropogenic emissions of chlorofluorocarbons (CFCs) and related compounds, some of the longer-lived ozone-depleting substances are still accumulating in the stratosphere and climate change is likely to prolong the effects of depletion. Temperature increases in the troposphere are projected to be accompanied by temperature decreases in the lower stratosphere, and there is already some evidence of this effect in the polar regions. Temperature decreases in the lower stratosphere are very likely to increase the frequency and extent of polar stratospheric clouds (PSCs) that catalyze CFC–ozone reactions, and result in a strengthening of the polar vortex, which in turn is likely to lead to longer-lasting conditions for ozone depletion (Staehelin et al., 2001). The minimum winter temperatures in the arctic stratosphere are very close to the threshold for the formation of PSCs and the chlorine reactions that lead to ozone loss, and the Arctic remains vulnerable to large-scale ozone depletion (Dahlback, 2002). It is also possible that temperature increases could lead to increased zonal flow at midlatitudes causing the polar vortex to be more stable, again favoring ozone depletion and a delay in the eventual recovery of the ozone layer (Shindell et al., 1998). Furthermore, as greenhouse gas concentrations increase, the tropical tropopause is very likely to become warmer, resulting in the transport of more water vapor into the stratosphere, which in turn is likely to lead to the formation of PSCs at higher temperatures (Kirk-Davidoff et al., 1999). Therefore, the ozone in the arctic stratosphere would be at greater risk of depletion (see section 5.6.2 for further discussion).

The underwater UV radiation environment changes dramatically with a decrease in snow- and ice-cover duration, especially if this occurs during periods of greatest UV radiation flux and ozone depletion. Analyses of the effects of melting arctic sea and lake ice show that this process results in order-of-magnitude increases in biological UV radiation exposure that greatly exceed those caused by moderate ozone depletion (Box 8.9; Vincent and Belzile, 2003). Lake and river ice are relatively transparent to UV radiation because of CDOM exclusion from the ice during freeze-up (Belzile et al., 2002a). Small changes in snow cover and white ice, however, can radically influence the below-ice UV radiation levels in arctic waters (Belzile et al., 2001).

In arctic aquatic environments, variations in suspended particulates, and especially CDOM, affect transmission of UV radiation (see Box 8.10). These variations can be more important than ozone depletion in determining the UV radiation exposure in the water column of freshwater systems.

In some areas of the Arctic, climate change is very likely to be accompanied by increased vegetation, a concomitant increase in CDOM loading (Freeman et al., 2001), and reduced exposure to underwater UV radiation.

These positive effects are likely, however, to be offset by reduced availability of PAR (Arrigo and Brown, 1996; Neale, 2001; Pienitz and Vincent, 2000). Marked south–north gradients in present-day CDOM concentrations in arctic waters are associated with the latitudinal distribution of terrestrial vegetation. Colored dissolved organic matter loading of freshwater systems is less pronounced at higher latitudes. Lakes in the tundra and polar-desert biomes contain low amounts of these materials; small variations in CDOM concentration in these systems can cause major changes in underwater UV radiation exposure (Laurion et al., 1997; Vincent and Pienitz, 1996). Freshwaters in northern Scandinavia are low in dissolved carbon similar to water bodies in North America; the median DOC concentration for 25 lakes above the treeline in Finnish Lapland was 18 mg C/l (Rautio and Korhola, 2002b). Although acid precipitation enhances underwater UV radiation levels by reducing DOC concentrations in the water, increased thawing of permafrost with climate change is very likely to increase soil runoff and levels of DOC (or CDOM) in arctic freshwater systems. This is very likely to be accompanied by an increase in water turbidity, which will probably not only decrease PAR penetration but also increase the relative proportion of UV radiation, thereby hindering repair processes in aquatic organisms that are stimulated by longer wavelengths. Increased physical turbulence is also likely to expose planktonic organisms to unfavorable irradiance conditions (e.g., exposure to high levels of surface UV radiation and PAR), the effects of which are likely to be especially severe for species that cannot migrate.

8.6.2. Ultraviolet radiation effects on aquatic biota and ecosystems

The effects of UV radiation in the aquatic environment range from molecular to whole-ecosystem. Photobiological damage includes the direct effects of UV radiation in which photons are absorbed by biological molecules such as nucleic acids and proteins that then undergo photochemical alteration. An alternative damage pathway is via the interaction of UV radiation and organic compounds or other photosensitizing agents to produce reactive oxygen species such as superoxide and hydroxyl radicals. These can diffuse away from the site of production and cause oxidative damage to enzymes, lipid membranes, and other cellular constituents.

Aquatic biota have four main lines of defense against UV radiation damage: escape, screening, quenching (chemical inactivation), and repair. The net stress imposed by the UV radiation environment reflects the energetic costs of protection and repair in addition to the rate of photochemical degradation or alteration of cellular components (Vincent and Neale, 2000). These defenses are well illustrated by arctic zooplankton (see Box 8.11), but despite this protection these organisms remain vulnerable to ambient UV radiation levels (Zellmer, 1998), particularly in the cold, shallow, CDOM-poor waters that characterize many arctic lakes and ponds.

Changes in underwater UV radiation exposure are likely to directly affect the species composition of aquatic

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Box 8.9. Implications of changing snow and ice cover for ultraviolet radiation exposure

The warming northern climate is prolonging open water conditions. The loss of UV radiation-attenuating snow and ice earlier in the season, when water temperatures are still low but UV irradiances are maximal, is likely to be especially stressful for aquatic biota. As shown below, white ice (ice with air inclusions) has a strong attenuating effect on PAR (visible light) and an even greater effect on UV-A and UV-B radiation. This snow-clearing experiment on Hudson Bay showed that only 2 cm of snow reduced the below-ice exposure to UV radiation and to PAR by about a factor of three, with slightly greater effects at the shorter wavelengths.
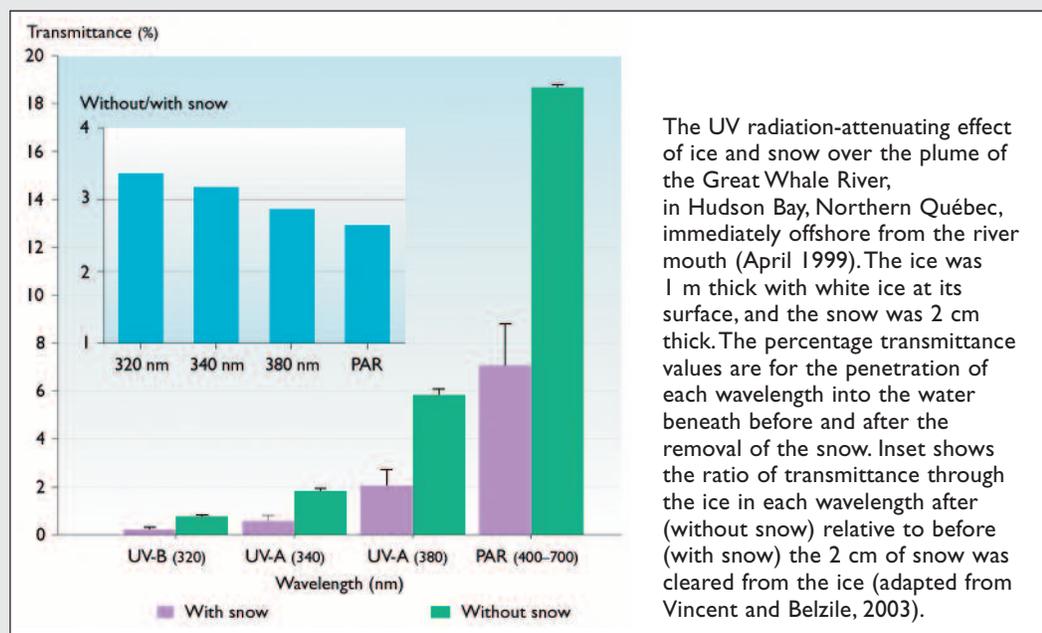
The UV radiation-attenuating effect of ice and snow over the plume of the Great Whale River, in Hudson Bay, Northern Québec, immediately offshore from the river mouth (April 1999). The ice was 1 m thick with white ice at its surface, and the snow was 2 cm thick. The percentage transmittance values are for the penetration of each wavelength into the water beneath before and after the removal of the snow. Inset shows the ratio of transmittance through the ice in each wavelength after (without snow) relative to before (with snow) the 2 cm of snow was cleared from the ice (adapted from Vincent and Belzile, 2003).

biota at each trophic level, as well as cause effects that cascade throughout the benthic (e.g., Bothwell et al., 1994) or pelagic (e.g., Mostajir et al., 1999) food webs and the coupling between them. Some trophic responses are likely to be "bottom-up effects" in that UV radiation exposure reduces the quantity or quality of prey and thereby reduces food supply to the next level of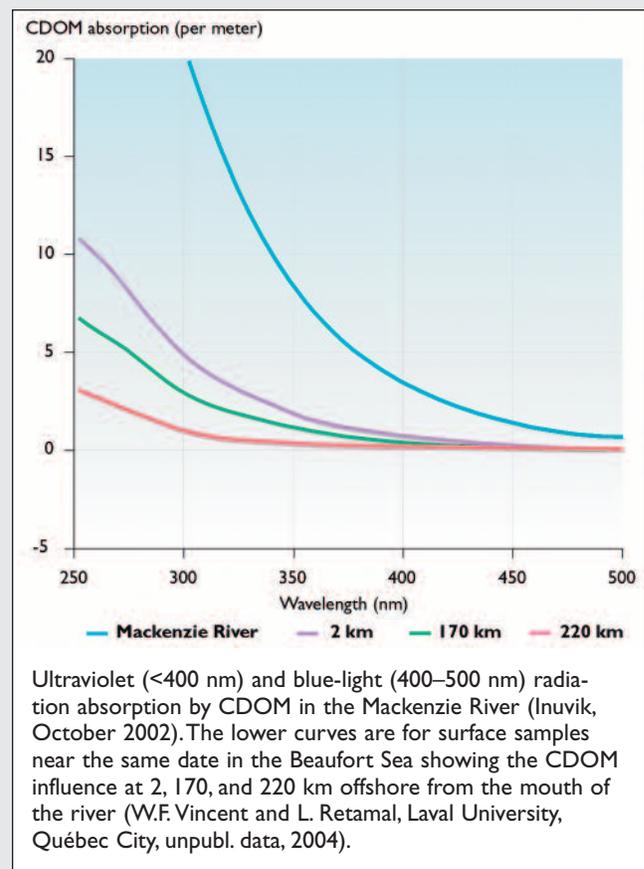 consumer organisms. This could occur, for example, via shifts towards inedible or less digestible algal species (Van Donk and Hessen, 1995; Van Donk et al., 2001) or by reducing the nutritional value of food organisms (Scott J. et al., 1999). The effects of variations in UV-B radiation on the quality of phytoplankton photosynthetic products have received little attention except for studies at the pigment level (e.g., Buma et al., 1996; Zudaire and Roy, 2001). Any alteration in the biochemi-

cal composition of primary producers is likely to change the nutritional value of food consumed by grazers (thus influencing energy flow throughout the food web) as well as restrict the production of photoprotective compounds against UV radiation. Short-term exposure to enhanced UV-B radiation levels in phytoplankton populations of various lakes in the Canadian High Arctic influenced the allocation of newly fixed carbon into the major macromolecular classes (Perin, 2003). Generally, synthesis of both protein and polysaccharides was inhibited by enhanced UV-B radiation levels, and the photosynthate would remain or accumulate in the pool of low molecular weight compounds. Lipid synthesis was insensitive to UV-B radiation levels and represented the most conservative and uniform class, accounting for about 20% of total carbon fixed.

Box 8.10. Colored dissolved organic matter: the natural sunscreen in arctic lakes and rivers

Colored dissolved organic matter (CDOM) is composed of humic and fulvic materials (average to low molecular weight) that are derived from terrestrial soils, vegetation, and microbial activities, and is known to be an effective protective screen against UV radiation for freshwater biota (e.g., plankton, Vincent and Roy, 1993; amphibians, Palen et al., 2002). These compounds absorb UV-A and UV-B radiation and short-wavelength visible light, and in high concentrations such as in arctic rivers they stain the water yellow or brown. Colored dissolved organic matter is now known to be the primary attenuator of underwater UV radiation in subarctic and high-arctic lakes (Laurion et al., 1997); Toolik Lake, Alaska (Morris et al., 1995); arctic ponds (Rautio and Korhola, 2002a); and arctic coastal seas influenced by river inflows (Gibson J.A. et al., 2000; Vincent and Belzile, 2003). The concentrations of CDOM in natural waters are influenced by pH (acidification can cause a severe decline; Schindler D.W. et al., 1996b), catchment morphology, runoff, and the type and extent of terrestrial vegetation. The latter aspects are especially dependent on climate.

