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General Features of the Arctic Relevant to Climate Change in Freshwater Ecosystems

Large variations exist in the size, abundance and biota of the two principal categories of freshwater ecosystems, lotic (flowing water; e.g., rivers, streams, deltas and estuaries) and lentic (standing water; lakes, ponds and wetlands) found across the circumpolar Arctic. Arctic climate, many components of which exhibit strong variations along latitudinal gradients, directly affects a range of physical, chemical and biological processes in these aquatic systems. Furthermore, arctic climate creates additional indirect ecological effects through the control of terrestrial hydrologic systems and processes, particularly those associated with cryospheric components such as permafrost, freshwater ice and snow accumulation/ablation. The ecological structure and function of arctic freshwater systems are also controlled by external processes and conditions, particularly those in the headwaters of the major arctic rivers and in the adjacent marine environment. The movement of physical, chemical and biotic components through the interlinked lentic and lotic freshwater systems are major determinants of arctic freshwater ecology.

INTRODUCTION

The nature and severity of climate and weather have a strong influence on the hydrology and ecology of arctic freshwater ecosystems (e.g., 1–6). 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 (7). 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 (8). 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 (8). Migratory organisms such as waterfowl occupy a variety of habitats both seasonally and over their lifetime (9). Hence, aquatic biota display a wide range of adaptation strategies to cope with the severe environmental conditions to which they are exposed (2, 9). 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.

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 (10). 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 (11–13). 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 (14). 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 paleo-limnological investigations (e.g., 15, 16).

During the summer, sources of water include not only rain, but also late or perennial snow patches, glaciers, thawing permafrost, and groundwater discharges (13, 14). 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 (1). 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 (6, 14, 17, 18) 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.

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 manuscript.

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 (19). Migratory birds, including geese, ducks, swans, and gulls, can be particularly abundant in arctic coastal and inland wetlands, lakes, and deltas (20–22; for comprehensive review see 9). 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 23) 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 (9, 24, 25). 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 (26, 27).

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, 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 (see ACIA region descriptions in 28) and as such act as conduits of heat, water, nutrients, contaminants, sediment, and biota northward (e.g., 29). 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 30, 31). 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 (32), 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 (33). 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 (34, 35).

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., 36).

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, 36). 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. 1) 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 (37, 38, 39, 40). 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

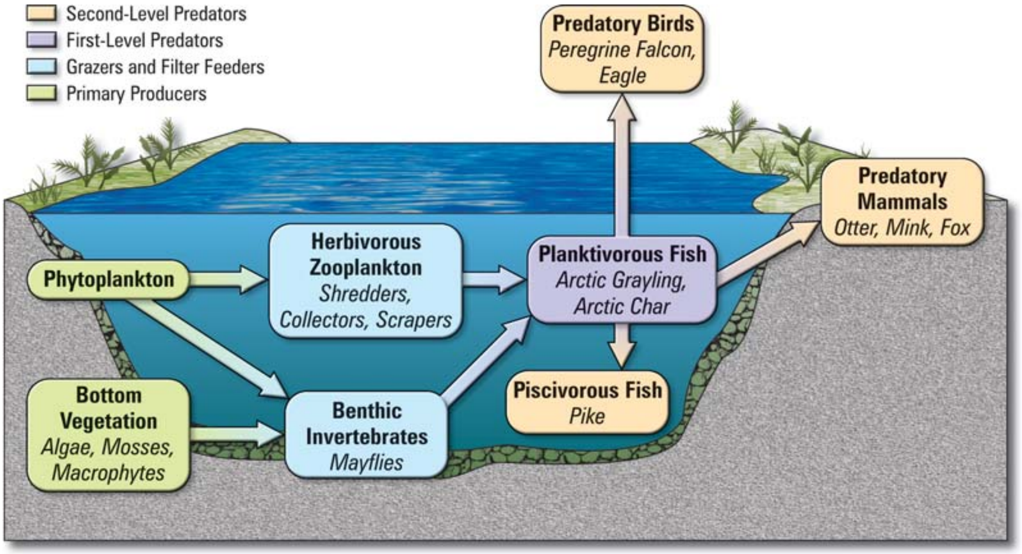

Figure 1. Representative arctic river and stream food web.

