11. LANDSCAPE CONTROL OF HIGH LATITUDE LAKES IN A CHANGING CLIMATE

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Bergstrom DM, Convey P and Huiskes AHL (Editors)
Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator, xx-xx.

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Introduction

Lakes are the downstream integrators of their surrounding catchments and are therefore highly responsive to variations in landscape properties. High latitude lakes share many characteristics with those of temperate latitudes and are subject to many of the same landscape controls. However, polar lakes and their catchments also experience persistent low temperatures, extreme seasonality and severe freeze-thaw cycles and these distinguishing features are likely to amplify their responsiveness to landscape and climate change.

General circulation models vary in their prediction of the future magnitude of regional climate change, but almost all converge on the conclusion that the polar regions will experience greater temperature increases than elsewhere and that these changes are likely to occur ever faster because of the positive feedback effects of melting snow and ice. Observations in the north polar region have shown that there have been significant rises in temperature throughout much of the area in recent decades, with effects on permafrost, lake ice cover, glacial extent and ice shelf break-up (Serreze et al. 2000, Mueller et al. 2003, ACIA 2004). Recent analysis of long term monitoring data from maritime Antarctic Signy Island (South Orkney Islands) and the McMurdo Dry Valleys in continental Antarctica has provided evidence of large regional variations in climate change and has shown that south polar lakes respond strongly to warming and cooling trends (Doran et al. 2002, Quayle et al. 2002, 2003).

In this review, we take a two-step approach towards examining climate-landscape-lake interactions in high latitude environments. First, we examine the general effects of landscapes on lake ecosystems through factors such as geomorphology, solute transport, vegetation and hydrology. We then examine how these properties are linked to climate, resulting in a set of mechanisms whereby climate change can have pronounced impacts on lakes. Throughout this review, we have drawn on examples from both polar regions. Lake ecosystems are an important part of the Arctic landscape and there are limnological similarities to Antarctica. In both regions permanently frozen soils exert a strong influence on catchment properties such as hydrological processes and geochemical interactions. Similarly in both regions, snow and ice cover are major controls on the structure and functioning of aquatic ecosystems. There is a long history of limnological research in high northern latitudes and much of this information is directly relevant to Antarctica. Current observations and model predictions indicate that the Arctic is much more sensitive to climate change and will continue to experience more rapid shifts in its temperature regime than Antarctica (Overland et al. 2004a, b). Much of the Subarctic and Arctic became ice-free in the early Holocene and the limnology and paleolimnology of northern lakes therefore provide a window into the potential future states of Antarctic lakes undergoing climate change.

Landscape Controls on Lakes

In this section we describe and illustrate the variety of ways in which landscape can exert control on the structure and dynamics of lake ecosystems. These effects take place at multiple time-scales: from pre-Holocene and Holocene (thousands of years), to recent changes observed over the last few decades. We have placed emphasis on examples from lakes in the polar regions to illustrate their distinctive properties and features that may make them particularly sensitive to climate change.

GEOMORPHOLOGY

Geomorphology exerts the most fundamental control on lakes and their surrounding catchments by dictating the shape of the landscape and the size and morphometry of basins that can receive, transport and store water. These properties also influence the geochemical weathering of substrates, the relative importance of hydrological flow pathways above and below soils and the transfer of solutes from land to water. A wide range of limnological characteristics are affected by the ratio of catchment to lake area, and by the area-volume and volume-depth relationships of lakes, including temperature, light availability for photobiological and photochemical processes, oxygen levels, nutrient retention times and habitat availability (Wetzel 2001, Kalff 2001). The geomorphological control on lakes include not only surface effects, but also underground processes where lithology and geological structure play an important role in the water and solute supply. Lakes can be classified according to their geomorphological origins such as tectonic (eg folds, fractures), lithological (eg volcanics, karst), differential erosion (eg rock bars, dykes), glacial erosion (eg excavation, moraines), ice dynamics (eg thermokarst), coastal processes (eg lagoons) and slope processes (eg rotational slumps, avalanches).

In the polar regions, many geomorphological features of the landscape have been shaped by glacial processes and continue to respond to ice dynamics. In the most extreme systems, ice dams the outlet of lakes. Some of the most impressive of these proglacial lakes (eg lakes Agassiz and Barlow-Ojibway) formed during the last deglaciation in the Northern Hemisphere, especially in areas surrounding Hudson Bay, Canada. Glacial retreat beyond certain threshold areas often resulted in catastrophic floods (eg the 8.2 ka event, Barber et al. 1999) that had global impacts on climate. There are many examples of proglacial lakes today in Antarctica (eg Lake Hoare, McMurdo Dry Valleys, Lake Untersee, Dronning Maud Land). Ice and snowpack can also act as a temporary dam to lakes (eg Lake Limnopolar on Byers Peninsula, Livingston Island and Boeckella Lake on Hope Bay, both in the Antarctic Peninsula) and such effects are also well known for northern rivers (Prowse and Culp 2003).

Epishelf lakes are a form of proglacial lake in which ice dams retain freshwater over the sea. This lake type is now rare in the Arctic, and one of the few examples was recently lost by climate change and break-up of the ice shelf at its mouth, with subsequent draining of the freshwater into the sea (Mueller et al. 2003). Many examples are known from Antarctica, including Moutonnée and Ablation lakes on the coast of Alexander Island (Heywood 1977, Hodgson et al. 2004), epishelf lakes in the Schirmacher Oasis (Korotkevich 1960) and Bunger Hills (Korotkevich 1972, Doran et al. 2000, Gibson and Andersen 2002, Verkulich et al. 2002) and Beaver Lake associated with the Amery ice shelf (Adamson et al. 1997, Laybourn-Parry et al. 2001). In some cases, the sea ice can be folded by the thrusting of glaciers and forms a series of synclinal troughs and anticlinal ridges roughly parallel to the edge of the glacier. Freshwater lakes of a few hundreds of meters long, tens of meters wide and a few meters deep can occupy the synclinal troughs during the summer months before the break-out of the sea ice, as in the Marguerite Bay area in Antarctica (Nichols 1960). Most of these systems formed during earlier periods of relative sea-level rise, lifting grounded ice masses and allowing sea water to penetrate into the lower part of the water column, or by connection to marine waters during periods of reduced freshwater input (Gibson and Andersen 2002, Gibson et al. this volume). A review of the formation and dynamics of Antarctic lake ecosystems (including epishelf lakes, epiglacial, subglacial and supra-glacial lakes) and their paleolimnology is provided by Hodgson et al. (2004).

Extensive flat terrains corresponding to erosive raised platforms of marine origin are relatively common in Antarctic coastal areas, due to glacioisostatic uplift and often contain numerous lakes. Examples include many ice-free peninsulas of the South Shetland Islands such as Fildes Peninsula on King George Island and Byers Peninsula on Livingston Island. In the Byers Peninsula, raised surfaces are extensive and contain more than 60 lakes and 50 pools, some of them up to 50,000m^2 in surface area and 9m deep. The flat, raised platforms show recent glacial erosion and absence of well-defined divides. There are diffuse boundaries and small differences in altitude between drainage basins, and this favours recent capture of meltwaters and precipitation, and sporadic connections between basins (López-Martínez et al. 1996).

Lithology and the geological structure exert a strong influence on high latitude lakes. Some lakes are located in craters (eg on Deception and Penguin Islands, South Shetland Islands) or in tectonic troughs. In many cases, faults and diaclases control the location of the lakes and the characteristics of the basins and the drainage network. Many lakes are located in glacial over-deepened, tectonically controlled sites. Lakes most strongly influenced by fractures are, in general, more elongate and commonly aligned parallel to each other, for example on Byers Peninsula, Livingston Island (López-Martínez et al. 1996).

Coastal lakes of lagoon origin are very common in the lower beaches of the maritime Antarctica. They have gently sloping edges and are either subcircular or elongate in plan (Jones et al. 1993, Cuchi et al. 2004). Their salinities tend to be high because of intermittent exchange with the sea (see below).