The paleoecological record has been helpful in examining past impacts of climate on biological underwater UV radiation exposure, specifically by using fossil diatoms in lake sediments as quantitative indicators of variations in CDOM. This record also underscores the large regional differences in the magnitude and direction of change in underwater UV radiation levels (Ponader et al., 2002; Saulnier-Talbot et al., 2003). Shifts in vegetation and hydrology caused by warming or cooling trends are very likely to affect the quantity of CDOM exported from catchments to their receiving waters, in turn affecting underwater UV radiation levels. For example, an analysis of the past underwater climate (paleo-optics) of subarctic treeline lakes indicated that recent Holocene cooling (from about 3500 years ago to the present) was accompanied by a southward retreat of the treeline and a large decrease in CDOM concentrations in lake waters. This decreasing CDOM resulted in an increase in biological UV radiation exposure that was two orders of magnitude greater than that associated with moderate (30%) ozone depletion (Pienitz and Vincent, 2000). Saulnier-Talbot et al. (2003) reported large decreases in biological UV radiation exposure (starting about 3000 years BP) in a coastal lake in subarctic Québec that were associated with the establishment of terrestrial vegetation in its catchment.

Ultraviolet (<400 nm) and blue-light (400–500 nm) radiation absorption by CDOM in the Mackenzie River (Inuvik, October 2002). The lower curves are for surface samples near the same date in the Beaufort Sea showing the CDOM influence at 2, 170, and 220 km offshore from the mouth of the river (W.F. Vincent and L. Retamal, Laval University, Québec City, unpubl. data, 2004).

Overall, these results were similar to those observed for Lake Ontario (Smith R. et al., 1998). However, the various classes of lipid may respond differently to variations in UV-B radiation levels. For example, exposure to UV radiation influenced fatty acid composition in algal cultures (Goes et al., 1994; Wang and Chai, 1994). Other studies observed that the effect of UV-B radiation on the major lipid classes is species-specific (De Lange and Van Donk, 1997).

Higher trophic levels are dependent on phytoplankton either directly as food or indirectly via trophic cascades. Inhibition of growth and cell division in phytoplankton will most often affect the food quality of these cells by placing stoichiometric constraints on the grazer (Hessen et al., 1997). Hessen and Alstad Rukke (2000) also showed that water hardness could be a major determinant of susceptibility to UV radiation damage among calcium-demanding species such as *Daphnia*. They suggested that calcium, which is an important element for invertebrates with calcified exoskeletons, in low concentrations (low-pH lakes, acidification) could reduce the stress tolerance of organisms. Although several studies of freshwater invertebrate species have reported increased mortality in response to increased UV radiation levels, especially zooplankton (Hurtubise et al., 1998; Leech and Williamson, 2000; Rautio and Korhola, 2002a; Siebeck and Böhm, 1994; Vinebrooke and Leavitt, 1999a; Williamson et al., 1994), the variation in UV radiation tolerance is high among species and life stages (Leech and Williamson, 2000). In general, small zooplankton (small rotifers) are considered to have a high UV radiation tolerance, while large species vary in their tolerance both among and within species. Leech and Williamson (2000) found that cladocerans had the lowest UV radiation tolerance and exhibited high variability among species. *Daphnia* was one of the most sensitive groups of organisms, while adult calanoid and cyclopoid copepods had high UV radiation tolerances. In a comparison of lakes across a successional gradient of catchment vegetation and thus CDOM content, three zooplankton species (*Asplanchna priodonta*, *Ceriodaphnia quadrangula*, and *Bosmina longirostris*) were absent from low-CDOM, UV-transparent waters, and perished when transplanted from a CDOM-rich lake in the series and held at 0.5 m depth under full UV radiation exposure in a clear lake. In contrast, two species that avoided high UV radiation exposure in the near-surface waters (*Daphnia pulicaria* and *Cyclops scutifer*, a highly UV-tolerant species) occurred in even the clearest lakes (Williamson et al., 2001). Morphotypic and biochemical differences among populations of a given species may also play an important role. Pigmented clones of *Daphnia* were more tolerant of UV radiation than transparent clones (Hessen et al., 1999), and pigmentation appears to increase in response to increased UV radiation exposure (Rautio and Korhola, 2002b; Box 8.11). Studies of the effects of natural and enhanced UV radiation levels on fish are rare, but laboratory experiments have shown that high-latitude species of trout have sunburns,

increased fungal infections, and higher mortality when exposed to increased dosages of UV radiation (Little and Fabacher, 1994).

Other trophic responses are likely to be top-down effects, in which some species are released from grazing pressure or predation by UV inhibition of the consumers and thereby achieve higher population densities (Bothwell et al., 1994). This complex combination of direct and indirect effects makes any future shifts in aquatic ecosystem structure extremely difficult to project. In addition, the deleterious effects of UV-B radiation at the community level are difficult to assess since they are generally species-specific. For example, Wickham and Carstens (1998) showed that the responses of the planktonic microbial communities in Greenland ponds to ambient UV-B radiation levels varied greatly between species, especially rotifers and ciliates.

Multiple factors seem to affect amphibians negatively. These factors include both site-specific, local effects (e.g., pesticide deposition, habitat destruction, and disease) as well as global effects (e.g., increased UV-B radiation exposure and climate change; e.g., Häder et al., 2003). Amphibians have been the focus of special interest at temperate latitudes because of the recent widespread decline in many frog populations and the recognized value of these organisms as sensitive indicators of environmental change. Although many amphibians can be relatively resistant to UV-B radiation, it can cause deformities, delays in development, behavioral responses, physiological stress, and death in frogs. The rise in UV-B radiation levels associated with stratospheric ozone depletion has been widely promoted as one of several hypotheses to account for their decline (Collins and Storfer, 2003, and references therein). However, the effects are controversial and in many habitats where the frogs are declining, the animals are well protected by CDOM (Box 8.10). A small number of frog species occur in the subarctic and the Arctic, including the common frog (*Rana temporaria*) and the wood frog (*Rana sylvatica* – North America), with distributions extending north of the Arctic Circle. Contrary to expectation, however, these populations may experience higher UV radiation exposures under natural conditions relative to temperate regions, and therefore be more pre-adapted, because of lower concentrations of UV-screening CDOM in high-latitude waters (e.g., Palen et al., 2002) and life-cycle characteristics (phenology: higher UV-B radiation doses during the breeding season at higher latitudes; Merilä et al., 2000). There is considerable variation in UV radiation tolerance between amphibian strains and species; for example, a latitudinal comparison in northern Sweden found that *R. temporaria* embryos were relatively tolerant of UV-B radiation, with no clear latitudinal differences (Pahkala et al., 2002). The positive and negative effects of climate change on arctic habitats (e.g., duration of open water, extent of wetlands) are likely to have much greater impacts on amphibians than changes in UV radiation exposure.
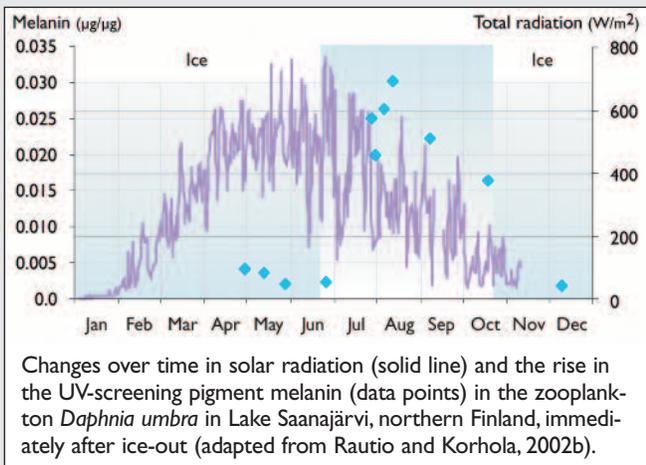
8.6.3. Impacts on physical and chemical attributes

The large arctic rivers are relatively protected from UV radiation exposure because of their high CDOM content (Gibson J.A. et al., 2000). Conversely, natural and increased UV radiation levels are likely to be important for photochemical loss of carbon from these systems. For example, there is evidence that the duration of ice-free conditions has increased in the Mackenzie River, Canada (Magnuson et al., 2000) and the River Tornio, Finland. The resultant increased exposure to UV radiation is likely to favor increased annual rates of UV degradation of riverine DOC, with possible impacts on the inshore coastal waters that receive these inputs.

Box 8.11. Ultraviolet radiation protection and recovery mechanisms in arctic freshwaters

Aquatic organisms have varying abilities to counter the effects of UV radiation. Photoprotective and repair processes are particularly important in preventing and reversing UV radiation damage to photosynthetic mechanisms. A range of potential repair processes is stimulated by longer wavelengths to counteract the damaging effects of UV radiation. The relative importance of repair versus protection will vary depending on specific conditions and the physiological characteristics of the species assemblage (Banaszak and Neale, 2001). Organisms living in arctic lakes have evolved several strategies to cope with UV radiation, which play an important role in shallow and highly UV-transparent arctic lakes and ponds. Some species of algae and zooplankton have an ability to reduce their exposure to UV radiation by vertical migration, which may be a response to high intensities of UV radiation (Huntsman, 1924). Leech and Williamson (2001) and Rhode et al. (2001) provided further evidence that organisms avoid highly irradiated areas by escaping the brightly lit surface zone.

Changes over time in solar radiation (solid line) and the rise in the UV-screening pigment melanin (data points) in the zooplankton *Daphnia umbra* in Lake Saanajärvi, northern Finland, immediately after ice-out (adapted from Rautio and Korhola, 2002b).

In addition to avoidance, aquatic organisms can escape from UV radiation by reducing the effective radiation that penetrates the cell. A number of UV-protecting compounds have been described; the three major types are carotenoids, mycosporine-like amino acids (MAAs), and melanin. The photoprotective properties of carotenoids are mainly associated with antioxidant mechanisms and inhibition of free radicals, as opposed to direct UV radiation screening (Hessen, 1994). Carotenoids absorb wavelengths in the visible light spectrum and do not therefore provide direct protection from UV radiation. Mycosporine-like amino acids have absorption maxima ranging from 310 to 360 nm within the UV wavelength range. They are present in alpine phytoplankton and zooplankton (Sommaruga and Garcia-Pichel, 1999; Tartarotti et al., 2001) and also occur in arctic freshwater organisms although there is no research on this. Animals are unable to synthesize MAAs and carotenoids, and must therefore acquire these compounds from their diet.

Cladocera and fish produce melanin, with absorption maxima between 250 and 350 nm. Melanin acts by absorbing radiation before it enters the body tissues, and its synthesis seems to be a direct response to UV radiation (Hobæk and Wolf, 1991). Melanic zooplankton are typically found in clear arctic waters where the absorbance of UV radiation is low, and in shallow ponds where high DOC levels may not provide enough protection from UV radiation (Hebert and Emery, 1990; Rautio and Korhola, 2002b). It has also been shown that melanin synthesis followed the annual variation in UV radiation levels (i.e., synthesis peaked at the time of maximum underwater UV irradiance, see figure). Aquatic organisms can also repair damage from UV radiation by nucleotide excision repair or by photoreactivation mechanisms, such as photoenzymatic repair (Leech and Williamson, 2000).

Brief exposure to UV radiation triggers only the initial UV radiation stress response. However, responses over long periods show that organisms can acclimate to the UV radiation stress and/or recover growth rates with the development of photoprotective strategies (e.g. the synthesis of photoprotective compounds). A long-term enclosure experiment conducted in a high-arctic lake on Ellesmere Island (Nunavut, Canada) showed an initial decrease in phytoplankton productivity with enhanced UV-B radiation exposure, with recovery after 19 days (Perin, 2003). Long-term acclimation to and recovery from increased levels of UV radiation were also observed in a cultured marine diatom (Zudaire and Roy, 2001). Antecedent light conditions, temperature, nutrient availability, and/or variations between species are all factors that can affect acclimation of organisms to high intensities of UV-B radiation (Zudaire and Roy, 2001).

In addition to having low CDOM concentrations and resultant deep penetration of UV radiation, many arctic lakes, ponds, and wetlands are shallow systems. The mean measured depth for more than 900 lakes in northern Finland was less than 5 m (Blom et al., 1998), and was about 5 m for 31 lakes in the vicinity of Tuktoyaktuk (Northwest Territories; Pienitz and Smol, 1994) and 46 lakes on Ellesmere Island (Nunavut; Hamilton et al., 1994). Consequently, all functional groups, including the benthos, are often exposed to UV radiation throughout the entire water column. In addition, many aquatic species stay in the offshore pelagic zone. Even species that are more benthic or littoral are protected minimally by macrophytes, as arctic waters, especially those in barren catchments, often contain little aquatic vegetation.

Changes in UV radiation exposure in these northern ecosystems are amplified by the low CDOM concentrations. Most have concentrations of DOC below 4 mg DOC/l, the threshold below which there are marked changes in UV radiation penetration through the water column, and in the ratio of wavelengths controlling the damage–repair balance, with only minor changes in CDOM (Laurion et al., 1997).