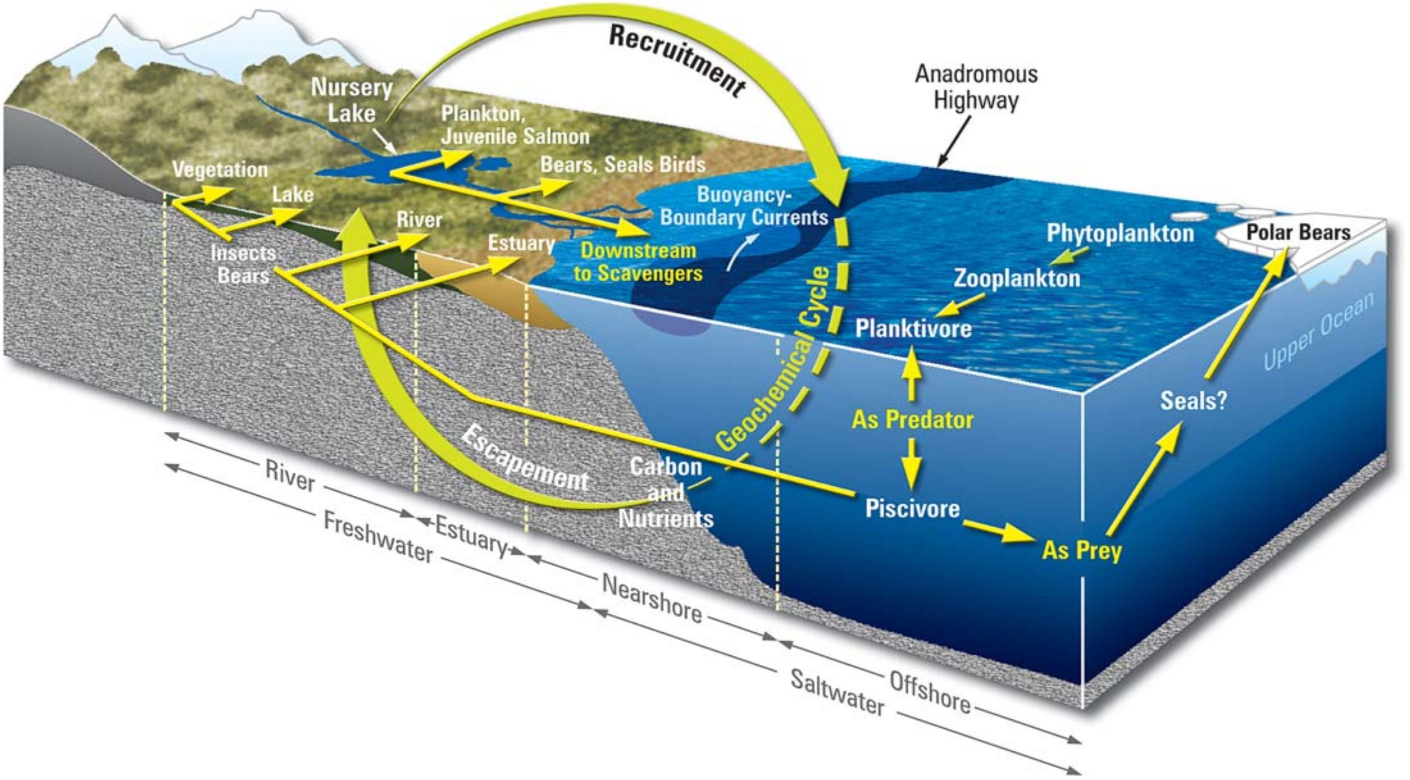

Figure 2. A stylized portrayal of the use of estuaries and the keystone role of anadromous fish in the trophic dynamics of arctic nearshore estuarine and marine ecosystems (56).

