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Abstract

Following deglaciation, the long-term pattern of change in diatom communities and the inferred history of the aquatic environment are affected by a hierarchy of environmental controls. These include direct climate impacts on a lake's thermal and hydrologic budgets, aswell as the indirect affects of climate on catchment processes, such as weathering, soil development, microbial activity, fire, and vegetation composition and productivity,which affect the transfer of solutes and particulates from the terrestrial ecosystem into the lake. Some of these catchment influences on lacustrine systems operate as time-dependent patterns of primary succession that are set in motion by glacier retreat. This paper provides a conceptual model of some dominant pathways of catchment influence on long-term lake development in glaciated regions and uses a series of paleolimnological examples from arctic, boreal, and temperate regions to evaluate the relative role of direct climate influences and of catchment processes in affecting the trajectory of aquatic ecosystems during the Holocene in different environmental contexts.

Keywords: Diatom, Ontogeny, Succession, Paleoclimate, Catchment, pH, Nutrients, DOC

Introduction

A hierarchy of environmental controls that change with time drives variation in lake ecosystemstate over periods of decades to millennia (Figure 1). Climate is a first-order control on aquatic structure and function via a complex series of direct and indirect mechanisms. These include direct impacts on a lake's thermal and hydrologic budgets and the resultant influences on biogeochemistry and organisms, as well as the direct impacts of temperature on metabolic rates of aquatic organisms. Climate also influences lake ecosystems indirectly by affecting catchment structure and function, including weathering, soil development, microbial activity, fire, and vegetation composition and productivity, which, in turn, influence the transfer of solutes and particulates from the terrestrial system into the lake. In glaciated landscapes, where glacial retreat sets in motion a sequence of change associated with primary succession, these catchment processes can be time-dependent; this directional series of changes is commonly referred to as ontogeny (e.g. Battarbee 1991; Engstrom *et al.* 2000 and references therein).

Here we consider the role of catchment processes on long-term lake evolution during the Holocene

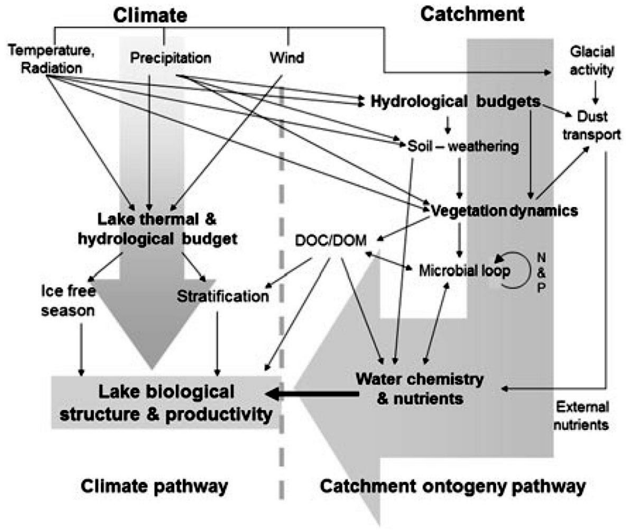

Figure 1 A conceptual model showing direct climate forcings and catchment-mediated processes that affect biological community structure and productivity. Details of the processes and their ecological affects are summarized in Table 1, together with relevant examples from the literature.

(Table 1). We review both climate-driven changes in terrestrial structure and function and time-dependent successional processes that affect weathering, soil development, hydrology, and nutrient cycling—hence catchment processes that have the potential to alter the fluxes of materials to lakes embedded within the landscape. Although we recognize the over-arching influence of climate on aquatic ecosystem dynamics (Battarbee 2000), we focus on indirect catchmentmediated processes, which filter the influence of natural climatic variability (Leavitt *et al.* 2009). We also present examples from the paleolimnological literature that illustrate the role of these catchment processes in a range of environments and evaluate settings where catchment processes are likely to be most important relative to settings where direct climate impacts dominate changes in ecosystem structure and function. We focus our review on lakes formed by glaciation and therefore on landscapes where primary succession following ice retreat interacts with climate to affect lacustrine ecosystem state. We also focus our review primarily on studies that infer ecosystem changes from sedimentary diatom assemblages.