Igneous rocks often show abundant 'roches moutonnées' and the development of 'rock bars' and 'riegels' that act as dams for lakes in many cases. Lakes of karstic origin are rare in high latitudes due to the scarcity of limestone and other rocks suitable for karst development, in addition to the lack of water. However, thermokarst lakes of permafrost origin, are common in the polar regions (see below).

Under certain circumstances, liquid water masses can be maintained beneath the Antarctic ice sheet by geothermal heat fluxes to produce subglacial lakes. These lakes are likely to have been isolated for very long periods of time from the above-ice communities (over 15 million years, Bulat et al. 2004) and the potential for life in these waters is presently an intriguing frontier of research in polar microbial ecology.

Ice dams or other geomorphological features such as moraines or rock bars and riegels may produce arheic lakes in which there is no flushing and outflow, with the only loss of water via evaporation or ice ablation. This type of landscape effect results in hypersaline environments in which the solutes in the inflowing waters are concentrated by evaporation or freeze-concentration. This produces a stratified dense brine at the bottom layer of deeper lakes, or extreme salinities throughout the water column of shallower lakes. Winter freeze-up of shallow waters may impose a severe constraint on biodiversity in some high latitude environments by exposing organisms to extreme osmotic stress and sub-zero liquid water temperatures (Hawes et al. 1999).

A well studied example of geomorphological evolution and its effects on lakes is in the Toolik Long Term Ecological Research (LTER) site, Alaska. In this region, the broad retreat of ice sheets has left behind landscapes in which the glacial activity in the past has a strong effect on modern-day surface waters. In fact, three different glacial advances have left a legacy of different ecologies of lakes and streams. During the Pleistocene, most of northern Alaska was unglaciated except for mountain glaciers that flowed north from the peaks and valleys of the Brooks Range and spread out over the foothills. In the Toolik region, the till of the earliest glaciation, from the early Pleistocene, has been overlapped by till from three advances (Hamilton 2003). Lakes and streams on these three glacial surfaces have been studied: a ~10,000 year old surface (10ka), a ~60,000 year old surface (60ka) and a greater than 300,000 year old surface (300ka). The youngest surface (~10ka) has numerous kettle lakes, many isolated from streams. Flanking slopes are steep and may have slumps along the banks. Soils are well drained but surface drainage is poorly integrated. On the next surface (60ka) kettle lakes are still present but many have grassy slopes and marshy shores where solifluction has deposited silt. Drainage networks are well integrated and lakes are connected by small streams. The oldest surface (>300ka) is a subdued landscape that reflects a long period of postglacial modification. Moraines have broad crests and gentle flanking slopes. Crests and upper slopes have a cover of windblown silt (loess). Solifluction has redistributed much of the loess from upper to lower parts of moraine flanks. Soils are fine-grained and hold more moisture than those on the younger surfaces. Slopes are drained primarily by water tracks rather than by incised stream channels. Kettle lakes are rare but small thaw ponds have developed in swales. Drainages have silty channels with beaded thaw ponds. Even the hydrology is somewhat different in older terrestrial landscapes as there is better development of water tracks, narrow troughs that run downslope every few 10s of metres. The differences among landscapes are shown in Table 1. Similar studies are required in Antarctica

Table 1. Lake and stream averages for landscape of different ages in Alaska. Conductivity includes ranges. Assembled by W.J. O'Brien.

Landscape age	Lake depth (m)	Number of lakes (#/km^2)	Lake area (ha)	Stream length (km)	Conductivity (μS/cm) and range
Young <10ky	16	1.24	3.1	0.65	80 (45-105)
Intermediate ~60ky	11.3	0.77	5.7	0.74	40 (28-70)
Old >300ky	9.1	0.18	1.6	1.03	20 (8-35)

Hobbie et al. (2003) hypothesized that younger surfaces support more varied biotic communities because there are more types of habitat. On the younger surface, more lakes lead to greater buffering of stream hydrology, longer residence times of water in the aquatic systems and less stream disturbance. More lakes lead to more trapping of nutrients in sediments and to accumulation of nutrients in photosynthetic algae and secondary consumers. Downstream, the stream biota are more abundant because of the material from lakes. Isolated lakes in the youngest surfaces may lack fish, which drastically changes the food web and have a very small drainage basin. The evolution of stream network structure is important because watershed disturbance interacts with stream network structure to create a distribution of habitats that affects the function of the entire stream network (Benda et al. 2004).

HYDROLOGY

The hydrologic properties of high latitude catchments are especially complex given the importance of freeze-thaw cycles and the influence of permafrost on surface and subsurface flow. Seasonal freezing and thawing processes play a major role by altering the amount of liquid water in the catchment and the pathways of flow to downstream lakes.

The heterogeneity of the permafrost and the active layer makes it very difficult to predict hydrological pathways in high latitude landscapes. Permafrost acts as a non-permeable layer, restricting the water exchange or movement to the active layer that thaws on a seasonal basis. Although groundwater is mostly frozen and immobile within permafrost, some groundwater movement can occur there by two mechanisms. First, ice within permafrost retains a small percentage of liquid water in films that can potentially exist at temperatures down to -50°C. This water may creep through the tortuous pore channels that pervade all frozen ground. There may be also salt brines in soils that are not flushed by precipitation. These brines are sufficiently concentrated to remain liquid to very low temperatures and migrate as groundwater. These reservoirs of liquid water occur at different levels and can be interconnected (Woo 2000).

In spring the soil is still frozen and infiltration from snowmelt only takes place through cracks or interstices through coarse elements of the soil. In Arctic soils, infiltration represents only 5-20% of the snowmelt (Marsh and Hey 1989). This infiltrated water may refreeze, further increasing the impervious nature of the soils. The spring flows may be very intense (up to 70% of the snow cover, Landals and Gill 1972) and largely restricted to the surface, washing the first centimetres of the soil and transporting moderate amounts of solutes. This spring flow is especially important for organisms inhabiting the soil surface, for example cyanobacterial mats and moss turfs that commonly grow on gentle slopes without permanent water supply. The active layer starts thawing after disappearance of the snow-cover and subsurface infiltration and flow pathways become more important at that time. Some groundwater flow may occur into lakes via taliks, unfrozen substrata that underlie lakes in permafrost regions. At some sites in the polar regions, groundwater fed by snowmelt and rainfall comes to the surface as springs that then flow into streams and lakes (Andersen et al. 2002).

The low albedo of barren high latitude soils causes surface heating and evaporation to be important features in the hydrological cycle of the polar regions (Woo 2000). Evaporative losses are highly variable, for example accounting for 15% of the 300-350mm precipitation in northern Alaska (Hobbie 1973, cited by Schindler et al. 1974) and a potential 165% of the 350-400mm precipitation in the Schirmacher Oasis, Antarctica (Haendel 1995). In polar desert catchments where precipitation is extremely low, the scarce snowmelt water is readily absorbed by the uppermost centimetres of unfrozen soil and then largely evaporated because of the dryness of the air and high winds. This results in an extreme negative water balance, for example an annual loss of ice of 305mm at Lake Vanda compared with only 10mm annual precipitation (Chinn 1993). Thus groundwater contributes only sporadically to surface water bodies in permafrost regions (Fig. 1).

In certain areas of low-lying ground, snowmelt or precipitation can saturate the active layer and accumulate at the surface, producing extensive wetlands. This type of landscape is found throughout both polar regions, for example on Livingston Island in Antarctica and in the Canadian High Arctic. These polar wetlands provide persistent liquid water 'oases' in summer, and they are typically highly productive, well developed ecosystems with a diverse biota (Woo and Young 2000). The thawing of permafrost and the resulting decrease of soil volume and even slumping of shorelines gives rise to thermokarst lakes, small, shallow water bodies that are especially abundant throughout the Subarctic and Arctic (see below).