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 (1). 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 (37). 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 (1). 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 factors such as deglaciation events and timing also figure prominently in determining biodiversity at higher trophic levels in these systems (41).

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 (23). 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 (42), 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 (43, 44). Spring overland floods are critical to the recharge of delta lakes, such as those of the Yukon, Colville (45, 46), Mackenzie (47, 48), and Slave Rivers (49) in North America, and the Yenisey, Lena, Kolyma, and Indigirka Rivers in Siberia (50, 51). Flooding during spring breakup also provides sediments and nutrients to deltas (e.g., 52), 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., 53). 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 (54), 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 (55). 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 (56). Hence, estuaries provide a significant food source for anadromous species compared to what is available to them from adjacent freshwater streams (8). This productivity typically results in large populations of fish that are important to local fisheries (e.g., Arctic char – *Salvelinus alpinus*, Atlantic salmon – *Salmo salar*) 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. 2). 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*), rednecked 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 (57). 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., 58) and contaminants (e.g., 59), and are thereby capable of producing both positive and negative impacts on the aquatic biota in these systems.

LAKES AND PONDS, 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 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; 60, 17). 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 (18, 61, 62). Spring runoff originates from snow accumulation on lake ice, hillslope runoff (62), and lateral overflow from wetlands and streams (47). Outlets of small lakes may be snow-dammed, and eventually release rapid and large flows downstream (61, 62). 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 (6, 65).

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; 66, 67). 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 (68). In contrast, many high-arctic lakes mix vertically, thereby reducing thermal stratification (17, 67). 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 (66, 69). 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. 3). 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

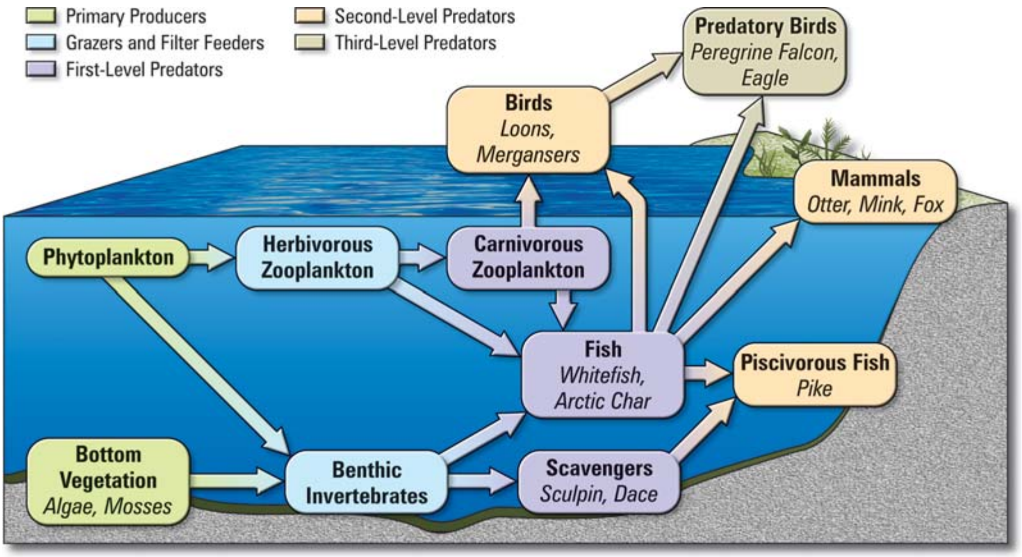

Figure 3. Representative food web in arctic lakes (24).