The initial impacts of climate change are likely to be associated with the loss of permanent ice covers in the far northern lakes: this appears to have already recently taken place in the Canadian High Arctic (Belzile et al., 2002a). These effects are likely to be amplified by prolonged open-water conditions in lakes and ponds. However, other physical changes in these environments (e.g., wind-induced mixing) are likely to have greater perturbation effects than those associated with increased UV radiation exposure. Although increases in CDOM are very likely to mitigate the effects of increased UV radiation levels, decreases in PAR are very likely to hamper photosynthesis. Furthermore, increased turbidity associated with thawing permafrost is likely to further reduce the exposure of organisms to damaging UV radiation (for turbidity effects on UV radiation, see Belzile et al., 2002b).

The photochemical effects of increased UV radiation levels are also likely to influence the toxicity of contaminants (see also section 8.7). Mercury (Hg) is the principal toxic chemical of concern in the Arctic and elsewhere. Methyl mercury (MeHg) is the most toxic form and the only form that biomagnifies in food chains. It was recently shown that:

- ultraviolet radiation exposure photoreduces divalent mercury (Hg^{2+}, the soluble form in lakes) to elemental mercury (Hg^0, the form that can volatilize from lakes; Amyot et al., 1997);
- ultraviolet radiation can also influence photooxidation (the conversion of Hg^0 to Hg^{2+}; Lalonde et al., 2001);
- the formation of MeHg in arctic wetlands is very sensitive to temperature;
- ultraviolet radiation photodegrades MeHg; and

- most of the Hg in recently fallen snow moves back to the atmosphere within a few days of exposure to solar radiation (Lalonde et al., 2002).

Not only is photochemical reduction of Hg important in the Arctic, but microbial reduction and oxidation may also occur as shown previously in temperate lake waters. Microbial oxidation is turned on by a hydrogen peroxide-dependent enzyme likely triggered by photochemical production of hydrogen peroxide (Scully et al., 1997). The interactions between UV radiation, temperature, and pH can alter Hg mobilization and speciation, and regulate the levels of Hg in organisms at the base of the food web. Photochemical events during spring are likely to be especially sensitive to rising UV-B radiation levels. Large quantities of Hg are photochemically oxidized and precipitate out of the arctic atmosphere with the first sunlight each spring, resulting in a rapid rise in Hg concentrations in snow; 24-hour variations in these atmospheric Hg-depletion events correlate with fluctuations in UV-B irradiance (Lindberg et al., 2002). Increasing spring levels of UV radiation due to stratospheric ozone depletion would probably enhance this so-called "mercury sunrise" phenomenon.

Wetlands and peatlands are rich in CDOM and the aquatic biota are therefore well protected from UV radiation exposure. Early loss of snow and ice, however, is likely to increase exposure during a critical growth phase. Photochemical processes may be especially active in these shallow waters, and this mechanism of CDOM loss is very likely to accelerate with temperature increases (snow-cover loss) and ozone depletion.

8.6.4. Impacts on biotic attributes

Mild increases in UV radiation levels are likely to stimulate biological processes via photochemical release of low molecular weight organic carbon substrates and nutrients. More severe increases are likely to cause damage and/or a shift toward UV-tolerant species with a potential loss of diversity or other unique ecosystem attributes (Fig. 8.20).

8.6.4.1. Rivers and streams

Benthic mats and films are a common feature of high-latitude streams as well as many ponds, lakes, and wetlands, and are often dominated by cyanobacteria, especially the nitrogen-fixing genus *Nostoc* and filamentous species of the order Oscillatoriales (Vincent, 2000). These communities commonly occur in shallow water systems where UV radiation exposure is likely to be high. Ultraviolet radiation has a broad range of deleterious effects on benthic cyanobacteria including on their pigment content, nitrogenase activity, photosynthesis, and respiration (Castenholz and Garcia-Pichel, 2000; Vincent and Quesada, 1994). Much of the literature, however, reports experiments conducted under unrealistically high UV radiation dosages provided by artificial lamps, and many of the effects are likely to be much less
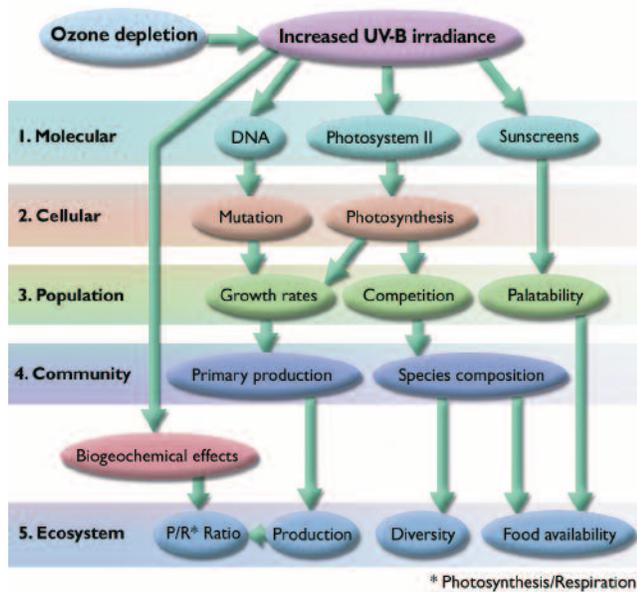
Ozone depletion → Increased UV-B irradiance

1. Molecular — DNA, Photosystem II, Sunscreens

2. Cellular — Mutation, Photosynthesis

3. Population — Growth rates, Competition, Palatability

4. Community — Primary production, Species composition

Biogeochemical effects

5. Ecosystem — P/R* Ratio, Production, Diversity, Food availability

* Photosynthesis/Respiration

Fig. 8.20. Ultraviolet radiation is the most photochemically reactive wavelength in the solar spectrum and has a wide range of effects, from molecular to whole ecosystem (Vincent and Roy, 1993).

apparent or absent in natural ecosystems, even under conditions of severe ozone depletion (Vincent and Neale, 2000). Periphyton and benthic invertebrates are well protected given their avoidance and sunscreen capacities. Zooplankton and phytoplankton communities are well developed in large arctic rivers (e.g., Rae and Vincent, 1998a), however, they are generally protected by high CDOM concentrations in these waters.

8.6.4.2. Lakes, ponds, and wetlands

In the Arctic, lake organisms have to cope with low nutrient conditions and/or low food availability, low temperatures, and short growing seasons (3–5 months). The UV radiation damage–repair balance may be especially sensitive to features of the arctic freshwater environment. Most of these ecosystems are oligotrophic and phytoplankton are therefore commonly limited by nutrient supply (Bergeron and Vincent, 1997) in addition to low temperatures (Rae and Vincent, 1998a). As a result, the photosynthetic rates per unit biomass tend to be extremely low, even in comparison with other low-temperature systems such as sea ice, polar oceans, and low-temperature cultures (Markager et al., 1999). Because of the low temperatures and low nutrients, phytoplankton photosynthetic rates are extremely low in Canadian high-arctic lakes (usually less than 1.5 µg C/µg Chl-a/hr) and phytoplankton perform very poorly under high-light regimes (Kalff and Welch, 1974; Perin, 2003; Rigler, 1978). There have been few explicit tests of the effect of temperature on UV radiation damage of planktonic systems (Rae and Vincent, 1998a). However, since enzymatic processes are temperature-dependent (whereas damage induction is not), the slow metabolic rates of northern phytoplankton are likely to have a direct effect on the net stress imposed by increased UV radiation exposure by reducing all cellular processes including the rate of repair of photochemical damage. In the antarctic

waters, for example, low temperatures drastically reduce repair to the extent that algal cells failed to show any photosynthetic recovery for at least five hours after UV radiation exposure (Neale et al., 1998). The low nutrient conditions that characterize northern lakes are likely to further compound this effect by reducing the availability of elemental resources for building enzyme systems involved in the functioning of the cell, including the repair of UV radiation damage, and are also likely to limit the investment in photoprotective mechanisms. Moreover, the lower temperatures probably reduce the affinity of the phytoplankton cells for nutrient uptake by membrane transport processes (Nedwell, 2000), thereby increasing nutrient limitation.

The paleoclimatic record has also provided insights into the possible effects of past climate change on UV radiation exposure in aquatic ecosystems. For instance, analyses of fossil diatom assemblages in northern and alpine lake sediments have indicated that variations in underwater UV irradiance during the Holocene had major impacts on algal community structure and productivity (Leavitt et al., 1997; Pienitz and Vincent, 2000). Paleo-optical studies from subarctic lakes have revealed large fluctuations in biologically damaging underwater UV irradiance over the last 6000 years, accompanied by pronounced shifts in algal species composition and changes in the balance between benthic and pelagic primary producers (Pienitz and Vincent, 2000). Vinebrooke and Leavitt (1999b) observed similar effects in low-CDOM mountain lakes.

There are only a few studies of temperature-dependent UV radiation damage to zooplankton (Borgeraas and Hessen, 2000). In general, it is assumed that low temperatures would slow down the UV radiation damage repair mechanisms such as DNA repair and detoxification of reactive oxygen species. However, contrary to expectations, Borgeraas and Hessen (2000) found that reduced temperatures increased survival among UV-irradiated *Daphnia*. They argued that although repair mechanisms are slower in the cold, UV-triggered activation processes (such as reactive oxygen species metabolism and lipid peroxidation) also slow down with decreasing temperature, thereby increasing *Daphnia* survival.

At ambient levels, UV-B radiation can contribute up to 43% of the photoinhibition of photosystem II function in phytoplankton populations of Canadian high-arctic lakes (as measured by both *in vivo* and dichlorophenyl-dimethyl urea-enhanced fluorescence) as well as decreasing (by up to 40%) phytoplankton productivity rates near the water surface (Perin, 1994). The smallest size fraction (i.e., picoplankton: 0.2–2 µm) usually represents more than 50% of total phytoplankton productivity in high-arctic lakes (Perin, 1994). Oligotrophic conditions tend to select for small cells with a high surface-to-volume ratio that favors nutrient transport at low substrate concentrations. Small cells are especially sensitive to UV radiation because they have high illumi-

nated surface-to-volume ratios, little self-shading, and low effectiveness of screening pigments (Karentz et al., 1991; Raven, 1998). Even the production of UV radiation sunscreens is unlikely to confer much protection given the short path length in these cells (Garcia-Pichel, 1994), and studies of a variety of organisms have shown that enhanced UV radiation exposure inhibits the growth of larger cells less than that of smaller cells (Karentz et al., 1991). Laurion and Vincent (1998) evaluated the size dependence of UV radiation effects on photosynthesis in subarctic lakes with a series of short-term photosynthetic experiments, which showed that, in contrast to expectations, the smaller cells were more resistant to UV radiation than larger cells. This smaller-cell fraction was dominated by cyanobacteria, a group known to have a broad range of effective UV-protective mechanisms (Vincent, 2000). Kaczmarska et al. (2000) also found low UV radiation susceptibility in a pico-cyanobacteria-dominated phytoplankton assemblage from a clear lake in southern Canada. On the other hand, short-term experiments in several high-arctic lakes showed that the relative contribution of picoplankton (0.2–2 μm) to phytoplankton production generally decreased with increased UV-B radiation exposure while the larger cells (>20 μm) were more UV-B radiation tolerant and their contribution to productivity usually increased after UV-B radiation exposure. Arctic lake experiments at Spitsbergen also indicated a greater sensitivity of the picocyanobacteria relative to larger colonial species to UV-B radiation exposure (Van Donk et al., 2001). A study by Boelen et al. (2001) showed that for marine tropical plankton, UV-B-induced DNA damage was not significantly different between two size classes (0.2–0.8 μm and 0.8–10 μm). Given the variability in results between studies, other aspects such as species-specific sensitivity, repair capacities, or cell

morphology might be more important than cell size (Boelen et al., 2001).

The level of photoinhibition by UV radiation in phytoplankton can be modified by many factors that influence the extent of exposure within the water column. For instance, vertical mixing can affect the time and duration of phytoplankton exposure to UV radiation and diminish or aggravate projected inhibition of photosynthesis obtained under simulated conditions (continuous UV radiation exposures). In a well-mixed water column, the planktonic community can seek refuge from UV-B radiation, and photo-repair in the deeper portion of the column. However, the formation of near-surface thermoclines caused by high solar irradiance, calm winds, and solar heating of the surface water can retain the phytoplankton under high irradiances for longer periods of times (Milot-Roy and Vincent, 1994) and result in UV radiation damages that can exceed what can be repaired (Xenopoulos et al., 2000). During the spring and summer in the Arctic, climatic conditions (e.g., clouds, rain, snow, fog, and wind) that change tremendously from day-to-day can affect the amount of UV radiation exposure as well as the ratios of UV radiation to longer wavelengths reaching the surface of the earth. In the coastal areas of northern Norway, variation in cloudiness was demonstrated to influence UV radiation levels. The relative amount of UV-A and UV-B radiation to PAR increased during periods of heavy cloud cover (Eilertsen and Holm-Hansen, 2000) because clouds reflect and return radiation (Madronich et al., 1995).