In continuous permafrost areas, the streams and rivers have little subsurface exchange and therefore respond rapidly to variations in precipitation (Woo 2000).

Maximum runoff is recorded during the spring snowpack and glacial melt period and diurnal variations in discharge may occur associated with the daily melt cycle. The interannual variations in flow in the Onyx River, feeding Lake Vanda in the McMurdo Dry Valleys, have been related to the number of positive °C days on the surface of the glaciers that feed it with meltwater (Chinn 1993). In discontinuous permafrost areas, the streams and rivers are fed by subsurface water via the active layer, taliks or subpermafrost springs and so there is much less of a direct coupling with precipitation and melt cycles.

The nature and length of the transport pathway, from the water source to the lake, also influences the extent of solute accumulation and transfer. For example, glaciers and snow in the McMurdo Dry Valleys provide most of the hydrological input to the lakes, but contain only low solute concentrations (Lyons et al. 1998). Much of the dissolved content of these inflows is derived from the inflows picking up salts that have been deposited by wind or solid precipitation, or released by weathering. Thus, stream length has a strong influence on the ultimate downstream concentrations of solutes and hence chemical loading into the receiving lakewaters.

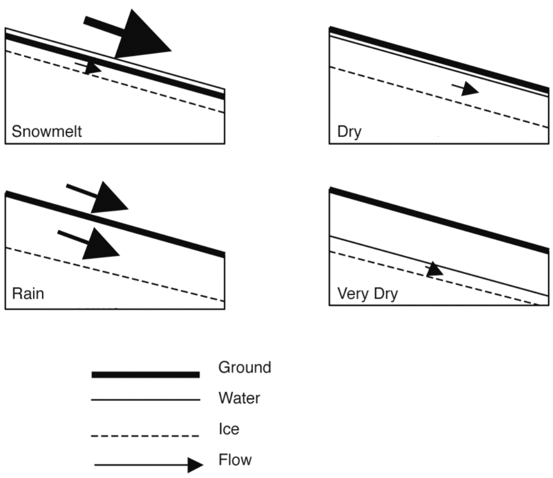

Figure 1. Water flows and relative position of the ice and water tables in a typical slope, under different meteorological conditions. The size of the arrows represents the difference in magnitude of the flow. The arrows above and inside the diagram represent the surface and the subsurface flow, respectively (redrawn from Woo 2000).

Subsurface flows are known in Antarctica, for example of increased salinity groundwaters in the Larsemann Hills. Widely fluctuating concentrations of subsurface nutrients have indicated patchily distributed soil brines and decaying buried organic matter as sources of salts (Kaup and Burgess 2002). Enriched by these sources, inflows have substantially increased the nutrient levels of lakes that they discharge into (Kaup et al. 2001). In dry soils, however, the subsurface transport of elements may be minimal. For example, in the McMurdo Dry Valleys region, Campbell et al. (1998) found that solute mobility ranged from 1m in very arid soils to 5m in wetter soils. With less soluble metals (Pb, Cu and Zn), movement was 0.5m or less in 30 years.

LITHOLOGY

Differences in geological substrates affect the extent of rock weathering and the chemical composition of soil water that ultimately discharges into lakes. This can be seen in lakes distributed across major geological boundaries, for example from highly alkaline sedimentary to acidic granite-gneiss formations in the region northeast of Yellowknife in the Canadian Arctic (Pienitz et al. 1997). As noted above, differences in glacial history can lead to different substrate types that in turn affect the solute chemistry of river and lake waters.

Geological differences also affect the type and productivity of vegetation that in turn will influence lakes through a variety of mechanisms (see below). For example, in their analysis of vegetation on the Arctic Slope, Alaska, Walker et al. (2003) found a significant statistical relationship between above ground phytobiomass and a summer temperature index (sum of mean monthly temperatures above 0°C). One conspicuous outlier, however, was at Atqasuk, where biomass was lower than at Barrow despite a more than two-fold higher temperature index. This anomaly was attributed to the sandy, nutrient-poor soils at Atqasuk. Similarly there are major differences in soil characteristics including pH and nutrients among glacial landscapes of different ages in the Toolik Lake LTER site, Alaska. This translates into differences in soil mineralization rates, foliar nutrient levels and plant community structure and biomass (Hobbie and Gough 2002).

On the Byers Peninsula, as an example of maritime Antarctic conditions, water conductivity shows a broad range of values from 4.8 - 1441µS cm^{-1}. Lowest values of conductivity are related to snow melt: 4µS cm^{-1} while rainfall varies between 17.3 and 53.7µS cm^{-1}, indicating the influence of marine aerosols. Groundwaters have conductivities from 246 to 715µS cm^{-1}, indicating rock weathering reactions, with differences according to lithology. Lakes and pools have higher conductivity values than snow/rain and underground water. Coastline lagoons have particularly high values due to overwash of brackish water, probably of marine origin. An inverse relationship between discharge and conductivity has been suggested (Cuchí et al. 2004). The hydrologic cycle during the end of the summer at Byers Peninsula indicates favourable conditions for rock-water interactions that increase conductivity of water according to rock type, temperature and interaction time. Permafrost plays an important role in the recharge and water flow, especially in interior areas of the peninsula.

Moisture and frequency of freeze-thaw cycles are key factors affecting chemical weathering (Haendel 1995). However, the relative importance of freeze-thaw cycles is under discussion. Hall (1992) indicated that in Byers Peninsula (Livingston Island) wetting and drying, salt weathering and chemical weathering could be more important than freeze-thaw, but Navas et al. (2005) suggested that the main processes in the same area seem to be related to cryogenic effects resulting from freeze-thaw cycles that lead to rock disintegration and the supply of solutes to the lakes. The migration of sulphatic, carbonatic and bicarbonatic solutions in soils and rocks has been documented by ionic content of water and in some cases by salt efflorescences in many ice-free areas (Simonov 1971, Wand et al. 1985). There is evidence of chemical weathering in the McMurdo Dry Valleys (Lyons and Mayewski 1993), although some authors argue that chemical weathering is reduced to negligible rates under conditions of extreme cold and dryness (Matsuoka 1995, Campbell and Claridge 1987). Chemical weathering is accelerated in aqueous environments, for example, silicate-based rocks in the stream beds of the McMurdo Dry Valleys (Lyons et al. 1998). Several studies (eg Conca and Malin 1986, Conca and Wright 1987) have shown that cations such as Fe^{3+}, Sr^{2+}, K^+ and Ca^{2+} are being weathered from the bedrock in Southern Victoria Land. However, it has been demonstrated that only a small proportion of the Mg^{2+} entering into the lakes in Taylor Valley, McMurdo Dry Valleys, is of weathering origin (Green et al. 1988), and that most of the Na^+, Cl^- and SO_4^{2-} enters as marine-derived aerosols. CO_3^{2-} and HCO_3^- may derive from dissolution of carbonate rocks in the drainage basins or via hydrolysis of silicate minerals. In less extreme areas, under higher humidity such as the Schirmacher Oasis, free water and temperatures above freezing are dominant in the soil for 2 to 3 months, causing release of K^+, Ca^{2+} and SO_4^{2-}. The residence time of water in the thawing zone has a strong influence on the extent of solute accumulation. As in the Taylor Valley, anorthosites contribute to Mg^{2+} deficit and high Ca^{2+} content of waters in Antarctic Lakes Untersee and Obersee (Haendel 1995). Alkaline solutes, released during weathering of anorthosites are also the most probable reason for pH values of up to 12 in these lakes (Haendel et al. 1995), combined with the low buffering capacity of the receiving waters.