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-plankton and invertebrates such as rotifers, copepods, and cladocerans increase with lake trophic status (37), 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/m^2/yr (70, 71), contrasting with extremely oligotrophic high-arctic lakes that have phytoplankton production levels of <10 g C/m^2/yr (37). 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 (72, 73). Benthic invertebrate species diversity and abundance also display high latitudinal and inter-lake variability and may be significant in shallow lakes and ponds (37, 38, 74, 75, 76). For example, in lakes of the Svalbard region, chironomid larvae are often numerically dominant but display low diversity ($\sim$10 species; 77, 78, 79), 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 (80), Iceland (81), 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 (82). 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 (81). Pond vegetation typically includes horsetail (*Equisetum* spp.), water smartweed (*Polygonum amphibium*), duckweed (*Lemna* spp.), and pondweed (*Potamogeton* spp.) (22), and the resulting plant detritus tends to be mineralized rather than grazed upon. Figure 4 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 brant (*B. bernicla*), eider (*Somateria mollissima*), long-tailed duck (*Clangula hyemalis*), redthroated loon (*Gavia stellata*), yellow-billed loon (*G. adamsii*), Arctic loon (*G. arctica*), tundra swan (*Cygnus*

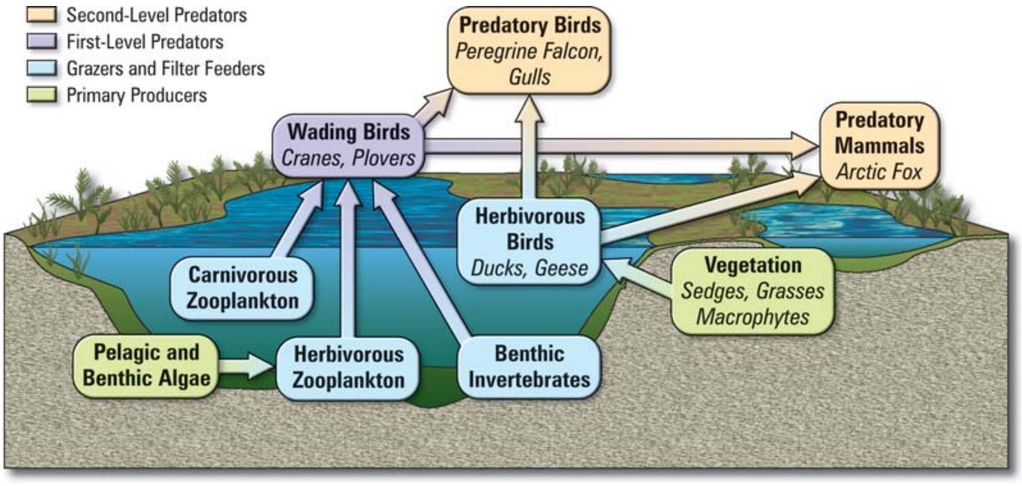

Figure 4. Representative food web in arctic tundra ponds (24).