Biogeochemical linkages between lakes and their catchments

Catchment processes that affect aquatic ecosystems include changes in hydrology, weathering, vegetation, and microbial dynamics, which in turn influence various biogeochemical pathways that link the catchment and the lake (Figure 1; Table 1). Some processes involve direct temperature or hydrological impacts on chemical weathering of parent material or on the character of soils in influencing the chemistry of surface waters; others involve changes in composition and biomass of vegetation or the microbial community, which subsequently alter soils, hydrology, and biogeochemical cycling.

The impacts of chemical weathering and vegetation change on base cations, pH, and dissolved organic carbon

Long-term natural acidification of lakes is common in regions with base-poor bedrock (Bigler *et al.* 2002; Engstrom *et al.* 2000; Ford 1990; Renberg 1990; Whitehead *et al.* 1989). Early studies of lake ontogeny posited that lakes become more acidic over time, because of the progressive leaching of base cations from soils (Iverson 1964; Whitehead *et al.* 1989). More recent studies from boreal and temperate forests dominated by conifers suggest that long-term lake acidification may be more tightly linked to vegetation change and its impacts on soil development and hydrology. The accretion of soil organic matter (SOM) over time increases the flux of dissolved organic carbon (DOC) in runoff, with consequent influences on the acid–base chemistry of down-gradient lakes (Pienitz *et al.* 1999). Podzolization in organic-rich soils also reduces hydrologic conductivity, groundwater recharge, and consequently the influx of base cations in groundwater inflow (Engstrom *et al.* 2000; Ford 1990). The net effect of the alteration of hydrological flow paths is to increase surface flow through organic-rich soils. Thus, in a variety of basepoor terranes the increased surface flux of organic acids and decreased flux of base cations in groundwater produces a net decline in lake pH over time. These processes operate in the cool humid forested areas of boreal and temperate regions, as well as in the treeless areas of arctic and sub-arctic regions, despite the lower plant biomass and shallower soils.

DOC transfer from land to lakes also has the potential to have profound limnological effects on the underwater light climate (Williamson *et al.* 1999), thermal budgets (Fee *et al.* 1995), other elemental cycles, and trophic interactions (Karlsson *et al.*

Table 1. A summary of the processes illustrated in Figure 1, together with an indication of the possible methods used to reconstruct the process/variable and its main environmental consequences and ecological effects.

Climate and catchment drivers (see Fig. 1)	Timescale (year)	Method for reconstruction and/or paleo proxy indicator	Process response in both catchment and lake	Ecological community response in lake	Problems	Literature examples
Lake morphometry and infilling	10^3	Modeling; 3-D reconstruction of basin infill	Altered stratification, mixing regimes; resuspension/tubidity	Expansion of littoral zone; macrophyte production; habitat changes	Detailed morphometry needed; multi-coring	Stone and Fritz (2006), Odgaard (1993)
Effective moisture (precipitation minus evaporation)	10^0–10^3	Diatoms; stable isotopes; geochemistry; modeling	Lake-level; salinity	Changed biological structure	Confounding influences on isotope signal	Anderson and Leng (2004), Aebly and Fritz (2009)
Thermal budgets						
Ice cover	Seasonal 10^{-1}	Modeling	Mixing regimes, light; seasonal CO_2, pH	Littoral/pelagial coupling;	Issues of temporal scaling	
Thermal stratification (for chemical stratification see below)	Seasonal 10^{-1}	Modeling	Anoxia, mixing regimes; seasonal CO_2 build-up; pH change; nutrient recycling	Phytoplankton dynamics	As above; difficulties of retrospective reconstruction	Stefan and Fang (1997)
Glacial activity						
Fluvioglacial input	10^1–102	Lithostratigraphy/grain size	Light climate	Decreased primary production		Bakke et al. (2005)
Dust/loess	10^1–10^3	Grain size	Nutrient input; alkalinity	Productivity changes	Diatom removal required	Neff et al. (2008), Psenner (1999)
Vegetation dynamics	10^2–10^3	Pollen, macrofossils, modeling	Terrestrial nutrient retention, soil acidification N_2 fixation	Productivity changes; pH changes	Spatial scaling problems	Birks and Birks (2006), Anderson et al. (2006)
Vegetation-driven soil development	10^2–10^3	Macrofossils (e.g. *Cenoccocum*), biomarkers; stable isotopes; geochemistry	Complex–nutrient recycling/retention; altered POC/DOC fluxes	Productivity changes; Acidity/pH changes		Heggen et al. (2010)
DOC/DOM export	10^1–10^3	NIR, porewater fluorescence; stable isotopes	Light climate; organic acidity	Reduced benthic production Community shifts		Rosen (2005)
Geochemical weathering and development of mineral soils	10^1–10^3	Geochemistry, sequential extraction; modeling	H^+ and nutrient export	Acidity pH changes, productivity changes	Problems with diatom-inferred pH	Battarbee et al. (2005), Boyle (2007)
Erosion	Events: 10^1 Trends 10^1–10^3	Geochemistry, magnetics	Silt loading	Light, nutrient inputs		Dearing (1991)
Fire	10^{-1} (10^1–10^3)	Charcoal	Increased nutrient loading, DOM/POM transfer	Nutrient input, primary production	Separating regional/ local fires	Birks (1997)
In-lake processes						
Anoxia and nutrient cycling	10^{-1} (10^1–10^2)	Geochemistry (Fe:Mn)	Internal nutrient cycling	Nutrient recycling, primary production	Separating internal and external nutrient sources	Engstrom and Wright (1984)