Ultraviolet radiation may impair the transfer of carbon from the microbial food web to higher trophic levels, including zooplankton and fish. However, increased pho-
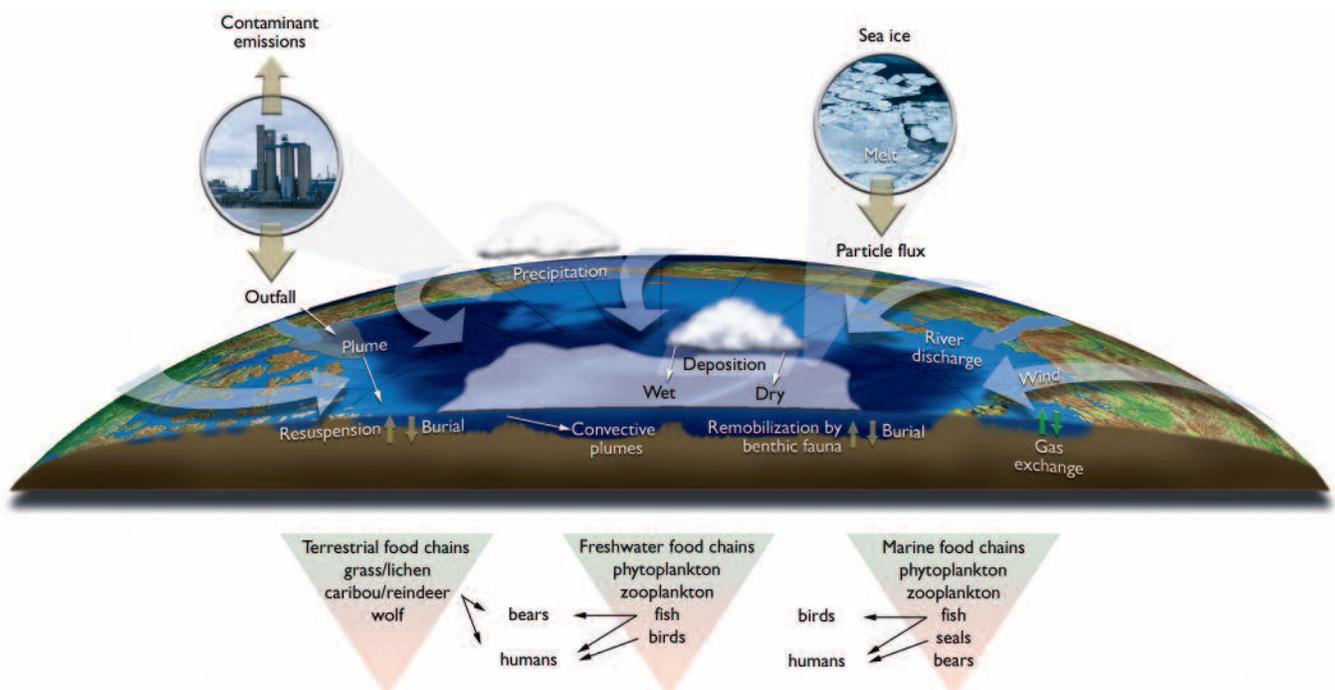

Fig. 8.21. Contaminant pathways, transfers, and exchanges in freshwater systems: land–atmosphere–water interactions (adapted from AMAP, 1998).

tochemical activity associated with UV radiation also has the potential to stimulate some heterotrophic species by causing the breakdown of high molecular weight organic compounds into a more available form (Bertilsson et al., 1999; Lindell et al., 1996; Reche et al., 1998; Wetzel et al., 1995) that can then be taken up for bacterial and protist growth. A study using large enclosures in a high-arctic lake with high levels of dissolved organic compounds showed that after long-term exposure to enhanced UV-B radiation, heterotrophic bacterial production and zooplankton density increased, which may have resulted from an increase in nutrient availability caused by photodegradation of organic compounds and the stimulation of heterotrophic pathways (Perin, 2003).

Some wetland biota such as amphibians are known to be highly sensitive to UV radiation, although sensitivity varies greatly among populations, and other factors such as climate effects on habitat extent are likely to have much greater impacts on northern species (section 8.6.2). A variety of complex responses have been observed to date in wetland plants. For example, UV-B radiation effects on the growth of high-latitude mosses appear to be a function of water supply as well as species. Field irradiation (UV-B radiation levels increased 15%) of *Sphagnum fuscum* caused a 20% reduction in growth, however, growth of the other moss species increased by up to 31% with the enhanced UV-B radiation. This stimulatory effect, however, ceased or was reversed under conditions of reduced water supply (Gehrke et al., 1996).

8.7. Global change and contaminants

During the past 50 years, persistent organic pollutants (POPs), metals, and radionuclides have been widely distributed into northern freshwater ecosystems by long-range atmospheric transport (Barrie et al., 1998; Macdonald R. et al., 2000). Within some catchments, deposition from the atmosphere may be augmented locally by industry or agriculture (AMAP, 1998) or biotransport (AMAP, 2004b; Ewald et al., 1998; Zhang et al., 2001). Figure 8.21 illustrates contaminant pathways, transfers, and exchanges in freshwater systems. This section briefly discusses how projected global change might alter these pathways, focusing especially on POPs and Hg because they have the greatest potential for change in risks to freshwater ecosystems as a result of climate change (Macdonald R. et al., 2003a,b).

8.7.1. Contaminant pathways and arctic freshwater ecosystems

There are two components of long-range transport pathways: transport to arctic freshwater catchments, and processes within the catchments (Fig. 8.22). Transports and transfers within each of these components are altered by climate change manifested in such things as wind fields, precipitation (amount, timing, form), snow cover, permafrost, extreme events, UV radiation exposure, the hydrological cycle, ice cover, the organic carbon cycle,

and food webs, and are very likely to result in enhanced bioaccumulation of contaminants (e.g., Box 8.12).

Before describing specifically how global change may alter contaminant pathways, it is important to understand how contaminants become concentrated in the environment. Macdonald R. et al. (2002) suggest that there are two distinct concentrating processes, which they term solvent switching and solvent depletion. Solvent switching can, for example, lead spontaneously to concentration amplification of hexachlorocyclohexanes (HCHs) in water because HCH partitions strongly out of air (Li et al., 2002), or high concentrations of PCBs in phytoplankton due to strong partitioning out of water and into lipids (Mackay D., 2001). Solvent depletion involves a reduction in the mass of solvent in which the contaminant is held, a process that can lead to fugacity amplification (i.e., POP concentrations exceeding thermodynamic equilibrium with the surrounding media). Examples include inefficient fat transfers in aquatic food webs (i.e., biomagnification, Kidd et al., 1995c), the loss of organic carbon in settling particles or during sediment diagenesis (Jeremiason et al., 1998; Larsson et al., 1998), the decrease of snow surface area as crystals become more compact during aging or the entire loss of snow surface during melting (Macdonald R. et al., 2002; Wania, 1999), or cryogenic concentration during the formation of ice (Macdonald R. et al., 2003b; Fig. 8.23). Many of the consequences of climate change for the solvent-switching processes are relatively easy to project and model because the effect of temperature on partition coefficients is known. For example, for contaminants that presently are saturated in arctic surface waters, increased temperatures will generally lead to net gas evasion (Harner, 1997) and the ocean is very likely to become a net source of those contaminants to the atmosphere. McKone et al. (1996) concluded that, with temperature increases, the risk hexachlorobenzene (HCB) presents to aquatic biota is likely to decrease slightly because HCB will partition less into water (McKone et al., 1996). The solvent-depleting processes, however, provide a much greater challenge to projection and have not yet been incorporated realistically into models.

8.7.2. Persistent organic pollutants in arctic catchments

The freeze, melt, and hydrological cycles and the organic carbon cycles of arctic lakes are likely to provide sensitive sentinels of change. As discussed in more detail in the previous sections and Chapter 6, probable changes as a result of projected temperature increases include reduced thermal contrast between winter and spring; reduced duration of snowmelt (later freeze-up, earlier melting); reduced ice formation; increased annual precipitation; thawing of permafrost producing a deeper active layer, enhanced soil erosion, mobilization of organic carbon, and reduced pond areas owing to drainage; more frequent extreme weather events; changes in catchment vegetation (i.e., more leaf-bearing plants); changes in nutrient availability; warming of
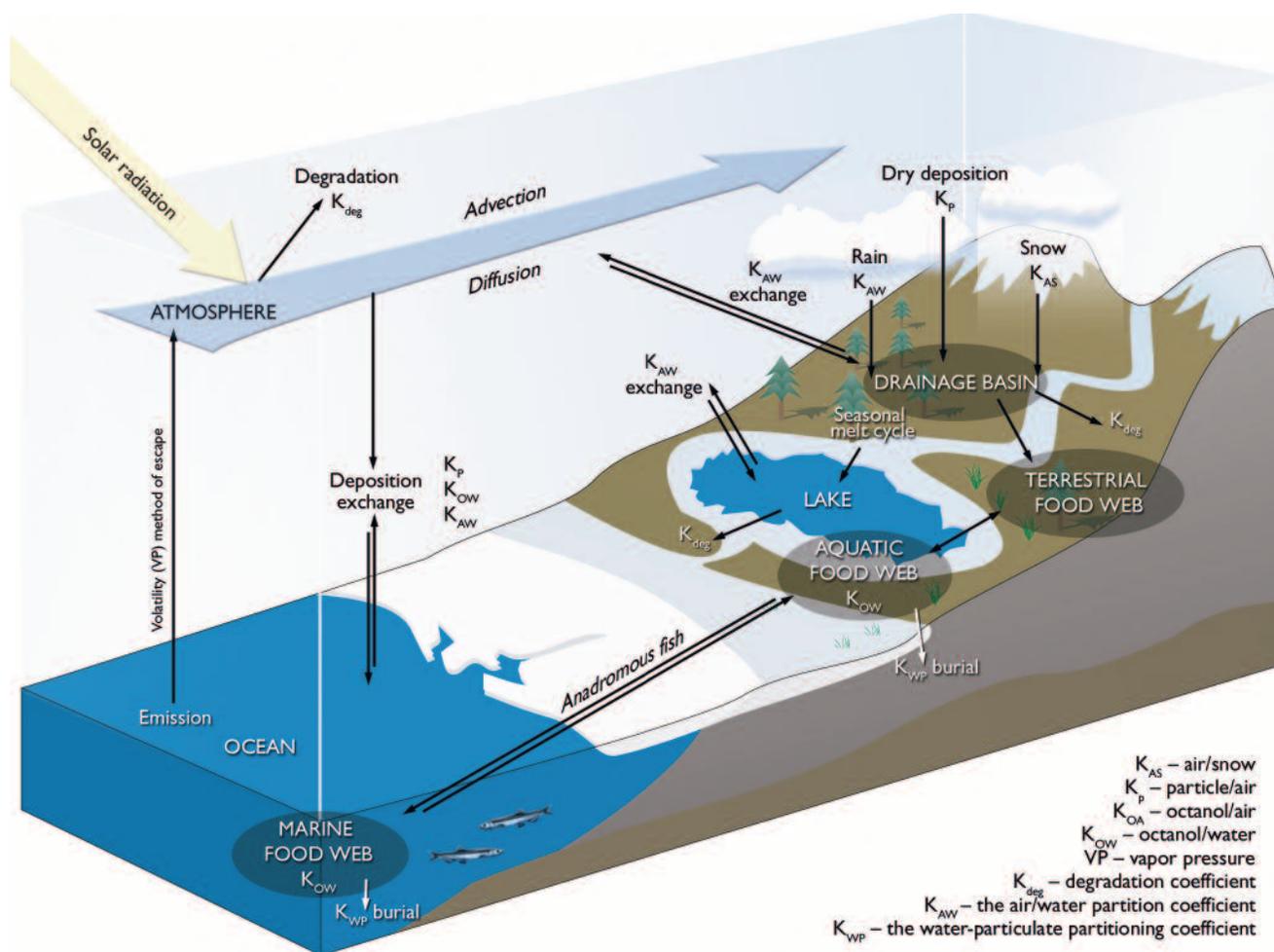
Fig. 8.22. Processes involved in transporting POPs to the Arctic and depositing them into terrestrial ecosystems. Transport, deposition, and exchange can occur anywhere along the transport pathway. Contaminants can also be transported within aquatic and terrestrial food chains. Climate change can alter the physical couplings between the systems (e.g., by changing rain or snowfall patterns), or alter the biological couplings by changing trophic structure or migratory pathways.

lakes; and an increase in the frequency of wildfires (e.g., Hinzman et al., in press; Schindler D.W., 1997; Schindler D.W. et al., 1996a, 1997; Vörösmarty et al., 2001). For some lakes, permafrost degradation together with reduced ice cover is very likely to result in enhanced nutrient and organic carbon loadings and higher productivity. Conversely, if dry summer conditions produce extensive fires, affected lakes are very likely to receive reduced spring melt, fewer nutrients from the catchment, reductions in productivity (Schindler D.W. et al., 1996a), and higher burdens of combustion PAHs.

Most arctic lakes receive their contaminant burdens from the atmosphere, with the catchment acting as a receptor through snow, rain, and dry deposition especially during winter, and a conveyor through snow and ice melt and runoff in spring (e.g., see Larsson et al., 1998; Macdonald R. et al., 2000). This section describes the stages from contaminant release to its final emergence in top freshwater predators (Fig. 8.22), noting in particular those components of the pathway likely to be altered as a result of climate change.