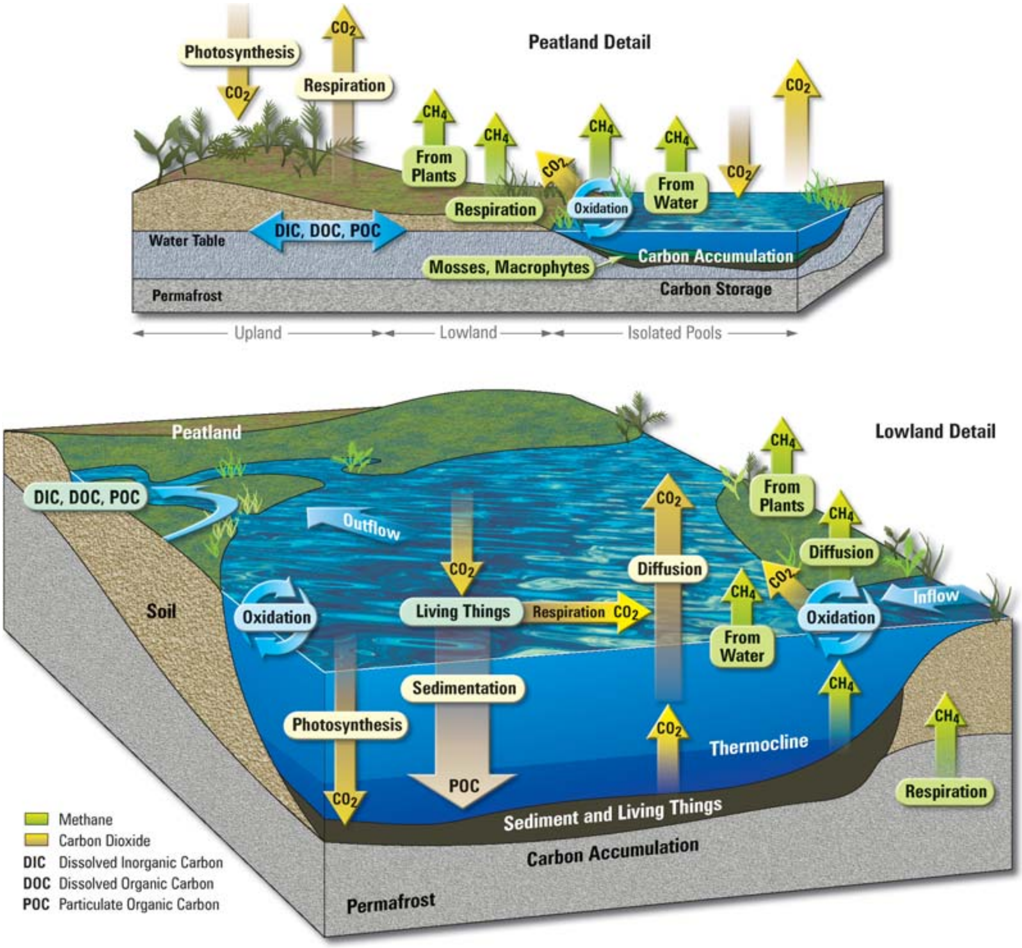

Figure 5. Simplified schematic of carbon cycling in high-latitude aquatic ecosystems.

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 (83).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 (9, 83). 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 (84, 85). Approximately 3.5 million km^2 of boreal and subarctic peatlands exist in Russia, Canada, the United States, and Fennoscandia (86). 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 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 micro-topography. 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 (87).

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 (88). Peatland pools in arctic Finland, for example, host thriving populations 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 (89).

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 (85), 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 (90). The role of arctic and subarctic wetlands as net sinks or sources of carbon (Fig. 5) 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; 91). 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., 92, 93, 94, 95, 96).The future status of wetlands as carbon sinks or sources will therefore depend on 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. (97) provide a more detailed treatment of carbon cycling and dynamics in arctic terrestrial and aquatic landscapes.

CONCLUSIONS

The Arctic is comprised of a suite of lentic and lotic freshwater ecosystems with large spatial diversity in size, abundance and associated biota. Many features of the arctic climate, which exhibit strong variations along latitudinal gradients, directly affect physical, chemical and biological processes in these aquatic systems. Furthermore, arctic climate creates a number of indirect ecosystem effects through the control of terrestrial hydrologic systems and processes, particularly those associated with cryospheric components such as permafrost, freshwater ice and snow accumulation/ablation. Many large arctic-river systems, however, are also strongly influenced by extra-arctic hydroclimatic conditions. In general, it is the southerly more temperate headwaters of the large arctic rivers that are the principal suppliers of water, heat, nutrients, sediment and biota to their downstream intra-arctic lotic components, including the major deltas and estuaries that ring the circumpolar. By contrast, the ecological structure and function of rivers and stream networks that wholly exist within the Arctic, as well as the diverse range of arctic lentic systems, are much more controlled by the hydroclimatology and physio-chemical characteristics of the various sub-regions of the Arctic. Wetlands in particular provide some of the most abundant and biologically productive aquatic ecosystems, their prominence largely due to surface ponding on permafrost and low rates of evapotranspiration that characterizes the Arctic. The ecology of all arctic lentic and some lotic systems (i.e., those with major flow linkages to stream networks) is also coupled to the arctic marine system through anadromy. Because of the dominance of some anadromous fishes in arctic freshwater ecosystems, variations in marine conditions, such as the quality of summer feeding grounds, can have a direct effect on the ecology of freshwater lentic and lotic systems.

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