Table 1, continued

Climate and catchment drivers (see Fig. 1)	Timescale (year)	Method for reconstruction and/or paleo proxy indicator	Process response in both catchment and lake	Ecological community response in lake	Problems	Literature examples
Meromixis bacterial activity (phototrophic)	10^1–10^2	Pigments: okenone	Light, altered nutrient cycling	Microbial loop		McGowan et al. (2008)
Bacterial activity (heterotrophic)	10^{-1} (10^1–10^2)	Biomarkers	Light; organic matter recycling; CO_2; pH	Microbial loop, heterotrophy	Heterotrophy per se difficult to identify	Spring et al. (2000), Coolen and Overmann (1998)

In terms of reconstructing a variable, we have excluded many biologically inferred approaches, such as chironomid-temperature and diatom-temperature reconstructions, because problems with secondary gradients limit the validity of many transfer functions (Juggins 2013). Also, use of biologically-inferred proxies precludes the use of the original biological data as a response variable (in a statistical analysis; see Lotter and Anderson (2012) for a discussion of this problem). A further layer of complexity is added by trophic interactions but is not discussed here. Recognition of the difficulties in reconciling seasonal processes (i.e. stratification) and the sediment record is implicit in this listing (see text for a discussion).

2009; Sobek *et al.* 2005; Williamson *et al.* 2001). Altered DOC fluxes are not only caused by primary succession and its subsequent influence on soil development but also climate change. In the Arctic, for example, increased temperature affects soil chemistry by deepening the seasonal active melt layer, with associated changes in microbial activity and biogeochemical cycling (Hobbie *et al.* 2002). These changes in microbial activity can increase particulate organic carbon and DOC transfer from the landscape to the lake, which may influence lake productivity and biological structure. Altered carbon flux also can fundamentally affect lacustrine trophic structure; for example, heterotrophy (net ecosystem respiration > primary production) is common in aquatic ecosystems with high DOC concentrations (>10 mg L^{-1}) (Sobek *et al.* 2005).

Climate, weathering rates, vegetation dynamics, and microbial influences on nutrient fluxes

Long-term weathering, changes in soil development driven by vegetation or climate change, and altered catchment hydrology can affect not only carbon fluxes but also nutrient transfer (Table 1). In the initial stages of catchment development, the weathering of newly exposed bedrock releases base cations and nutrients, which in turn may increase their concentration in runoff and in down-stream lakes (Boyle 2007). Organic acids that result from the development of SOM augment this weathering (Berner and Berner 2012). Thus, increased lacustrine nutrient concentrations and increased primary production can accompany stabilization of catchment soils and the early weathering of recently deglaciated substrates (Fritz *et al.* 2004). In the case of phosphorus, multiple products of long-term soil development bind phosphorus in sediments and soils, including calcium, iron and aluminum oxy-hydroxides, and organic compounds (Engstrom and Wright 1984). Thus, over some period of time, both the progressive leaching of apatite (Boyle 2007) and the binding of phosphorus during long-term soil development (Filippelli and Souch 1999; Norton *et al.* 2011) can reduce phosphorus concentrations in runoff, and as a result, lakes may become more oligotrophic (see below).