VEGETATION

Plant biomass, productivity and community structure are features of the landscape that have a wide-ranging influence on rivers and lakes. Vegetation alters the wind regime, the extent of snow cover and albedo, and the hydrological balance between evaporation and precipitation. The root structures of the vegetation in subantarctic and Arctic environments greatly influence the physical stability of the catchment and its susceptibility to soil erosion and particle transfer into waterways. The extent of permafrost development is also affected by vegetation cover, as are leaf litter, soil properties and terrestrial biota, including microbiota that can be eventually washed into streams and lakes.

One of the greatest controlling influences of terrestrial plants on aquatic ecosystems is through its effect on solutes in the waters that percolate through the leaf litter and root zones and eventually make their way into lakes via overland flow, streams and groundwater. Some nutrients and ions may be stripped out by biological uptake processes in the soil or by interactions with soil particles, while others may increase in concentration through decomposition, cation exchange and weathering. Dissolved organic matter (DOM) derived from vegetation breakdown in the soil has a particularly broad range of effects on lake and river ecosystems. Landscape processes control the quantity and quality of DOM entering the aquatic system (allochthonous DOM, ie that derived from outside the lake) with regional effects of climate, vegetation type and pH (acid rain) and strong gradients as a function of latitude and altitude (Schindler et al. 1990, Pienitz and Smol 1993, Vincent and Pienitz 1996, Lotter 1999, Laurion et al. 2000).

Even in Antarctic polar desert lakes, there is transfer of solutes from their surrounding catchments, including organic materials from mosses, lichens, algae and their associated decomposition products. Given the absence of vascular plants in such environments, the inputs will contain little complex humic material, but may be rich in other organic compounds. On Signy Island for example, polyols (sugar alcohols) from the catchment mosses may enter the lakes and be a substrate for certain bacteria (Wynn-Williams 1980). In the McMurdo Dry Valleys, more extensive lakes in the past have left residuals of organic material derived from previously submerged microbial mats. These occur in large quantities in the soils of some parts of the valleys and they constitute a legacy of organic carbon that today provides a supplemental input to the present lakes (Priscu 1998).

DOM derived from the breakdown of higher plants absorbs strongly in the ultraviolet as well visible (especially blue) wavebands. This coloured DOM (CDOM) therefore plays a central role in light availability and the underwater spectral regime of aquatic ecosystems (Williamson et al. 1996, Laurion et al. 2000, Markager and Vincent 2000), hence on photochemistry (Molot and Dillon 1997, Bertilsson and Tranvik 2000, Gibson et al. 2001) and photosynthesis (Carpenter et al. 1998, Williamson et al. 1999, Lehman et al. 2004). Absorption of solar energy by CDOM also has consequences for heat transfer in the water column and thermal stratification (Mazumder and Taylor 1994, Snucins and Gunn 2000). DOM is also a major energy source that can be used by bacteria and some of the energy of the bacteria may be eventually transferred to higher trophic levels (Schell 1983, Kirchman et al. 2004, del Giorgio and Davis 2003). DOM alters nutrient and micronutrient availability, for example phosphorus and iron, for autotrophic and heterotrophic communities and can thereby affect biological carbon and energy fluxes (Hessen 1992, Hobbie 1992, De Haan 1993).

ANTHROPOGENIC EFFECTS

Human activities are increasingly a major factor to consider in the landscape ecology of both polar regions, with consequences for downstream receiving waters. For example, construction and operational activities in addition to vehicle use at and near scientific stations in Antarctica are bringing about significant impacts upon the active layer and permafrost in the catchments of lakes. The damage to soils and vegetation from tracked vehicles has been evident or severe on King George Island, South Shetland Islands, with slopes eroded and tracks that penetrate to a depth of 0.5m. Drainage patterns have been altered and quagmires formed (Harris 1991). Land disturbances released considerable water content from permafrost and caused channelled flows, soil shrinkage, land slumping and salinization in the McMurdo Sound region (Campbell et al. 1994). In the Larsemann Hills, Antarctica, four stations and a network of roads have been established in a relatively small area. The roads run predominantly through gneiss that breaks down to fine sand and silt and this substrate is readily mobilized by water. Meltwaters from snowpacks and exposed permafrost have resulted in the roads becoming watercourses that channel the flow and alter lakes by changes in water input, salt loading and turbidity (Burgess and Kaup 1997, Kaup and Burgess 2003). These physically disturbed landscapes may also be more vulnerable to increased thaw and runoff associated with climate warming.

Human impacts are resulting also in chemical changes in surface and subsurface (active layer) waters of lake catchments. In the Larsemann Hills, these waters affected by anthropogenic inputs have up to an order of magnitude higher conductivities than those in natural catchments. The origin of salts has been attributed to direct salt inputs from station activities (wastewater and urine, chemicals, building materials) and to intensive rock crushing by tracked vehicles and subsequent increased weathering, indicated by considerable silt increases in certain areas. The latter changes may be translated into increased nutrient loading on lakes (Kaup et al. 2001), eutrophication and associated changes in limnological properties such as decreased lake water transparency (Ellis-Evans et al. 1997). There is evidence for changed trophic status of lakes brought about by human-generated nutrients in other Antarctic lake districts, including the Schirmacher Oasis (Haendel and Kaup 1995) and Thala Hills (Kaup 1998). These enriched systems may respond quite differently from pristine high latitude lakes to climate-dependent changes in their surrounding landscape.

Effects of climate on landscape and lakes

Lakes are transient features of the landscape and experience continuous evolution, from the first geological origins of a basin to its eventual infilling by biotic and abiotic sediments. Climate change has the potential to affect lake evolution through a variety of processes, especially in the polar regions where small changes in temperature can have a large impact on landscape properties such as snowpack, glacier melt, hydrological inputs, vegetation and soil stability. In this section, we illustrate some of the mechanisms whereby climate affects landscapes and lakes, at various timescales.

GEOMORPHOLOGY

The climate-induced recession of glaciers and ice caps has a wide ranging effect on landscape geomorphology that in turn affects the presence, distribution and form of lake basins. Climate change can result in modifications of pre-existing geomorphological patterns, for example through the thawing of permafrost or changes in precipitation and water-induced erosion. Such erosion processes also affect the transport of sediment from land to lakes and therefore the extent of infilling. As noted in Geomorphology (above), the exposure of moraines of various ages after glacial retreat also has an influence on lake water chemistry. The isostatic adjustment of land following glacial retreat can also radically alter the influence of the sea on coastal lakes and lagoons (see below).

Ice bound lakes are especially sensitive to small variations in climate. For example, the extensive Ellesmere Ice Shelf that once dammed the northern fiords of Ellesmere Island underwent considerable break-up and contraction during the 20th Century (Vincent et al. 2001). This has resulted in the loss of ice-dammed epishelf lakes, most recently that of Disraeli Fiord in which the freshwater layer completely drained away as a result of the break-up of the Ward Hunt Ice Shelf in 2002 (Mueller et al. 2003).

MARINE CONNECTIONS

Many Antarctic and Arctic lakes show a connection to some degree to the sea (see Gibson et al. this volume). For example, in the Vestfold Hills (Antarctica) some ends of paleoceanic bays became lakes (eg Peterson et al. 1988, Cromer et al. 2005) and the coastal aquatic ecosystems include meltwater influenced fjords (eg Ellis Fjord and Crooked Fjord) and lakes that are intermittently connected to the sea with seasonal marine inputs, including microbiota and fish. The latter includes Burton Lake that has an ice dam across its entrance sill, isolating it from the sea for up to 8 months of the year (Bayly 1986). These connections are strongly affected by climate over long timescales (hundreds to thousand of years).