Upon release, contaminants are transported through the atmosphere either as gases or adsorbed onto particles.

During atmospheric transport, washout and air–surface exchange remove some of the contaminant to the surface where it may become permanently sequestered or re-volatilized as a result of, for example, seasonal heating cycles, eventually arriving in the Arctic via a number of "hops" (Barrie et al., 1998). Accordingly, POPs undergo hemispheric-scale chromatography, with surfaces (soil, water, vegetation) providing the stationary phase and the atmosphere providing the moving phase. Global temperature increases will generally accelerate this cycling. Processes that are effective at capturing contaminants in arctic drainage basins (e.g., strong partitioning onto particles, into precipitation, into vegetation) are also effective at removing contaminants during transport. For example, Li et al. (2002) suggested that air–water partitioning alone restricts the entry of beta-hexachlorocyclohexane (β-HCH) into the Arctic by removing it to surfaces by rain and air–sea exchange. In the case of β-HCH, and in the case of contaminants that partition strongly onto particles (e.g., many PAHs, dichloro-diphenyltrichloroethane (DDT), and highly chlorinated PCBs), changes in rainfall patterns (amount and location) are very likely to alter the efficiency of transport to arctic locations and capture within the Arctic. Heavy metals provide an instructive example that

will likewise apply to many of the POPs. Presently, less than 20% of particulate metal entering the Arctic is captured there (Akeredolu et al., 1994). Since the five ACIA-designated models project that the Arctic will become a "wetter" place (section 4.4.3, see also Manabe et al., 1992; Serreze et al., 2000), the capture of particulates and contaminants that partition strongly into water is likely to significantly increase by a factor that could more than offset efforts to reduce global emissions.

Because much of the contaminant delivery to the Arctic occurs during late winter as "arctic haze" or as "brown snow" events (Hileman, 1983; Welch H. et al., 1991), it is clear that sequestering by snow is an important

Box 8.12. Temperature-induced metal accumulation and stress responses in fish from Canadian Arctic lakes

High-altitude and high-latitude lakes are very sensitive ecosystems, where even slight environmental changes will possibly substantially affect ecosystem function (Köck and Hofer, 1998; Köck et al., 2001). Environmental changes can alter fish habitat and toxicant accumulation from water and diet. Long-range transport of pollutants also tends to endanger fish populations by leading to highly elevated metal accumulation (Köck et al., 1996). Water temperature has been shown to be the driving force of excessive metal accumulation in these fish. A multi-year project, centered around small sensitive lake ecosystems in the Canadian Arctic Archipelago (Cornwallis Island, Somerset Island, and Devon Island), was designed to explain the interactions between short- or longer-term climatic variation, the bioaccumulation of metals, and various biochemical stress indicators in land-locked populations of Arctic char.

Arctic char were collected at monthly intervals from Resolute Lake (Cornwallis Island, Nunavut, 74° 41' N, 94° 57' W) during summers from 1997 to 2001. Fish were dissected and liver tissue subsampled for analysis of metal content (cadmium – Cd and zinc – Zn) and biochemical stress indicators (glutathione – GSH, glutathione disulfide – GSSG, glycogen, and Vitamin C). Glutathione is an antioxidant, which is reduced to GSSG in the presence of reactive oxygen species. The GSSG/GSH ratio is a sensitive indicator of oxidative stress in cells (Lackner, 1998). Stress response was indicated by a decrease in GSH accompanied by an increase in GSSG.

Interannual variation of the GSSG/GSH ratio in the liver of Arctic char (n=20 individuals per group) from Resolute Lake, showing means ± standard deviation (Köck et al., 2002).

Similar to Arctic char from Austrian high-mountain lakes, concentrations of Cd and Zn in the liver of high-latitude char exhibited a marked seasonal change during summer, and were significantly higher at the end of the ice-free period. A similar pattern was found for concentrations of metallothione (an inducible metal-binding protein) in the liver. Concentrations of Cd and Zn in the liver of char collected in August 1998 were significantly higher than those in fish collected during the same period in 1997, 1999, 2000, and 2001, which coincides with much higher lake water temperatures in the El Niño year of 1998 (Köck et al., 2002). Cadmium concentrations in the liver were positively correlated with frequencies of high temperatures (4–12 °C) and negatively with those of lower temperatures (<0–4 °C).

Interannual variation of the GSSG/GSH ratio, glycogen, and Vitamin C levels in the char studied indicate a higher level of stress in 1998 than in 1997 and 1999: the GSSG/GSH ratios in the livers of fish collected in 1998 were significantly higher than in 1997 and 1999 (see figure). Furthermore, concentrations of glycogen and Vitamin C were significantly lower in 1998. The severe depletion of glycogen energy reserves indicates that atypically high lake temperatures enhanced metal bioaccumulation and detoxification responses, diverting energy resources from other important physiological functions.

These results illustrate that Arctic char are extremely susceptible to even slight changes in lake water temperatures. Rising water temperatures lead to increased metabolic rates and thus pumping of higher volumes of water across the gills, which in turn results in increased uptake of dissolved metals from the water. The rapid increase in temperatures projected by various GCMs will possibly be a serious threat to the stability of Arctic char populations in high-latitude lakes.
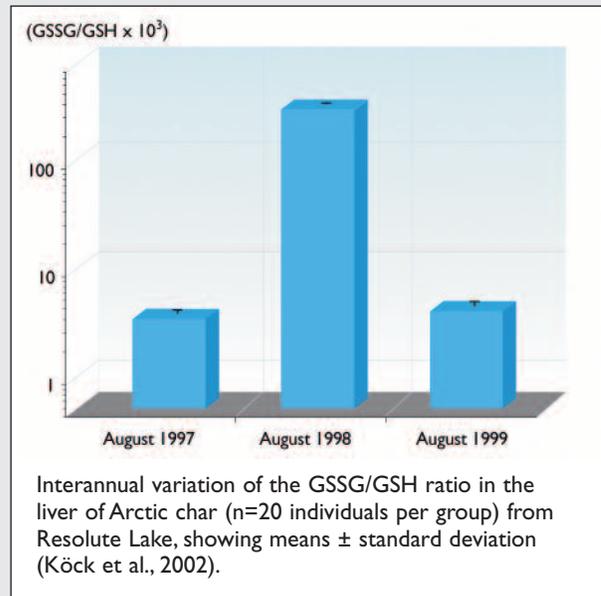
process. Hence, careful consideration must be given to any changes in arctic snow conditions. Newly formed snow has a large surface area (as much as 0.4 m^2/g, Hoff et al., 1998) that scavenges both particulate and gaseous POPs, eventually sequestering them into the snowpack (Gregor, 1990). Precipitation form (snow, rain, fog) is therefore important and, considering the seasonal modulation in atmospheric concentrations of contaminants (Heintzenberg, 1989; Hung et al., 2001; Macdonald R. et al., 2000), so is timing. For example, snowfall during a period of arctic haze would be much more important for transferring contaminants to the ground than at other times of the year.

As snow ages or melts, its surface area to volume ratio decreases, resulting in the removal of the solvent that captured the POPs (e.g., Wania, 1997). Macdonald R. et al. (2002) estimated that this process could lead to fugacity amplification of ~2000 times that of the air – clearly an enormous thermodynamic forcing. Depending on the exact circumstances under which snow loses its surface area, the POPs will be vaporized back to the air or partitioned into particles, soil, vegetation, or meltwater. Changes in the frequency and timing of snowfall, unusual events like freezing rain, or the rate and timing of snowmelt are likely to effect large changes in the proportion of POPs that enter the arctic hydrological cycle.

Terrestrial organic carbon in soils and vegetation has a large capacity to store many POPs (Simonich and Hites, 1994), with PCBs, DDT, HCH, and chlorobenzenes figuring prominently (AMAP, 2004b). Wania and McLachlan (2001) have shown that forests "pump" organochlorines from the atmosphere into foliage and subsequently to long-term soil reservoirs. Accordingly, increased proportions of leaf-bearing plants in arctic catchments will enhance this "pump". Increased metabolism of soil organic carbon owing to temperature increases, changes in soil moisture, or reduced snow cover will force POPs associated with soil organic carbon to redistribute, probably into groundwater or meltwater.

Climate variation results in the storage of contaminants in perennial snow and ice or in soils, vegetation, and delta/estuarine sediments during periods of cold climate (years to decades). These stored contaminants may subsequently be released during a period of warming and, although this process may not be sustainable, it is likely to produce episodes of high contaminant loadings into water (Blais et al., 1998, 2001). During permafrost degradation, a shift toward dendritic drainage patterns (e.g., McNamara et al., 1999) allows a more complete transport of contaminants into ponds and lakes and possibly re-mobilizes contaminants stored in soils. Simultaneously, the reduction of pond areas owing to drainage channels in permafrost (Hinzman et al., in press) is likely to enhance contaminant transport into the remaining surface water.

After POPs enter the hydrological cycle through the mechanisms discussed, a proportion of them will be stored in lakes and lake sediments. Evidence from a limited number of studies (Diamond et al., 2003; Helm et al., 2002; Macdonald R. et al., 2000) suggests that meltwater currently enters arctic lakes when they are thermally stratified beneath an ice cover. Therefore, much of the annual snowmelt traverses under the ice to exit at the outflow carrying its contaminant burden; that is, arctic lakes are not efficient at capturing POPs entering via streamflow. It is probable that many of the previously described alterations in freshwater systems induced by climate change (such as reduced ice cover, increased mixing and primary production, and increased loading of organic carbon and sediment from the contributing catchments) will also enhance contaminant capture in lakes (e.g., see Hinzman et al., in press).

Because most arctic lakes tend to be oligotrophic, only a small proportion of POPs is transported by vertical flux of organic particles and buried in sediments (e.g., Diamond et al., 2003; Muir et al., 1996; Stern and Evans, 2003). A second solvent-depletion process occurs due to organic carbon metabolism during particle settling and within bottom sediments (Fig. 8.23a). The loss of organic carbon can provide exceptionally strong thermodynamic forcing to drive the POPs off solid phases and into sediment pore water, where they may diffuse into bottom waters or partition into benthos (Gobas and MacLean, 2003; Jeremiason et al., 1994; Macdonald R. et al., 2002). An increase in the vigor of the organic carbon cycle (e.g., increased primary production, organic carbon loadings, and microbial activity) will enhance this thermodynamic pump. Cryogenic concentration (Fig. 8.23d) is likely to work together with organic carbon metabolism in sediments during winter to produce exceptionally high concentrations of POPs in bottom water. Although relatively poorly studied, contaminants are believed to be excluded from ice as it forms. For shallow water that freezes nearly to the bottom, dissolved contaminants are likely to be forced into a very small volume of remaining water and the resultant high contaminant concentrations will promote partitioning into remaining organic material including sediment surfaces, benthos, plankton, and larger animals. As noted previously, such under-ice zones are often a critical winter refuge for biota (e.g., Hammar, 1989). It is likely that a general reduction in the depth of ice formed during warmer winters will reduce cryogenic concentration. However, cryogenic concentration interacts with water levels, which are likely to decrease during permafrost degradation (Hinzman et al., in press).

The transfer of lipid-soluble POPs upward in aquatic food webs is one of the most important routes of exposure to apex feeders, including humans. In this solvent-depleting process, much of the lipid is metabolized at each trophic level while the organochlorines are retained. This results in higher trophic levels exhibiting organic carbon biomagnification factors of 3 to 100 in their lipids, and a net bioaccumulation of 10^7 to 10^9 times higher than in the water (Braune et al., 1999; Kidd et al., 1995a,c; Macdonald R. et al., 2003b). Changes in aquatic trophic structure either through

alteration of the number of food web steps or the size distribution of predatory fish will likewise change contaminant burdens. With climate change, wide-ranging shifts in zoogeographic distributions have the potential to affect every step in freshwater food chains (Hinzman et al., in press; Schindler D.W., 1997).

There are several other ways that global change can alter contaminant pathways in arctic aquatic ecosystems. As noted in section 8.5.4, recent evidence suggests that salmon migrations undergo large, climate-related variation (Finney et al., 2000, 2002) and that Pacific salmon may respond to change by invading arctic rivers (Babaluk et al., 2000). Given that these salmon biomagnify and bioaccumulate contaminants in the Pacific Ocean, they are an important means of contaminant transport into particular arctic catchments. In specific lakes, fish may supply more POPs than atmospheric deposition (Ewald et al., 1998). Similarly, bird migrations that change in location and intensity have the potential to concentrate, transport, and deposit contaminants in particular catchments (AMAP, 2004b, Braune et al., 1999; Hinzman et al., in press). For example, detailed studies of Lake Ellasjoen, Norway,

found that seabirds can serve as important biological pathways carrying contaminants (in this case POPs) from marine to freshwater environments (AMAP, 2002). Climate change or human intervention is also very likely to lead to the introduction of exotic species to the Arctic. Although probably not a risk to arctic lakes, the invasion of the Great Lakes by the zebra mussel (*Dreissena polymorpha*) provides an instructive example of just how disruptive an exotic species can be to organic carbon and POP cycles (Morrison et al., 1998, 2000; Whittle et al., 2000).