In shallow lakes and ponds in the Arctic, climate affects the duration of the ice-free season, and, in turn, lake productivity and the patterns of change in lacustrine diatom assemblages (Smol and Douglas 2007). Yet, seasonal and inter-annual changes in temperature, hydrology, and chemical weathering that affect nutrient fluxes and hence primary production may be equally important as drivers of ecological change. Jones *et al.* (2005) reported elevated nitrogen export from areas with discontinuous permafrost, a study that has clear implications for lake-catchment interactions in a warming world. Even in dry arctic environments, such as the interior of SW Greenland, where summer precipitation is insufficient for overland flow (Hasholt and Søgaard 1978), the period of spring melt is a significant contributor to lacustrine nutrient budgets (cf. Tye and Heaton 2007). Although chemical weathering in sparsely vegetated catchments of the high Arctic and in the fell-field landscapes at higher altitudes in the low Arctic is poorly understood, its role in surface-water chemistry merits more attention (Hall *et al.* 2002), particularly its potential to influence nutrient budgets of oligotrophic lakes.

The biomass and composition of catchment vegetation also influence nutrient fluxes from catchments into lakes by influencing microbial processes (Table 1). Microbial nitrogen fixation in soils is enhanced by several early successional plant species, such as *Dryas* and *Alnus* (Chapin *et al.* 1994), and by cyanobacteria. In arctic ecosystems today, estimates suggest that 25–80 % of nitrogen inputs to soils is due to fixation (Chapin and Bledsoe 1992). If terrestrial uptake does not consume the resulting soil pools of ammonium and nitrate, nitrogen export may increase during the early stages of terrestrial succession, in turn increasing primary production in nitrogen-limited aquatic ecosystems (Engstrom *et al.* 2000; Fritz *et al.* 2004; Goldman 1961; Hu *et al.* 2001). Vegetation development also can affect aquatic nitrogen availability by altering the flux of SOM to the lake and in turn affecting sediment redox and denitrification (Seitzinger *et al.* 2006).

Nitrogen export from catchments is influenced by rates of microbial processing and by direct uptake by plants, both of which are influenced by climate via a complex set of linkages. Plant phenology, both timing of the spring growth and of late-season senescence, can determine nitrogen uptake, loss to soil water, and hence nitrogen availability for utilization in aquatic systems. There is growing evidence for nitrogen mineralization during winter, with substantial inorganic nitrogen export from terrestrial systems during snowmelt, because terrestrial plants are unable to utilize the plant available N pool early in the season. Tye and Heaton (2007) found that soil-derived NO_3 loss increased in the late summer in tundra on Svalbard, possibly associated with reduced demand by plants during their late-season senescence. Although enhanced microbial activity associated with increased temperatures in late-season may increase NO_3 loss, continued warming may reduce its impact due to positive effects on plant growth and seasonality, possibly over-riding photoperiod (Tye and Heaton 2007). Changes in vegetation composition driven by climate change also can affect nitrogen fluxes. Thus, the greening of the Arctic—the expansion of shrubby vegetation across previously bare ground (Tape *et al.* 2006)—is likely to sequester nutrients in plant biomass, as well alter hydrology and other biophysical processes locally. The implications of these processes for lake nutrient budgets are, therefore, complex. A further complication for predicting catchmentlake nitrogen interactions is that greater nitrogen mineralization results in a positive feedback on decomposition rates, because the enhanced nitrogen inputs relieve bacterial N-limitation. Another level of complexity is that of catchment spatial heterogeneity (Hobbie *et al.* 2002) and the importance of site characteristics and successional stage (which influence plant growth and vegetation composition, which in turn control nutrient stoichiometry and the build-up of nutrient pools in soils, cf. Wookey *et al.* 2009). These processes vary considerably at the regional and local scale, and this heterogeneity can impart considerable variability to down-gradient lacustrine systems. This complexity needs to be fully considered in paleolimnological analyses and incorporated into multi-site paleolimnological studies (e.g. Fritz *et al.* 2004; Figure 2).