More than 20 lakes in the Vestfold Hills contain relict seawater that was isolated by isostatic uplift of the land after the last deglaciation, about 10,000 years ago (Gibson 1999). This climate-dependant process has resulted in meromictic lakes (lakes that never fully mix) in which dilute, oxygenated meltwaters lie over the ancient, saline, anoxic bottom waters. In the early stages of evolution of such lakes the formation of sea ice and associated brine drainage is likely to have contributed to the high salinities of their present-day bottom waters (Gallagher et al. 1989). Some of the lakes (eg Watts Lake (Pickard et al. 1986), Lake Druzby at the end of Ellis Fjord) have been gradually flushed out with meltwater and are now well-mixed freshwater systems. Sediment cores from Ace Lake in this region show three distinct phases of salinity as indicated by analysis of the fossil diatom flora (Roberts and McMinn 1999): a freshwater phase, followed by a period of inundation resulting in marine and sea ice biota, followed by the present-day hypersaline conditions. In this process, the local sea level, as the balance between the eustatic and isostatic components, is relevant. In the Holocene the sea level rose and then fell resulting in flooding of initially freshwater lakes and subsequent re-isolation (Zwartz et al. 1998)

Analogous effects are also known from the north polar region, again associated with climate change at millennial timescales, deglaciation and isostatic rebound. One set of these systems lie along the northern coastline of Ellesmere Island in the Canadian High Arctic where a series of lakes and fjords form a chronosequence illustrating the various stages in landscape evolution and degrees of connectivity to the sea: well mixed fjords, ice-dammed, meltwater-influenced, stratified fjords, saline, meromictic lakes and lakes that have been flushed out by meltwater and are entirely fresh (Fig. 2).

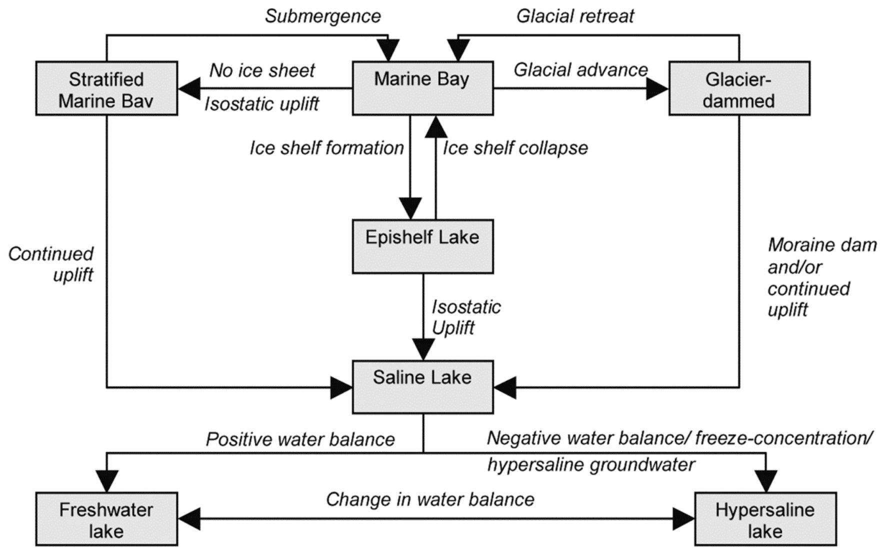

Figure 2. Postulated evolutionary sequence for coastal, high latitude landscapes, embayments and lakes. Reproduced by permission from van Hove et al. *(2006).*

Paleolimnological analysis of coastal Arctic and Antarctic lakes further to the south also show that their evolution began with a submerged phase beneath the sea. For example, analyses of the sediments of ultra-oligotrophic, freshwater Char Lake at Resolute Bay in the Canadian High Arctic show that it emerged from the sea ca. 6ka ago and subsequently became completely fresh ca. 4ka ago (Michelutti et al. 2003). Similarly, subarctic Lake Kachishayoot in coastal Hudson Bay has sediments indicating a marine then brackish water phase before isolation from the sea and shift to present-day freshwater conditions (Saulnier-Talbot et al. 2003).

Small changes in sea level can produce important variations in the properties of small coastal lakes that are separated from sea level by barrier-beaches. Moreover, the fresh water/marine water interface will change finding a new equilibrium with an increased freshwater flow and a sea level rise.

PERMAFROST EFFECTS

Permafrost is overlain by the active layer and the depth of this layer is a reflection of the dynamic equilibrium between hydrological and thermal properties of the soil and atmospheric conditions (Hinzman et al. 1991). Climate-related changes in this layer will have a wide-ranging influence on the transport of water, solutes and particulate materials to downstream receiving water bodies. No long-term (several decades) records of the depth of the permafrost active layer are available in the polar regions, however, several models (Frauenfeld et al. 2004) based on air temperatures identify potentially large variations in its thickness, deepening by 20cm in the period 1956-1990 in Russia. There are predictions for a 20-30% increase in the active layer thickness by the year 2050 in the Northern Hemisphere (Anisimov et al. 1997). This will expose upper permafrost to leaching with meltwater and also will produce shifts in the interconnections among subpermafrost, intrapermafrost and above-permafrost liquid water masses of unpredictable ecological consequences, since in many cases those groundwater masses are rich in solutes and only discharge on surface waters through permafrost discontinuities.

Permafrost may contain considerable stocks of ancient organic matter that can be liberated during melting. For example, in the Larsemann Hills and in Signy Island extensive vegetation beds (mosses, cyanobacterial mats) occurred over the upper permafrost during warmer climates of the past (Burgess et al. 1994, Smith et al. 2004). These can, by climate warming or other disturbances, increasingly contribute to the nutrients and DOM loads in the subsurface waters and, subsequently, in the lake inflows. In one case, gravel mining for road construction caused a drastic increase in permafrost thawing. Soil frozen for thousands of years began to weather and nutrients were released. The result was spring waters extremely rich in nutrients, mainly phosphorus, (Hobbie et al. 1999). Increased nutrient inflows will have a potential to alter trophic status in natural Antarctic lakes and such evidence has been indeed documented (eg Laybourn-Parry 2003).

The active layer in the Dry Valleys is mostly dry because evaporation and sublimation far exceeds the annual recharge into it (Campbell et al. 1998). The result is that the soils are barely leached and weathering products accumulate in the soil profile. In contrast, in oases such as Schirmacher, Thala, Larsemann and Bunger (coastal continental Antarctica) with more intensive recharge from increased meltwater supply, considerable subsurface flow of water occurs (Haendel 1995, Burgess and Kaup 1997). Each summer, the depth of thaw layer depends on temperature, solar radiation conditions and the extent of snow cover. With a snow cover more than 10cm thick, the solar radiation reaching the ground surface became almost negligible on King George Island (maritime Antarctic) where the active layer thickness varied between 0.5 - 3.5m. These conditions are probably representative for the entire maritime Antarctic region (Cannone and Guglielmin 2003) and also for the coastal continental Antarctica to a lesser extent.

The occurrence of many old soils at high inland elevation indicates that little response to global climatic change would be expected there. For the much younger soils in East Antarctica and the Antarctic Peninsula, when mean annual summer temperatures are higher, responses to global change and change in sea level may be significant (Bockheim et al. 1999). In these regions, the process of increasing the temperature due to global warming can, as in the Arctic, result in thawing of permafrost and an increase in active layer thickness. For example, a rise of ca. 1°C in summer air temperatures during the last 50 years due to local climate change on Signy Island (maritime Antarctic) has markedly increased chlorophyll *a* and nutrient levels in lakes. This response may be linked to deglaciation and also reductions in lake snow and ice cover (Quayle et al. 2002). However, if the climate warming in Antarctica is accompanied by increased precipitation then its effect on the active layer and on the lakes can be complex. If the summer snow cover in the oases is extended by increased precipitation, then chemical weathering and nutrient release from the catchments may also decrease.