Changes within arctic catchments that cause apex feeders (e.g., humans, bears, mink, birds) to switch their diet from aquatic to terrestrial food sources or vice versa have a large potential to alter contaminant exposure. Whereas arctic aquatic food webs exhibit endemic contamination from biomagnifying chemicals, arctic land-based food webs are among the cleanest in the world (AMAP, 2004b; de March et al., 1998). Dietary changes are forced by fluctuations in the populations of prey species or by changes in access to the species due to early ice melt or permafrost degradation (e.g., Fast and Berkes, 1998; Riedlinger, 2001).
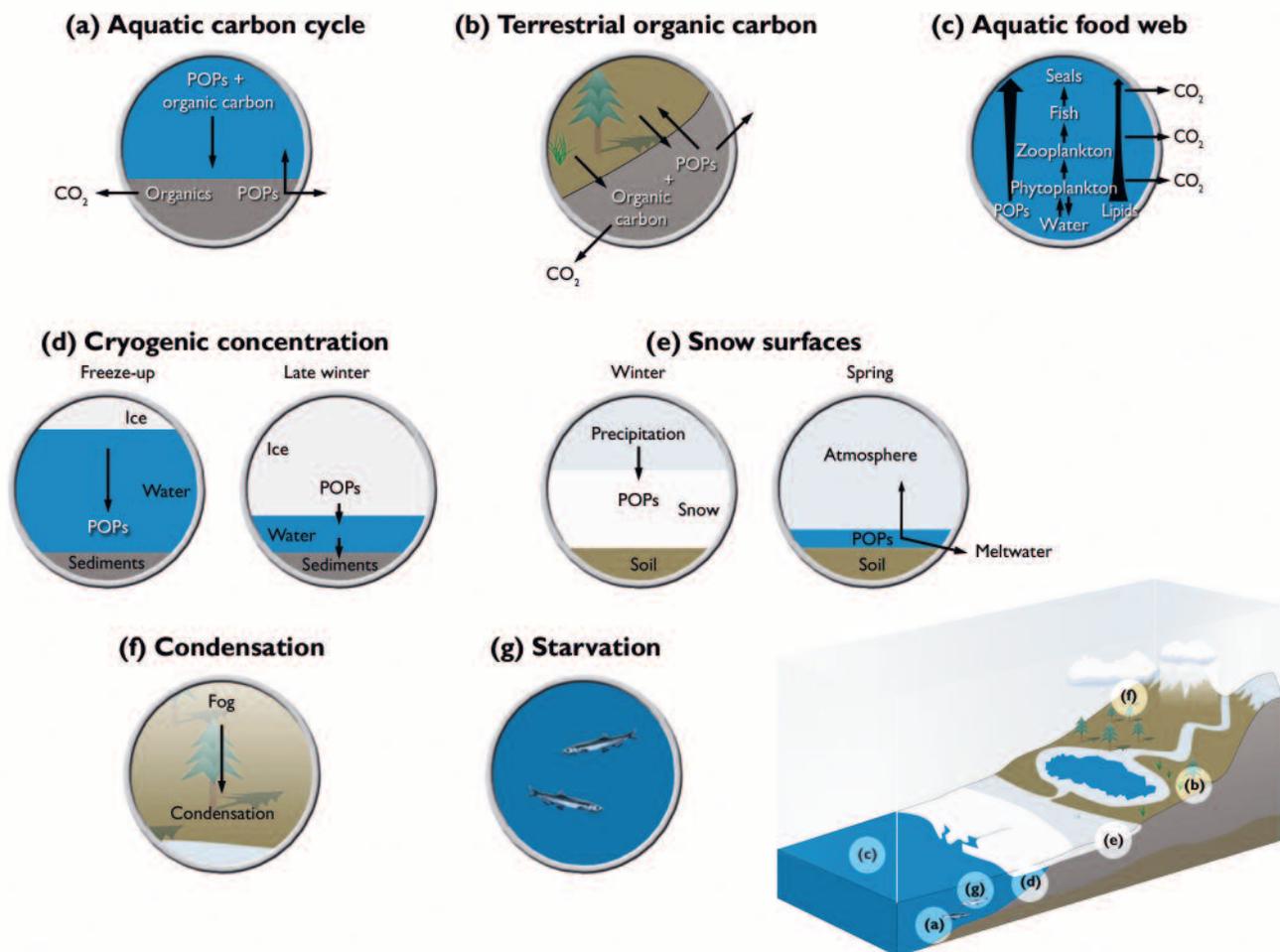
Fig. 8.23. In the illustrated solvent-depleting processes, POPs are concentrated beyond thermodynamic equilibrium through the removal of solvent by organic carbon metabolism in (a) aquatic and (b) terrestrial carbon cycles, by (c) inefficient lipid transfer in aquatic food webs, by (d) exclusion into a dwindling layer of water during the growth of ice, by (e) the loss of snow surfaces during aging or melting, by (f) the loss of surface area through condensation of fog into water droplets or onto surfaces, and (g) through loss of lipid pools during periods of starvation.

As conditions more suitable for domestic crops develop, agriculture or silviculture within arctic drainage basins and associated chemical use is likely to expand. Demographic shifts and population increases in northern regions could possibly lead to increased local release of contaminants. South of the Arctic, global temperature increases and alteration of hydrological cycles will probably result in insect and other pest outbreaks (e.g., West Nile virus or malaria), provoking the re-introduction of banned pesticides (Harner, 1997). Finally, contaminants in dumps or sumps presently contained by permafrost are very likely to be released by permafrost degradation (Williams and Rees, 2001).

Increased fluxes of PAHs are likely to result from the erosion of peat-rich soils (Yunker et al., 1993) or drying trends leading to an increase in wildfires, and are likely to have a greater impact on small rivers that presently receive most of their PAHs from combustion sources (Yunker et al., 2002).

8.7.3. Mercury in arctic catchments

Mercury exhibits a natural global cycle that has been enhanced by human activities such as coal burning, soft and ferrous metal smelting, cement production, and municipal waste with the consequence that two to three times as much Hg is now cycling through the atmosphere and surface waters than was before the rise of industry (Lamborg et al., 2002). Pacyna and Pacyna (2001) estimated that worldwide anthropogenic Hg emissions totaled 2235×10^3 kg in 1995, with fossil fuel consumption contributing over half of that. This value may be compared to the 2500×10^3 kg/yr estimate of natural emissions (Nriagu, 1989). The largest emitter of Hg from fossil fuel consumption is China (495×10^3 kg

in 1995), which is directly upwind from the Bering Sea, Alaska, and the western Arctic. In comparison, Russia released about 54×10^3 kg in 1995.

Many of the concentrating processes discussed for POPs (Fig. 8.23) apply equally to Hg. However, atmospheric Hg depletion events (MDEs) after polar sunrise provide a unique, climate-sensitive pathway to Hg deposition in arctic catchments (Fig. 8.24, Lindberg et al., 2002; Lu et al., 2001; Macdonald R. et al., 2000; Schroeder et al., 1998; Steffen et al., 2003). The process requires snow surfaces, solar radiation, and the presence of sea salts (bromides and chlorides). Although MDEs are initiated over the ocean, and especially over the marginal seas where halides are more available from frost flowers (crystals of ice that form directly from the vapor phase, often associated with new sea ice, which can become very salty by channeling brine upward from the ice) or first-year ice (Shepson et al., 2003), atmospheric advection can subsequently deposit reactive Hg in arctic catchments (Steffen et al., 2003). As with POPs, Hg can be transferred and concentrated during snow aging and melting, such that a large pulse of Hg is released to terrestrial and freshwater environments during spring melt (e.g., see AMAP, 2004a; Diamond et al., 2003; Stanley J. et al., 2002). Scott K. (2001) showed that Hg deposited through the MDE mechanism is in a form that can readily be taken up by biota. Once Hg enters the hydrological cycle, it can be concentrated and transferred through the carbon cycle and food webs, both of which are vulnerable to change. In addition, the efficiency of arctic lakes in capturing Hg is very likely to be altered by changes in the timing of freshet, ice melt, and productivity (Braune et al., 1999; Diamond et al., 2003; Kidd et al., 1995b; Macdonald R. et al., 2000).

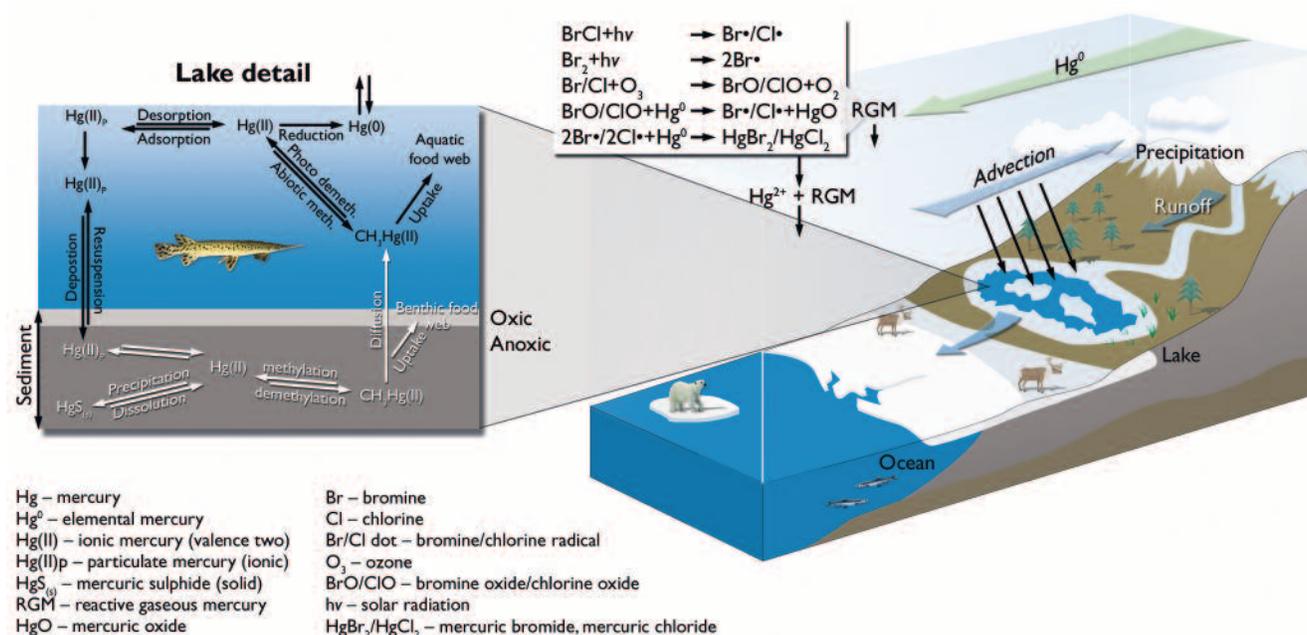**Fig. 8.24.** Production of particulate and reactive gaseous mercury over the ocean after polar sunrise (right side) and the advection of reactive and bioavailable forms of mercury into catchments where it is deposited. After deposition, the mercury enters lakes through meltwater and is then subject to reduction and methylation (meth.) processes. Methyl mercury ($CH_3Hg(II)$) is the most toxic form.

Table 8.5. Environmental factors affecting mercury concentration in aquatic top predators.

Projected change	Effect on mercury concentration in predatory fish	Reference
Flooding of soil	Increase	Bodaly and Johnston, 1992
Increased primary production	Reduce	Pickhardt et al., 2002
Increased number of trophic levels	Increase	Kidd et al., 1995b
Shift toward larger fish	Increase	Sherwood et al., 2001
Reduced lake size	Increase	Bodaly et al., 1993
Increased anadromous fish migration	Increase	Zhang et al., 2001

Once Hg has been deposited into arctic catchments, a number of processes may lead to elevated concentrations in old, predatory fish (Table 8.5). The coupling between Hg deposition on surfaces and its entry into lakes is likely to be enhanced by projected changes in the hydrological and organic carbon cycles (Diamond et al., 2003; Stanley J. et al., 2002). Apex feeders are most vulnerable to any change in the Hg cycle considering that biomagnification factors are 250 to 3000 (Atwell et al., 1998; Folt et al, 2002; Kidd et al., 1995b; Muir et al., 1999). Because MeHg presents a far greater health hazard than inorganic or elemental Hg, methylation is a crucial process upon which climate change operates. Wetlands and wetland sediments are net producers of MeHg (Driscoll et al., 1998; Suchanek et al., 2000), and Hg observed in fish from small lakes appears to correlate with the amount of watershed occupied by wetlands (Greenfield et al., 2001). Flooding of terrestrial landscapes has the well-known consequence of releasing Hg from submerged soils (Bodaly et al., 1984). Therefore, alteration of wetland distribution or area in the Arctic resulting from thawing permafrost (section 8.4.4.4) is very likely to release Hg, which will be more serious if arctic soils contain an inventory of contaminant Hg accumulated during the past century or two.