Long-term patterns of ecosystem change

Below we review a series of examples from arctic, boreal, and temperate regions to evaluate the relative role of direct climate influences and of catchment processes (Figure 1) in affecting the Holocene trajectory of aquatic ecosystem structure and function over time. Specifically, we evaluate (1) the settings in which changes in acid–base status driven by catchment processes are the first order influence on aquatic structure and function; (2) changes in nutrient status

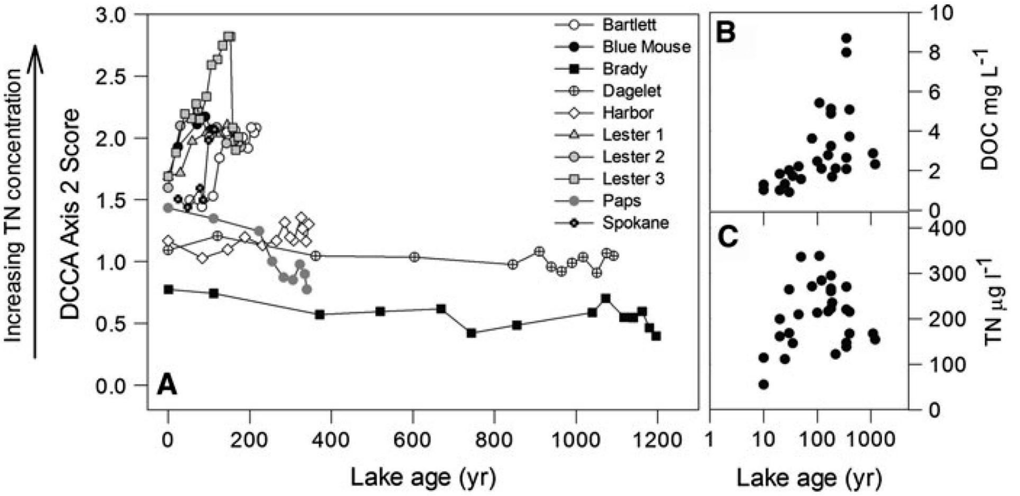

Figure 2. Spatial variability in developmental trends inferred from diatom assemblages in short cores from a chronosequence of lakes in Glacier Bay Alaska highlighting the complex response of lakes within a small geographic area. **a)** The diatom assemblage trajectory along the nutrient (nitrogen) axis (DCCA2, $\lambda = 0.37$ (axis 1 $\lambda = 0.63$), see Fritz *et al.* 2004) since the time of lake formation by retreating glaciers; **b)** contemporary lakewater DOC concentration plotted against lake age; **c** contemporary lakewater TN concentration plotted against lake age. Some lake trajectories vary very little on axis 2 but show change in inferred DOC (e.g. Brady, cf. **b**) whereas other lakes, e.g. Lester-3, do change along the N-concentration gradient, reflecting the changing TN gradient observed in contemporary chronosequence (**c**). See Fritz *et al.* (2004) for the diatom stratigraphies and additional information.

and productivity associated with primary catchment succession; (3) the relative role of direct climate influences versus catchment mediated changes in nutrient status in affecting the development of planktic diatom floras; and (4) settings where climate is the primary driver of long-term limnological change.

Long-term changes in pH and dissolved organic carbon in arctic and boreal lakes

Interactions among catchment geology, climate, and vegetation affect the acid–base status of lakes through time. In cool humid regions of northeastern US, the dominant trend in diatom species composition in lakes on crystalline bedrock is a progressive decrease in pH over time. This trend may reflect the loss of base cations during weathering and the increase in DOC inputs as vegetation density increased, particularly of conifers (Ford 1990; Whitehead *et al.* 1989). In the maritime regions of southeastern Alaska, high precipitation (>1,500 mm year^{-1}) leads to podzolization of soils and peatland expansion in areas of low elevation. As a result, even lakes on calcareous glacial till show long-term declines in lake pH (Engstrom *et al.* 2000; Fritz *et al.* 2004).

In high-latitude regions of Scandinavia, paleolimnological records from sites on base-poor bedrock also show a decline in pH over time, in most cases associated with increased terrestrial plant biomass and acidification of catchment soils. In contrast, in nearby sites on base-rich substrates, catchment vegetation was relatively stable during the early to mid-Holocene (Bigler *et al.* 2003), and similarly no major change is evident in the aquatic flora, although undoubtedly climate varied substantially over multiple millennia. A similar pattern of stasis in diatom community composition over multiple millennia is also observed in paleolimnological records from the alpine steppe of Siberia (Westover *et al.* 2006).