Climate warming is likely to have pronounced effects on thermokarst landscapes. In these regions, surface melting and slumping affects the morphology of the landscape that in turn influences the hydrologic cycle and aquatic biota and is related to the movement of the tree line in the arctic tundra (Hinzman et al. 2004). These regions are abundant in parts of the Arctic and contain lakes and ponds in vast complexes that variously exchange water with each other and with rivers. The water bodies are typically shallow (< 1m depth) with low phytoplankton and stocks, but often with a productive, nutrient-rich benthic layer of cyanobacteria and other organisms. These luxuriant benthic mats appear to be a major food source for zooplankton that in turn supports other wildlife such as ducks and shorebirds. The formation processes and dynamics of the landscape in the thermokarst regions are illustrated in Fig. 3. The process of thermokarst formation starts by the degradation of the ice wedge, then the subsidence of the surface and the presence of ice beneath the sunken area, allows pond formation. The pond then increases the speed of thermokarst formation since the surface underneath does not freeze during winter. Eventually the reduction of permafrost can drain the pond, which may allow the colonization by terrestrial vegetation (shrubs in the Arctic). If the permafrost is completely destroyed the pond can dry up and the vegetation disappear. If the atmospheric conditions are favourable, palsas may form after refreezing of the surface and new permafrost is formed.

Variations in permafrost, and particularly in the active layer thickness, can be important for man-made constructions. The variation in the thickness of the active layer also affects the stability of the structures since much of the existing infrastructure erected in northern regions is located in areas of high hazard potential and could be affected by thaw subsidence under conditions of global warming (Nelson et al. 2001). These activities are in turn likely to influence the sediment transport to lakes.

Human impacts are resulting also in chemical changes in surface and subsurface (active layer) waters of lake catchments. In the Larsemann Hills, waters subject to human impacts have up to an order of magnitude higher conductivity than those in natural catchments, the origin of salts being attributed to direct salt inputs from station activities (wastewater and urine, chemicals, building materials) and to intensive rock crushing by tracked vehicles and subsequent increased weathering, indicated by considerable silt increases in certain areas. The latter changes may result in the eutrophication, loss of transparency in lakes and major shifts in their ecosystem properties (Ellis-Evans et al. 1997).

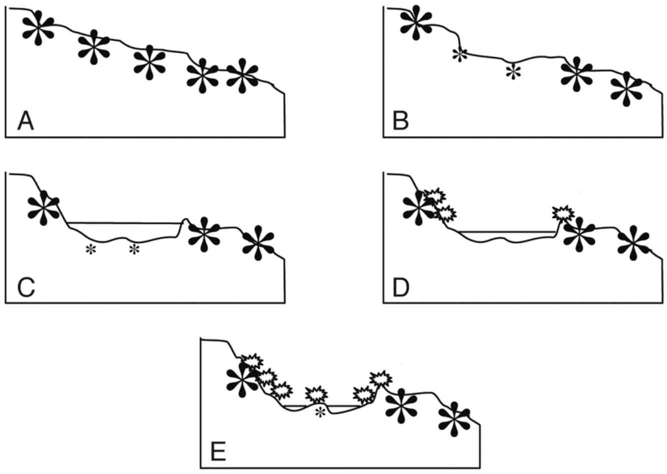

Figure 3. Hypothetical landscape evolution through thermokarst formation. A. Initial situation, permafrost is continuous. B. Some disturbance weakens the permafrost that becomes thinner leading to surface subsidence. C. Permafrost becomes very much reduced, the surface sinks considerably and ponds are formed. D. Vegetation colonizes this more humid and protected area. Pond drains, because permafrost degrades more deeply. E. Plant colonization, almost complete drainage of the ponds, refreezing of some areas (palsa formation). The size of the symbol represents the permafrost thickness (adapted from Hinzman et al. *2004).*

GLACIERS AND HYDROLOGY

Increased temperatures in the polar regions will be accompanied by a reduction of ice thickness and snowpack extent, the retreat of glaciers and also a shift in precipitation from snow to rain in some months (see Convey this volume). These variations are likely to induce modifications in the hydrology of the catchment and so in receiving lakes and wetlands.

Glacial retreat typically produces new lakes, when land depressions that originated from ice erosion are inundated with glacial meltwater. The glacial deposits left behind during retreat are prone to be eroded, weathered and transported by running waters. Moreover, the new land surfaces are also left open for running waters and wind erosion. Sediments are eventually carried to lakes that act as sediment traps. The amount and the size of the sediments in suspension will depend, apart from the water availability, upon the available energy in the ecosystem. In frozen systems, the available energy for transportation is very low and probably not enough to mobilise the sediments since most particles will be glued and/or protected by ice and snow. In such situations sediment reaching the lake will be small in size and low in quantity. On the other hand, where increased temperature results in ice melt and glacial retreat, the available energy for transportation will be higher and the sediment transported will cover a range from fine to larger in size and will be more abundant. The sediment cores collected from lakes in polar areas demonstrate a shift from coarse to fine size of the particles, indicating different stages of available energy and thus probably different climatic conditions (Björck et al. 1991, 1993), such as alternating warm and cold periods.

In shallow lakes fine sediments will remain in suspension during periods of open water since wind mixing will not allow the sedimentation of these inorganic particles. The presence of fine particles under open water conditions will increase the turbidity of the water reducing the available light for the photosynthetic organisms, both planktonic and benthic, likely limiting total autotrophic production in the ecosystem (see below).

An important effect of age on the biogeochemistry of the landscapes arises from the weathering of the glacial till. In the Alaska LTER, the till from all glaciations originated in a limited area of the Brooks Range (Hamilton 2003) so all the parent tills have similar chemistry. The effect of weathering and other important soil processes connected to vegetation and moisture results in a soil chemistry that reflects a similarity of origin and an evolution with age on all three glacial surfaces. The basic till in the region contains carbonates, apatite (calcium phosphate) and some calcium sulphate. Over time, the carbonates leach out and soil waters become more acidic (eg pH of the 10ka = 5.5-7, 60ka = 3.5-5.0). In streams and lakes, the pH and base cation content vary across the region in a pattern reflecting landscape age. For example, conductivity varies strikingly with landscape age (Table 1) and calcium and bicarbonate are more abundant in the lakes and streams of the younger surfaces. Within a drainage basin, the headwater streams and lakes receive the lowest concentrations of major ions while downstream freshwaters receive higher concentrations (Kling et al. 2000). Soil mineral phosphorus content is much greater in soils on younger landscapes (Walker et al. 1989, Giblin et al. 1991), while N availability is greater in older soils. Hobbie and Gough (2004) compared nutrient availability on the 10ka and the 60ka soils while Gebauer et al. (1996) documented the nutrients in the 300ka soils in the detailed study of Imnavait Creek. However, nutrients do not move as freely downslope as water and major cations. The uptake of nutrients by plants is increased by the shallow runoff due to permafrost thereby limiting nutrient inputs to freshwaters.

How do differences in biogeochemistry affect the functional aspects of aquatic ecology? Levine and Whalen (2001) found that the planktonic chlorophyll content (a proxy for algal biomass) was very similar in all of the numerous lakes they sampled in this region. Thus, pelagic production in lakes may not show a strong connection to landscape age but a stronger linkage appears to exist with benthic production (Fig. 4, Gettel 2006).

In shallow oligotrophic lakes benthic processes are especially important, light reaches the bottom and water column production is low (Ramlal et al. 1994). In lakes around Toolik Lake, shallow benthic primary production (< 6m) is similar to, or greater than water column production. The benthos also is important in nutrient cycling, benthic N_2 fixation can contribute up to 1 mg N $m^{-2}.d^{-1}$ during the summer months (Gettel 2006). In a survey of 15 lakes, Gettel (2006) found that shallow benthic N fixation showed a pattern of decreasing N_2 fixation among lakes on older landscapes (Fig. 4). However, Gettel (2006) also showed that fixation is controlled by a number of processes, including light and snail grazing, which co-vary with landscape age. In calcium rich lakes on the younger landscape, snail grazing can suppress N_2 fixation, altering the expected pattern of decreasing lake N_2 fixation with increasing landscape age. Benthic N_2 fixation is clearly important in shallow arctic lakes where benthic primary productivity can dominate.