8.8. Key findings, science gaps, and recommendations

In general, changes in climate and UV radiation levels in the Arctic are very likely to have far-reaching impacts, affecting aquatic species at various trophic levels, the physical and chemical environment that makes up their habitat, and the processes that act on and within freshwater ecosystems. Interactions of climatic variables such as temperature and precipitation with freshwater ecosystems are highly complex and can be propagated through the ecosystem in ways that are not readily predictable. This reduces the ability to accurately project specific effects of climate and UV radiation change on freshwater systems. This is particularly the case when dealing with threshold responses (i.e., those that produce stepwise and/or nonlinear effects). Forecasting ability is further hampered by the poor understanding of arctic freshwater systems and their basic interrelationships with climatic and other environmental variables, as well as by a paucity of long-term freshwater monitoring sites and integrated hydro-ecological research programs in the Arctic.

A significant amount of the understanding of potential impacts is based on historical analogues (i.e., historical evidence from past periods of climate change), as well as from a limited number of more recent studies of ecosystem response to environmental variability. Paleo-reconstructions indicate that during the most recent period of climatic warming, which followed the Little Ice Age, the Arctic reached its highest average annual temperatures observed in the past 400 years, resulting in glacier retreat, permafrost thaw, and major shifts in freshwater ecosystems. Examples of ecosystem effects included altered water chemistry, changes in species assemblages, altered productivity, and an extended growing-season length. Importantly, however, past natural change in the Arctic occurred at a rate much slower than that projected for anthropogenic climate change over the next 100 years. In the past, organisms had considerable time to adapt; their responses may therefore not provide good historical analogues for what will result under much more rapid climate change. In many cases, the adaptability (i.e., adaptation, acclimation, or migration) of organisms under rapidly changing climate conditions is largely unknown. Unfortunately, no large-scale attempts have been made to study the effects of rapid climate change on aquatic ecosystems using controlled experiments, as have been attempted for terrestrial systems (e.g., see International Tundra Experiment studies of tundra plant response in section 7.3.3.1). However, field studies in areas that have recently experienced rapid changes in climate have provided important knowledge. Information about ongoing climate change impacts is provided by results from long-term environmental monitoring and research sites in the Arctic, including the case studies presented in this chapter: Northern Québec and Labrador, Canada (Box 8.1), Toolik Lake, Alaska (Box 8.3), Lake Saanajärvi, Finnish Lapland (Box 8.4), and the Zackenberg Valley in northeastern Greenland (Box 8.5).

8.8.1. Key findings

This section lists a number of broad-scale findings for major components of arctic freshwater ecosystems. Although it was possible in this assessment to evaluate mesoscale regional differences in, for example, the timing and severity of the freshet and/or breakup on large rivers, difficulties in ecological downscaling of most climatic and related hydrological changes precluded regional discrimination of variations in impacts. Hence, most of the following statements are broad-scale and not

regionally specific. To indicate the probability of each impact occurring, the ACIA lexicon regarding the range of likelihood of outcome (section 8.1.2) has been applied to the findings (i.e., the bold-text statement(s) in each bullet). Each assigned likelihood is the product of a multi-author scientific judgment based on knowledge synthesized from the scientific literature, including the previously noted case studies, and the interpretation of effects deduced from the ACIA-designated model projections. The same level of likelihood of occurrence is applied to the subsequent, more detailed descriptions following each major finding.

Ecological impacts of changes in runoff, water levels, and river-ice regimes

- **A probable shift to a more pluvial system with smaller and less intense freshet and ice breakup is very likely to decrease the frequency and magnitude of natural disturbances, and reduce the ability of flow systems to replenish riparian ecosystems, particularly river deltas.** As rainfall becomes a more prominent component of high-latitude river flow regimes, and as temperatures rise, freshets will be less intense and ice breakup less dramatic. Furthermore, differential changes in climatic gradients along the length of large arctic rivers will produce varying responses in freshet timing and breakup severity. Decreased frequency and intensity of physical disturbances will result in decreased species richness and biodiversity in riverine, deltaic, and riparian habitats.

- **Reduced climatic gradients along large northern rivers are likely to alter ice-flooding regimes and related ecological processes.** Projected differential rates of temperature increases across the major latitudinal ranges of some large northern rivers and the corresponding reduction in the latitudinal spring temperature gradient are likely to reduce the frequency and magnitude of dynamic river-ice breakups and lead to more placid thermal events. Because such disturbances play a major role in maintaining habitat complexity and associated species richness and diversity, this will have significant implications for ecosystem structure and function.

- **A very probable increase in winter flows and reduced ice-cover growth is very likely to increase the availability of under-ice habitat.** High-latitude rivers that typically freeze to the bottom during the winter will experience increased flow in response to increasing precipitation and winter temperatures, increasing base flow, and declining ice thickness. The subsequent presence of year-round flowing water in these river channels will increase habitat availability, ensuring survival of species previously restricted by the limitation of under-ice habitat. Migration and the geographic distribution of aquatic species (e.g., fish) may also be affected.

- **A probable decrease in summer water levels of lakes and rivers is very likely to affect quality and quantity of, and access to, aquatic habitats.** In areas where combinations of precipitation and evaporation lead to reductions in lake and/or river water levels, pathways for fish movement and migration will be impaired, including access to critical habitat. In addition, declining water levels will affect physical and chemical processes such as stratification, nutrient cycling, and oxygen dynamics.

Changes in biogeochemical inputs from altered terrestrial landscapes

- **Enhanced permafrost thawing is very likely to increase nutrient, sediment, and carbon loadings to aquatic systems.** This is very likely to have a mixture of positive and negative effects on freshwater chemistry. As permafrost and peat warm and active layers deepen with rising temperatures, nutrients, sediment, and organic carbon will be flushed from soil reserves and transported into aquatic systems. Increased nutrient and organic carbon loading will enhance productivity in high-latitude lakes, as well as decrease exposure of biota to UV radiation. Conversely, heavily nutrient-enriched waters (i.e., systems with enhanced sediment and organic matter loads), may result in increased light limitation and reduced productivity.

- **An enhanced and earlier supply of sediment is likely to be detrimental to benthic fauna.** As soils warm in high-latitude permafrost landscapes and become more susceptible to erosion, surface runoff will transport larger sediment loads to lakes and rivers. Aerobes in lake and river bottom sediments will initially be threatened by oxygen deprivation due to higher biological oxygen demand associated with sedimentation. Larger suspended sediment loads will also negatively affect light penetration and consequently primary production levels. Similarly, negative effects such as infilling of fish spawning beds associated with increased sediment loads are also likely in many areas.

- **Increases in DOC loading resulting from thawing permafrost and increased vegetation are very likely to have both positive and negative effects.** The balance will be ecosystem- or site-specific. For example, as DOC increases, there will be a positive effect associated with reduced penetration of damaging UV radiation, but also a negative effect because of the decline in photochemical processing of organic material. An additional negative effect would be a decrease in primary production due to lower light availability (quantity and quality).

Alterations in ponds and wetlands

- **Freshwater biogeochemistry is very likely to be altered by changes in water budgets.** As permafrost soils in pond and wetland catch-

ments warm, nutrient and carbon loading to these freshwater systems will rise. Nutrient and carbon enrichment will enhance nutrient cycling and productivity, and alter the generation and consumption of carbon-based trace gases.

- **The status of ponds and wetlands as carbon sinks or sources is very likely to change.** High-latitude aquatic ecosystems function as sinks or sources of carbon, depending on temperature, nutrient status, and moisture levels. Initially, arctic wetlands (e.g., peatlands) will become sources of carbon as permafrost thaws, soils warm, and accumulated organic matter decomposes. Decomposition rates in aquatic ecosystems will also increase with rising temperatures and increases in rates of microbial activity. Increases in wetland water levels could enhance anaerobic decay and the production and release of methane.

- **Permafrost thaw in ice-rich environments is very likely to lead to catastrophic lake drainage; increased groundwater flux is likely to drain others.** As permafrost soils warm, freshwater bodies will become increasingly coupled to groundwater systems and experience drawdown. Lake drawdown will result in a change in the limnology and the availability and suitability of habitat for aquatic biota. Over the long term, terrestrial habitat will replace aquatic habitat.

- **New wetlands, ponds, and drainage networks are very likely to develop in thermokarst areas.** Thawing permafrost and melting ground ice in thermokarst areas will result in the formation of depressions where wetlands and ponds may form, interconnected by new drainage networks. These new freshwater systems and habitats will allow for the establishment of aquatic species of plants and animals in areas formerly dominated by terrestrial species.

- **Peatlands are likely to dry due to increased evapotranspiration.** As temperatures increase at high latitudes, rates of evapotranspiration in peatlands will rise. Drying of peat soils will promote the establishment of woody vegetation species, and increase rates of peat decomposition and carbon loss.

Effects of changing lake-ice cover

- **Reduced ice thickness and duration, and changes in timing and composition, are very likely to alter thermal and radiative regimes.** Rising temperatures will reduce the maximum ice thickness on lakes and increase the length of the ice-free season. Reduced lake-ice thickness will increase the availability of under-ice habitat, winter productivity, and associated dissolved oxygen concentrations. Extension of the ice-free season will increase water temperatures and lengthen the overall period of productivity.

- **A longer open-water season is very likely to affect lake stratification and circulation patterns.** Earlier breakup will lead to rapid strat-

ification and a reduction in spring circulation. In certain types of lakes this will cause a transfer of under-ice oxygen-depleted water to the deep water of stratified lakes in the summer (i.e., lakes will not get a chance to aerate in the spring). A longer open-water season will result in an increase in primary production over the summer that will lead to increased oxygen consumption in deeper waters as algae decompose. Correspondingly, fish habitat will be substantially reduced by the combination of upper-water warming and the low-oxygen conditions in deeper water. As a result, certain fish species (e.g., lake trout) may become severely stressed.

- **Reduced ice cover is likely to have a much greater effect on underwater UV radiation exposure than the projected levels of stratospheric ozone depletion.** A major increase in UV radiation levels will cause enhanced damage to organisms (biomolecular, cellular, and physiological damage, and alterations in species composition). Allocations of energy and resources by aquatic biota to UV radiation protection will increase, probably decreasing trophic-level productivity. Elemental fluxes will increase via photochemical pathways.

Aquatic biota, habitat, ecosystem properties, and biodiversity

- **Climate change is very likely to affect the biodiversity of freshwater ecosystems across most of the Arctic.** The magnitude, extent, and duration of the impacts and responses will be system- and location-dependent, and will produce varying outcomes, including local and/or regional extinctions or species loss; genetic adaptations to new environments; and alterations in species ranges and distributions, including invasion by southern species.

- **Microbial decomposition rates are likely to increase.** Rates of microbial decomposition will rise in response to increasing temperatures and soil drying and aeration. Enhanced decomposition of organic materials will increase the availability of dissolved organic carbon and emissions of carbon dioxide, with implications for the carbon balance of high-latitude lakes and rivers and, in particular, wetlands, which are significant carbon reserves.

- **Increased production is very likely to result from a greater supply of organic matter and nutrients.** Organic matter and nutrient loading of rivers, lakes, and wetlands will increase as temperatures and precipitation rise. Thawing permafrost and warming of frozen soils with rising temperature will result in the release of organic matter and nutrients from catchments. Rising temperatures will increase the rates and occurrence of weathering and nutrient release. Organic matter contributions may also increase with the establishment of woody species. Primary productivity will rise, the effects of which may

translate through the food chains of aquatic systems, increasing freshwater biomass and abundance. In some instances, high loading of organic matter and sediment is very likely to limit light levels and result in a decline in productivity in some lakes and ponds.

- **Shifts in ranges and community composition of invertebrate species are likely to occur.** Temperature-limited species from more southerly latitudes will extend their geographic ranges northward. This will result in new invertebrate species assemblages in arctic freshwater ecosystems.

Fish and fisheries

- **Shifts in species ranges, composition, and trophic relations are very likely to occur.** Southern species will shift northward with warming of river waters, and are likely to compete with northern species for resources. The ranges of anadromous species may shift as oceanic patterns shift. The geographic ranges of northern or arctic species will contract in response to habitat impacts as well as competition. Changes in species composition at northern latitudes are likely to have a top-down effect on the composition and abundance of species at lower trophic levels. The broad whitefish, Arctic char complex, and the Arctic cisco are particularly vulnerable to displacement as they are wholly or mostly northern in their distribution. Other species of fish, such as the Arctic grayling of northern Alaska, thrive under cool and wet summer conditions, and may have less reproductive success in warmer waters, potentially causing elimination of populations.
- **Spawning grounds for cold-water species are likely to diminish.** As water temperatures rise, the geographic distribution of spawning grounds for northern species will shift northward, and is likely to contract. Details will be ecosystem-, species-, and site-specific.
- **An increased incidence of mortality and decreased growth and productivity from disease and/or parasites is likely to occur.** As southern species of fish migrate northward with warming river waters, they could introduce new parasites and/or diseases to which arctic fish species are not adapted, leading to a higher risk of earlier mortality and decreased growth.
- **Subsistence, sport, and commercial fisheries will possibly be negatively affected.** Changes in the range and distribution of fish species in northern lakes and rivers in response to changing habitat and the colonization of southerly species have implications for the operation of commercial fisheries and will possibly have potentially devastating effects on subsistence fishing. Changes in northern species (e.g., range, abundance, health) will diminish opportunities for fisheries on such species, calling for regulatory and managerial

changes that promote sustainable populations. Subsistence fisheries may be at risk in far northern areas where vulnerable species, such as the broad whitefish, the Arctic char complex, and Arctic cisco, are often the only fish species present. Fisheries will have to change to secure access, and to ensure that fishery function and duration of operation are effective, given a change in fish species and habitat. Alternatively, new opportunities to develop fisheries may occur.