In regions proximal to the forest-tundra boundary, DOC export may vary with climate and produce fluctuating limnological trajectories. For example, in eastern Canada, a warmer and moister climate in the mid-Holocene enabled the northward movement of boreal forest into tundra. As a result, the build-up of organic-rich soils enhanced both DOC and nutrient inputs into regional lakes (Pienitz *et al.* 1999). As the climate cooled and tree line moved south, productivity and DOC concentrations declined. Similar patterns of change have been observed in the Eurasian Arctic (Jones *et al.* 2011). In both of these studies, major limnological change was associated with climate-driven impacts mediated through the catchment.

In arctic lakes of West Greenland, the long-term limnological trajectory is of gradual change along an axis from high pH to lower values over time, but with varied timing and rate (Perren *et al.* 2012). This common trajectory yet variable rate among sites suggests the major role of time-dependent catchment processes, such as the long-term leaching of base cations and increased transfer of organic acids, in affecting changes in ecosystem state (Table 1).

Boyle (2007) evaluated the relative roles of abiotic versus biotic processes as drivers of long-term lake acidification by modeling the concentration of mineral phases in runoff during the weathering of granite. Because the time-dependent loss of apatite via chemical weathering effectively tracks the magnitude and rate of long-term acidification reconstructed in multiple paleoecological studies from boreal latitudes of Europe and North America, Boyle concluded that abiotic processes (weathering) are more important than vegetation impacts on DOC and soil development in regulating early interglacial acidification. The model predicts that changes in mean annual runoff and soil thickness have significant impacts on long-term leaching rates, whereas the impact of DOC concentration is limited.

In some regions of the Canadian Arctic, long-term lake acidification is not caused by the loss of basecations over time, based on the lack of correlation between diatom-inferred pH and sediment geochemical measurements (Wilson *et al.* 2012). In these settings long-term acid–base chemistry is apparently climate driven, such that the higher productivity and CO_2 uptake associated with warm intervals increased lake pH, whereas during cold periods reduced productivity and reduced evasion of pH to the atmosphere because of ice cover caused pH to decline (Michelutti *et al.* 2007; Wolfe 2002). In this setting, long-term pH decline during the Holocene is attributed to Neoglacial cooling rather than to catchment processes. These sites are all in areas characterized by cold-based and nonerosive glaciation, which preserved relict landscapes through several glacial cycles and produced surfaces with little accumulation of till. As a result the role of soil development and vegetation change in driving long-term pH changes is limited (Wilson *et al.* 2012).

Trajectories of change in nutrient status and productivity following deglaciation

A dominant influence of catchment successional processes and vegetation change on lake ecosystems is evident during the first few millennia following deglaciation throughout temperate and high-latitude sites in the Northern Hemisphere. In the Arctic, benthic algal communities dominated following deglaciation, likely developed as a result of low nutrient concentrations associated with unstable and weakly developed catchment soils (Bigler *et al.* 2002, 2003; Birks *et al.* 2000; Bradshaw *et al.* 2000; Perren *et al.* 2012). In sub-arctic lakes of Sweden and Norway during the late-glacial period (Bigler *et al.* 2002, 2003; Birks *et al.* 2000; Bradshaw *et al.* 2000), increased benthic diatom diversity and fluctuations between benthic and planktic diatoms are associated with changes in nutrient input from the catchment and clastic load rather than directly with fluctuations in temperature or precipitation. Strong catchment influences continue into the early and mid-Holocene at most sites, but the magnitude, nature, and rate of influence are strongly influenced by catchment geology and elevation.