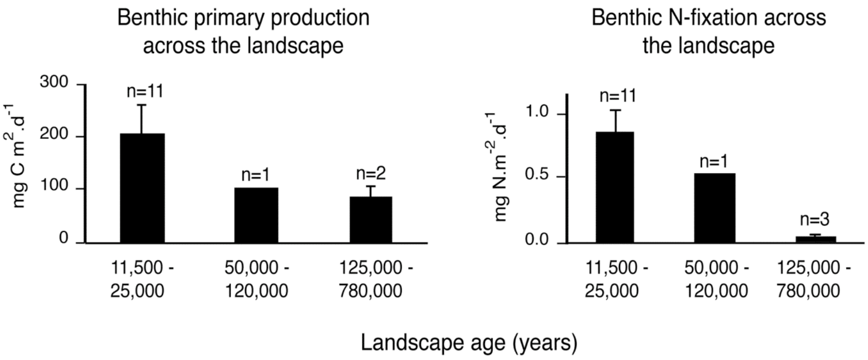

Figure 4. Benthic N_2 fixation and primary productivity on different landscape ages near Toolik Lake.

While soil dissolved organic carbon (DOC) increases with landscape age, DOC concentrations in lakes are under more complex controls because of the intensive processing of DOC in streams and lakes (Bowden and Group 1999). There are more snails and clams in lakes on the younger landscapes because the calcium concentrations are high. There is also evidence of more N_2 fixation in the younger networks possibly because of increased P (Fig. 4, Gettel 2006) and calcium. Position and morphometry also exert an important influence on primary production and these factors also vary with age. The older landscape has fewer, shallower lakes, which are less likely to be part of a network of lakes (Table 1). Lakes in a network tend to act as nutrient filters, so we expect that lake productivity will tend to decrease in long stream/lake sequences. For example, lakes at the headwaters of the Toolik inlet series of lakes (I-1 and I-2) have low primary productivity, but not as low as two lakes lower in the drainage (Kling et al. 2000). Lake I-8, which receives its water directly from streams, has higher productivity. Toolik Lake, which receives its water through nine intervening lakes, has the lowest primary productivity in the chain. This illustrates that the greater development of the stream-lake network on younger surfaces may serve to limit primary production in downstream freshwaters.

Lakes in both polar regions have undergone considerable changes in size associated with expansion and contraction of ice in their catchments. For example, Lake Vanda in the McMurdo Dry Valleys appears to have undergone major expansion 2000 - 3000 years ago, with evidence of ancient shorelines 64m above 1970s lake levels. This has been attributed to a brief period of climatic warming that increased the volume of meltwater from glaciers, and raised the snowline, causing the tributary glaciers to move to higher elevations. This meant than when conditions subsequently cooled, the higher glaciers were unable to provide substantial meltwater and Lake Vanda almost evaporated to dryness. This desiccation event is believed to have been the primary cause of the hypersaline bottom waters that now characterize this meromictic lake (Smith and Friedman 1993).

The long term water chemistry record at Toolik Lake has shown a doubling of the average acid neutralizing capacity (alkalinity) due primarily to changes in calcium and magnesium concentrations (Hobbie et al. 2003). There are no corresponding changes in the chemistry or amount of the precipitation that would account for these changes. It is suggested that dust from the road is causing the changes, but similar changes in alkalinity have been found in streams and lakes quite distant from the road (Hobbie et al. 2003). The most reasonable explanation is that alkalinity is an indicator of changes in soil and groundwater chemistry. For instance, it is possible that small, climate-dependent increases in active layer depth have exposed new soil material to weathering. Temperature however may not be the sole or even dominant factor affecting chemical weathering rates. For example, Lyons et al. (1997) compared weathering in Taylor Valley streams versus warm rivers in Alabama and found more than three times faster weathering rates in the former. In this comparison, lithology and water availability were likely to be the overriding controls on weathering.

Variations in temperature also affect the precipitation regime in polar regions, causing the increasing likelihood of rain rather than snow in the summer period. This change will have a major effect on the soil and geomorphology of the polar landscapes, since precipitation in solid form (snow) typically shows more gentle erosion effects because of the slower water release during thawing. However, rain produces an immediate effect eroding unstable soils, as those typical from polar regions. This also will also affect soil organisms, since the slow water release from snow, allows the biota to maintain an appropriate water content for survival during longer periods. However, the same amount of precipitation in the form of rain saturates the active layer of soil but disappears quickly because of flow or evaporation (see above) limiting water availability for biological processes.

Temperature rise itself has direct effects on the lakes through several landscape processes. An increase in air temperature will produce a direct increase in water temperature but also will warm the rocks and soils of the catchment. These will transfer more heat to the lake via warmer water from the catchment entering the lake ecosystem. For instance, a physical model of Toolik Lake, Alaska, uses daily weather data as the input and simulates the annual thermal cycle (Hobbie et al. 1999). Under a scenario of a 5°C air temperature increase, lake temperatures increased by 3°C while the ice-free season increased by seven weeks. This reduced effect on water temperature could be critical, because in polar regions lake water temperature typically ranges between 0 and 6°C. If stream water that is warmer (less dense) and richer in solutes enters the lake after the spring runoff, it will float over the colder (more dense) lake water, triggering a stratification of the water column that will last until wind mixes the different density layers. In this potential stratification period surface waters will have higher growth rates of photosynthetic organisms due to higher nutrient concentrations. This change will have profound consequences on the lakes ecology.

DISSOLVED ORGANIC MATTER

As summarized in Vegetation (above), the transport of dissolved organic matter (DOM) is a primary mechanism coupling lakes to their surrounding landscapes, and it exerts a wide-ranging physical, chemical and biological influence on aquatic ecosystems. The export of DOM from land to water is affected by vegetation type, biomass and productivity, and by the mobilization of stored reserves of organic matter in the catchment. Each of these in turn is likely to be highly susceptible to climate change.

The effect of climate on vegetation and DOM export has been illustrated in a series of paleoecological studies in northern high latitudes (reviewed in Pienitz et al. 2004 and Vincent et al. 2005) including limnological changes accompanying the shift of the northern tree line during the Holocene (ca. last 10 ka) in the Canadian Northwest Territories (MacDonald et al. 1993, Pienitz et al. 1999, Pienitz and Vincent 2000, Lehmann et al. 2004), the succession of vegetation types during ice retreat and soil development at Glacier Bay Alaska (Engstrom et al. 2000, Williamson et al. 2001), and the isostatic uplift, isolation from the sea and plant colonisation of catchments in coastal subarctic Québec following deglaciation (Saulnier-Talbot et al. 2003). In the latter paleo-optical study (study of past underwater light regimes), the authors found that there had been abrupt increases in diatom-inferred DOC concentrations and water colour that coincided with the retreat of postglacial marine waters and the arrival of spruce trees within the surrounding landscape. Their investigation also revealed large changes in the underwater irradiance environment over the course of the postglacial period, from extremely high UV exposure following the initial formation of the lake and its isolation from the sea, to an order-of-magnitude lower exposure associated with the development of spruce forests in the catchment. The use of additional macrofossil markers revealed that underwater UV penetration remained low even following forest retreat due to the development of alternate DOC sources in the catchment such as *Sphagnum* wetlands (Saulnier-Talbot et al. 2003).

These effects of vegetation on DOM loading in the past provide insights into how climate change may affect landscapes and lakes in the future. Regions such as the Canadian Arctic contain latitudinal bands of ecozones that differ in vegetation type and standing stocks (Gould et al. 2003), and there is evidence that the DOM content of lakes generally follow this vegetation gradient, with highest concentrations in waters of the boreal forest and lowest concentrations in lakes fed by polar desert catchments with sparse, discontinuous plant communities (Pienitz and Smol 1993, Vincent and Pienitz 1996). However, there are exceptions to this general pattern associated with local oases of vegetation. Overall, there appears to be a statistical relationship between the density of phytobiomass and temperature, specifically the extent of summer warming (Walker et al. 2003) and thus in the future it is likely that these ecozones will move northwards. Already such effects are noticeable at some locations. There is evidence of increased densities of shrubs associated with recent warming of the Alaskan tundra (Sturm et al. 2001) and on the Seward Peninsula, Alaska, there is evidence of tree line advance (Lloyd et al. 2002). This arrival of larger plants with more lignin-containing tissues is likely to increase the amount of CDOM transferred to lakes, as has been inferred from the paleorecord.