Aquatic mammals and waterfowl

- **Probable changes in habitat are likely to result in altered migration routes and timing.** Migration routes of aquatic mammals and waterfowl are likely to extend northward in geographic extent as more southerly ecosystems and habitats develop at higher latitudes with increasing temperature. Migration may occur earlier in the spring with the onset of high temperatures, and later in the autumn if high temperatures persist. Breeding-ground suitability and access to food resources will be the primary drivers of changes in migration patterns. For example, wetlands are important feeding and breeding grounds for waterfowl, such as geese and ducks, in the spring. As permafrost landscapes degrade at high latitudes, the abundance of thermokarst wetlands may increase, promoting the northward migration of southerly wetland species, or increasing the abundance and diversity of current high-latitude species.
- **An increased incidence of mortality and decreased growth and productivity from disease and/or parasites will possibly occur.** As temperatures rise, more southerly species of mammals and waterfowl will shift northward. These species may carry with them new diseases and/or parasites to which northerly species are not adapted, which is likely to result in both an increased susceptibility to disease and parasites, and an increase in mortality.
- **Probable changes in habitat suitability and timing of availability are very likely to alter reproductive success.** Aquatic mammals and waterfowl are highly dependent on the availability and quality of aquatic habitats for successful breeding, and in the case of waterfowl, nesting. Northern species may have diminished reproductive success as suitable habitat either shifts northward or declines in availability and access. Northward migration of southern species may result in competitive exclusion of northern species from habitat and resources.

Climate–contaminant interactions

- **Increases in temperature and precipitation are very likely to increase contaminant capture in the Arctic.** Projected increases in temperature and changes in the timing and magni-

tude of precipitation will affect the deposition of contaminants at high latitudes. Climate change will accelerate rates of contaminant transfer. Climate scenarios currently project a "wetter" Arctic, increasing the probability of wet deposition of contaminants such as heavy metals and persistent organic pollutants.

- **Episodic releases of high contaminant loadings from perennial snow and ice are very likely to increase.** As temperatures rise at high latitudes, snow and ice accumulated over periods of years to decades will melt, releasing associated stored contaminants in the meltwater. This will increase episodes of high contaminant loadings into water, which may have toxic effects on aquatic organisms. Permafrost degradation may also mobilize contaminants. Lower water levels will amplify the impacts of contamination on high-latitude freshwater bodies.

- **Arctic lakes are very likely to become more prominent contaminant sinks.** Spring melt waters and associated contaminants typically pass through thermally stratified arctic lakes without transferring their contaminant burden. Contaminant capture in lakes will increase with reduced lake-ice cover (decreased stratification), increased mixing and primary production, and greater organic carbon and sediment loading. Contaminants in bottom sediments may dissociate from the solid phase with a rise in the rate of organic carbon metabolism and, along with contaminants originating from cryogenic concentration, may reach increasing levels of toxicity in lake bottom waters.

- **The nature and magnitude of contaminant transfer in the food web are likely to change.** Changes in aquatic trophic structure and zoogeographic distributions will alter biomagnification of contaminants, including persistent organic pollutants and mercury, and potentially affect freshwater food webs, especially top-level predatory fish (e.g., lake trout) that are sought by all types of fisheries.

Cumulative, synergistic, and overarching interactions

- **Decoupling of environmental cues used by biota is likely to occur, but the significance of this to biological populations is uncertain.** Photoperiod, an ultimate biological cue, will not change, whereas water temperature, a proximate biological cue, will change. For arctic species, decoupling of environmental cues will probably have significant impacts on population processes (e.g., the reproductive success of fish, hatching and feeding success of birds, and the migratory timing and success of birds and anadromous fish may be compromised).

- **The rate and magnitude at which climate change takes place and affects aquatic systems are likely to outstrip the capacity of many aquatic biota to adapt or acclimate.**

Evolutionary change in long-lived organisms such as fish cannot occur at the same rate as the projected change in climate. The ability to acclimate or emigrate to more suitable habitats will be limited, thus effects on some native arctic biota will be significant and detrimental. Shorter-lived organisms (e.g., freshwater invertebrates) may have a greater genetic and/or phenotypic capacity to adapt, acclimate, or emigrate.

- **Climate change is likely to act as a multiple stressor, leading to synergistic impacts on aquatic systems.** For example, projected increases in temperature will enhance contaminant influxes to aquatic systems, and independently increase the susceptibility of aquatic organisms to contaminant exposure and effects. The consequences for the biota will in most cases be additive (cumulative) and multiplicative (synergistic). The overall result will be higher contaminant loads and biomagnification in ecosystems.

- **Climate change is very likely to act cumulatively and/or synergistically with other stressors to affect physical, chemical, and biological aspects of aquatic ecosystems.** For example, resource exploitation (e.g., fish or bird harvesting) and climate change impacts will both negatively affect population size and structure.

8.8.2. Key science gaps arising from the assessment

In conducting this assessment, a number of key gaps in scientific understanding became evident. These are noted throughout the chapter, and include:

- the limited records of long-term changes in physical, chemical, and biological attributes throughout the Arctic;
- differences in the circumpolar availability of biophysical and ecological data (e.g., extremely limited information about habitat requirements of arctic species);
- a lack of circumpolar integration of existing data from various countries and disparate programs;
- a general lack of integrated, comprehensive monitoring and research programs, at regional, national, and especially circumpolar scales;
- a lack of standardized and networked international approaches for monitoring and research;
- the paucity of representative sites for comparative analyses, either by freshwater ecosystem type (e.g., small rivers, wetlands, lakes) or by regional geography (ecozone, latitude, elevation);
- the unknown synergistic impacts of contaminants and climate change on aquatic organisms;
- a limited understanding of the cumulative impacts of multiple environmental stressors on freshwater ecosystems (e.g., land use, fisheries, forestry, flow regulation and impoundment, urbanization, mining, agriculture, and poleward transport of contaminants by invasive/replacement species);

- the unknown effects of extra-arctic large-river transport on freshwater systems induced by southern climate change;
- a limited knowledge of the effects of UV radiation–temperature interactions on aquatic biota;
- a deficient knowledge of the linkages between structure (i.e., biodiversity) and function of arctic aquatic biota;
- a poor knowledge of coupling among physical/chemical and biotic processes; and
- a lack of coupled cold-regions hydrological and ecological theories and related projective models.

Filling these gaps, the most outstanding of which include inter-regional differences in the availability of, and access to, circumpolar research (hence the North American and European bias in this assessment), would greatly improve understanding of the effects of climate and UV radiation change on arctic freshwater ecosystems. Furthermore, comprehensive monitoring programs to quantify the nature, regionality, and progress of climate change and related impacts require development and rapid implementation at representative sites across a broad range of the type and size of aquatic ecosystems found within the various regions of the Arctic. Coupling such programs with ongoing and new research will greatly facilitate meeting the challenges sure to result from climate change and increased UV radiation levels in the Arctic.

8.8.3. Science and policy implications and recommendations

A number of the above gaps in scientific understanding could be addressed by the following policy and/or program-related adjustments:

- Establish funding and mechanisms for the creation of a coordinated network of key long-term, representative freshwater sites for comparative monitoring and assessment studies among arctic regions (e.g., creation of a Circumpolar Arctic Aquatic Research and Monitoring Program).
- Based on the results of this assessment, establish a science advisory board (preferably at the international level) for targeted funding of arctic freshwater research.
- Secure long-term funding sources, preferably for an international cooperative program, for integrated arctic freshwater research.
- Adjust current northern fisheries management policies and coordinate with First Nations resource use and consumption.
- Establish post-secondary education programs focused on freshwater arctic climate change issues at both intra- and extra-arctic educational institutions, preferably involving a circumpolar educational consortium.

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Appendix. Scientific names of arctic fishes alphabetically listed by common name used in the text and boxes

(see Fishbase, http://www.fishbase.org/home.htm for further details on species). See also Box 8.6.

Common Name	Scientific Name or Group	Family
Alewife[c]	*Alosa* spp.	Alosidae
Arctic char[c,b]	*Salvelinus alpinus*	Salmonidae
Arctic cisco[c]	*Coregonus autumnalis*	Salmonidae
Arctic cod[a]	*Boreogadus saida*	Gadidae
Arctic grayling[b]	*Thymallus arcticus*	Salmonidae
Arctic flounder[a]	*Pleuronectes glacialis*	Pleuronectidae
Atlantic salmon[c]	*Salmo salar*	Salmonidae
blackfishes[b]	*Dallia* spp.	Umbridae
bluegill[b]	*Lepomis macrochirus*	Centrarchidae
broad whitefish[c]	*Coregonus nasus*	Salmonidae
brook trout[c]	*Salvelinus fontinalis*	Salmonidae
brown trout[b,c]	*Salmo trutta*	Salmonidae
bull trout[b]	*Salvelinus confluentus*	Salmonidae
burbot[b]	*Lota lota*	Gadidae
carp bream[b]	*Abramis brama*	Cyprinidae
chars	*Salvelinus* spp.	Salmonidae
cisco	*Coregonus (Leucichthys)* subgenus	Salmonidae
common dace[b]	*Leuciscus leuciscus baicalensis*	Cyprinidae
coregonines	whitefishes and ciscoes, Coregoninae	Salmonidae
cyprinids	minnows	Cyprinidae
Dolly Varden[c]	*Salvelinus malma*	Salmonidae
emerald shiner[b]	*Notropis atherinoides*	Cyprinidae
European eel[d]	*Anguilla anguilla*	Anguillidae
European perch[b]	*Perca fluviatilis*	Percidae
European whitefish[b,c]	*Coregonus lavaretus*	Salmonidae
fourhorn sculpin[a]	*Myoxocephalus quadricornis*	Cottidae
goldeye[b]	*Hiodon alosoides*	Hiodontidae
ide[b]	*Leuciscus idus*	Cyprinidae
lake chub[b]	*Couesius plumbeus*	Cyprinidae
lake cisco[b]	*Coregonus artedi*	Coregonidae
lake trout[b]	*Salvelinus namaycush*	Salmonidae
lake whitefish[b,c]	*Coregonus clupeaformis*	Salmonidae
lampreys[c,b]	*Lampetra, Petromyzon* spp.	Petromyzontidae
least cisco[c]	*Coregonus sardinella*	Salmonidae
ninespine stickleback[b,c]	*Pungitius pungitius*	Gasterosteidae
northern pike[b]	*Esox lucius*	Esocidae
northern redbelly dace[b]	*Chrosomus eos*	Cyprinidae
Pacific salmon[c]	*Oncorhynchus* spp.	Salmonidae
percids[b]	perch family	Percidae
pink salmon[c]	*Oncorhynchus gorbuscha*	Salmonidae
pond smelt[c,b]	*Hypomesus olidus*	Osmeridae
rainbow smelt[c]	*Osmerus mordax*	Osmeridae
rainbow trout[b]	*Oncorhynchus mykiss*	Salmonidae
roach[b]	*Rutilus rutilus lacustris*	Cyprinidae
round whitefish[b]	*Prosopium cylindraceum*	Salmonidae
ruffe[b]	*Gymnocephalus cernuus*	Percidae
salmon	*Oncorhynchus* spp.	Salmonidae
salmonines	trouts, chars, salmons	Salmonidae
sculpins	*Cottus* spp.	Cottidae
Siberian whitefish[c]	*Coregonus pidschian*	Salmonidae
slimy sculpin[b]	*Cottus cognatus*	Cottidae
smallmouth bass[b]	*Micropterus dolomieu*	Centrarchidae
sockeye salmon[c]	*Oncorhynchus nerka*	Salmonidae
sticklebacks	*Pungitius, Gasterosteus* spp.	Gasterosteidae
stone loach[b]	*Noemacheilus barbatulus*	Cobitidae
suckers[b]	*Catostomus* spp.	Catostomidae
threespine stickleback[c,b]	*Gasterosteus aculeatus*	Gasterosteidae
trout perch[b]	*Percopsis omiscomaycus*	Percopsidae
vendace[c,b]	*Coregonus albula*	Salmonidae
walleye[b]	*Sander vitreus*	Percidae
whitefishes	*Coregonus (Coregonus)* subgenus	Salmonidae
yellow perch[b]	*Perca flavescens*	Percidae
zander[b]	*Sander lucioperca*	Percidae

Dominant life history exhibited in arctic areas; more than one note indicates multiple life history types with order indicating primary mode in the Arctic as defined in this assessment: [a]marine species found in nearshore, brackish, and estuarine areas; [b]freshwater species found in freshwater or freshened brackish water areas only; [c]primarily anadromous species (although freshwater forms are also present); [d]primarily catadromous species (although freshwater forms may be present).