In addition to affecting the above ground, living stocks of carbon and associated plant detritus, climate change may also cause the mobilization of stored organic carbon reserves in the catchment. This aspect is of major concern in the Arctic and Subarctic. Northern high latitude regions contain the largest peat-bog systems on Earth with as much as one third of global organic carbon stocks (Gorham 1991, McGuire et al. 2002, Smith et al. 2004). Changes in air temperature and precipitation could potentially mobilize part of the sequestered carbon of these systems (Agafonov et al. 2004, Christensen et al. 2004) through physical (hydrology, freeze-thaw cycles), chemical (photoreactions, oxidation) and biological mechanisms (respiration, biodegradation of DOM, energy transfer through the food web). The stability of the soil carbon pool appears sensitive to the depth and duration of thaw (Goulden et al. 1998). It has been shown that rising temperatures can stimulate the export of DOC from peatlands (Freeman et al. 2001). Since the Little Ice Age (ca. AD 1550-1850), permafrost degradation has resulted in the loss of forested lands and an increase in long-term net accumulation of organic matter (Vitt et al. 2000, Turetsky et al. 2002) that may eventually be mobilized.

There is considerable interest at present on the influence of DOM on the inorganic carbon balance of high latitude aquatic ecosystems, and the potential role of rivers and lakes as systems that may decompose and ventilate organic matter from the tundra into the atmosphere. Work by Kling et al. (1991) illustrates how carbon movement through streams and lakes can change the carbon balance of an entire watershed. These authors found that Alaskan tundra lakes and streams are typically supersaturated in carbon dioxide. The CO_2 concentration in 25 lakes averaged 1162ppmv, with calculated positive fluxes of CO_2 from water to the atmosphere averaging 20.9mmol $m^{-2}.d^{-1}$. These high amounts of CO_2 came from groundwater that contained up to 46,500ppmv. Groundwater is likely confined by permafrost to shallow organic-rich soil layers where CO_2 produced by plant and microbial respiration can accumulate. Carbon loss by this aquatic pathway could equal the terrestrial carbon accumulation. They estimated the global C loss from tundra lakes and rivers to be between 7 - 20% of the current estimated C sink for arctic tundra, this estimation being conservative since part of the carbon exported to the ocean (POC and DOC) can also be respired and lost to the atmosphere. Kling et al. (1991) also measured CH_4 concentration in eight lakes and one river averaging 270ppmv, some 150 times the concentration partial pressure at atmospheric saturation. Supersaturation of methane, and thus net efflux of this potent greenhouse gas, has also been reported by Whalen and Reeburg (1990) in Alaskan freshwaters.

BIOLOGICAL CYCLES AND BIODIVERSITY

Most models predict that climate change will lead to an increase in temperature and precipitation regime in polar regions. Experimental increases of temperature in non-aquatic ecosystems as Antarctic terrestrial soils have shown large variations such as an increase in cyanobacterial colonizers, and the size of the micro-arthropod and nematode populations (Kennedy 1994, Wynn-Williams 1996, Convey 2003, Convey this volume). These variations are already being detected in polar regions under natural conditions, since they are more sensitive to these changes than other ecosystems. The onset of these effects is now being observed, such as an increase in the distribution of the higher plant *Deschampsia antarctica* on King George Island from 1984 to 2001 (Gerighausen et al. 2003). Variations in the vegetation and edaphic communities of catchments are likely to have large effect on the downstream receiving waters, shifting the amount and the type of DOC and POC entering into the lake (see above).

In terms of non-marine aquatic ecosystems the predicted changes include variations in the physical and chemical characteristics of the ecosystems. An increase in the open water period is expected, making light available during more time to deeper layers. An expanded open waters period will also allow more active mixing and through this will make available, in shallow lakes, more nutrients released from the lake sediments, therefore increasing nutrient availability for primary producers in these typically ultra-oligotrophic waters. The consequences of the exponential increase of primary producers are unpredictable but most probably will imply important variations in further steps of the food web. Apparently simple food webs, such as those found in polar freshwaters, can be strongly impacted by variations in organism numbers in any of the trophic levels (A. Camacho et al. unpubl. data). It is also likely that there will be an increase in the solute concentration of waters incoming into the lakes due to hydrological variation (see above). Both processes will most probably result in increased eutrophication. Typically eutrophication processes are characterised by an increase in biomass but also a decrease in biodiversity.

Another important factor is the increase of solids in suspension entering the lakes due to an increase of erosion in the catchments, or to higher discharge of streams into the lake. The effects of such an increase are unpredictable but most likely will reduce light availability in the water column shifting the biomass composition towards low light adapted primary producers (eg planktonic cyanobacteria). This increase in solids in suspension would also affect the benthic communities, which in some cases is the dominant biomass in some polar lakes (Imura et al. 1999). Most benthic communities are dominated by slow growing organisms so that rain of sediment on them may limit their survival (Imura et al. 1999). Any shifts in the underwater light regime will be a function of the balance between reduction caused by solids in suspension and increase due to reduction in ice cover duration and thickness. How these two factors will counteract is unknown at the moment, but most likely they will affect aquatic biodiversity.

After glacial retreat, milder conditions will make the new lands or aquatic ecosystems more suitable for invader species from non-polar latitudes. Clarke et al. (2005), as other authors suggested before (eg Ellis-Evans 1996), cast doubts on the biological isolation of Antarctica. In fact, redistribution and expansion of native populations and invaders have been documented for microalgal, invertebrate and plant taxa (Karentz 2003, Convey et al. this volume, Hughes et al. this volume). Several recent invasions have been documented, such as a carabid beetle at South Georgia (Ernsting et al. 1995). The subantarctic islands have been subject to the majority of recent introductions (Frenot et al. 2005), including taxa from many different phylogenetic groups. This topic is extensively treated by Gibson et al (2005), in relation to the biogeographical distribution of the Antarctic organisms.

Biodiversity change and species redistribution will be more conspicuous in the Arctic since there are no boundaries to limit the free distribution of organisms. However, landscape variations due to climate change could also strongly affect aquatic ecosystems if new connections are formed among different water masses. Fish are one group of organisms that would quickly move into the new habitats. Evidence from the Arctic indicates that any invasions triggered by climate change in Antarctica will have substantial impacts and will profoundly modify these simple ecosystems in terms of biodiversity and ecosystem functioning.

Conclusions

Landscape exerts a broad range of controls on the properties and dynamics of lakes in both polar regions. The primary effect over long time scales is on basin and catchment geomorphology, hydrological flow patterns and connections with the sea. Over shorter timescales, climate can have a strong effect on permafrost degradation, rock weathering, soil formation, erosion and vegetation development. Each of these processes in turn affects the chemical, physical and biological properties of downstream receiving waters. Most of the variations that have been observed over the last few decades are the result of slow or continuous change in climatic conditions. In the future, however, more rapid and pronounced alterations are likely. In high latitude landscapes where permafrost, glaciers, snowpack and other cryogenic features are so dependent upon persistent cold, small temperature changes are likely to have abrupt, threshold-dependent effects that in turn impact strongly on lakes.

Acknowledgements

This study was supported by grant REN2000-0435-ANT from the Ministerio de Ciencia y Tecnología (Spain), grant SAB2003-0025 from Ministerio de Educación y Ciencia (Spain) and the Networks of Centres of Excellence program ArcticNet (Canada). The work of E Kaup was supported by the grant SF0332089s02 from the Ministry of Education and Science (Estonia).

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