In temperate latitudes in regions with moderate to high precipitation in the period following deglaciation, catchment processes also are a primary control on lake ecosystem state immediately following lake formation. Diatom assemblages and pigment data from various temperate sites in North America and Europe indicate that primary production was low in the first centuries to millennia following deglaciation, but as the catchment stabilized and during the initial phases of weathering and soil formation, planktic floras developed and production increased, which suggests higher nutrient concentrations in the water column (Bennett *et al.* 2001; Florin 1970; Haworth 1976; Laird *et al.* 1998; Lotter 2001; Norton *et al.* 2011). The rate of change in nutrient concentration and primary production is likely highly variable among sites, dependent on site-specific differences in geology and vegetation history (Fritz *et al.* 2004) (Figure 2). Unfortunately the temporal resolution of most late-Glacial stratigraphic records is not sufficiently high to clearly establish rates of change.

Evaluating the role of nitrogen limitation in the early ontogeny of boreal and arctic ecosystems is complicated by in-lake successional processes, because nitrogen-fixing cyanobacteria can dominate in early stages after deglaciation, possibly because of their preference for alkaline conditions and their ability to use HCO_3 as well as fix N_2 directly (Reynolds 2006). This is suggested in pigment records from lakes in SW Greenland, where cyanobacterial pigments are dominant immediately after lake formation and subsequently decline, perhaps because the net nitrogen subsidy from land increased in-lake nitrogen availability (Anderson *et al.* 2008; McGowan *et al.* 2008). It is unclear whether these pigments are associated with picophytoplankton or benthic cyanobacterial mats. In many arctic lakes, *Nostoc* colonies are common in the littoral zone, and presumably their presence (and decay) increases nitrogen availability locally within the benthos. One likely beneficiary of this locally fixed nitrogen is benthic diatoms, which are abundant in arctic and boreal lakes; primary production in Arctic lakes is commonly concentrated in the littoral zone (Vadeboncoeur *et al.* 2003).

Although long-term Holocene oligotrophication is predicted in theoretical terms by declining apatite abundance during weathering (Boyle 2007), relatively few studies clearly demonstrate declining nutrient concentrations over time independent of long-term acidification. At a site in European Russia, maximum organic carbon content of the sediments (a gross measure of system productivity) occurred in the oldest sediments, yet diatom accumulation rates were uniform throughout the early to mid Holocene and did not decline until around 3,000 year BP, when catchment vegetation switched from forest to tundra and planktonic diatoms increased (Jones *et al.* 2011). In the early history of a site inSWGreenland, both planktic diatoms and cyanobacterial pigmentswere abundant suggesting enhanced productivity, and subsequently declined. Yet planktic diatoms return intermittently later, which suggests other controls on planktic production (Anderson *et al.* 2008). As suggested above, cyanobacterial dominance during early lake development may reflect high pH and inorganic forms as much as nutrient concentrations. In Glacier Bay (Alaska, USA) temporal trends in diatom production follow changes in catchment derived N inputs associated with nitrogen-fixing vegetation rather than long-term trends driven by weathering (Engstrom and Fritz 2006; Fritz *et al.* 2004).

Because of the high dry-mass accumulation rates during the early phases of catchment ontogeny (due to slope instability, low vegetation cover, etc.) and associated dilution effects on the sediment matrix, organicmatter, carbon content or biogenic silica should be presented as accumulation rates. For example, Anderson *et al.* (2012) compared C accumulation rates for four lakes in Greenland; at none of the sites were C accumulation rates at their maximumduring the earliest periods of lake development but instead occurred later due a range of to climate-catchment mediated processes. A more systematic assessment of lake productivity trends (using biogenic silica and/or carbon accumulation rates together with pigment analyses) over a range of sites is required to evaluate more critically the concept of long-term oligotrophication, as opposed to qualitative inferences from diatom assemblages where thecommunity changes can be interpreted in a number of different ways.

Direct climate versus catchment influences in affecting planktic diatom floras

Both direct climate influences and catchment-mediated processes have been posited to play a role in the development of planktic diatom floras in arctic and alpine lakes. A common feature in arctic lake records of moderate depth is a Holocene expansion of planktic diatoms, particularly in the genus *Cyclotella*. This expansion has been related to direct climate impacts on lake thermal structure and to altered nutrient inputs, particularly of nitrogen. In a large lake below tree line in Sweden, for example, the expansion of a *Cyclotella* flora during the early Holocene is attributed to both catchment-controlled nutrient inputs, as well as climate conditions suitable for the development of summer stratification (Bigler *et al.* 2002). *Cyclotella comensis* declined with the expansion of *Pinus* in the catchment around 7500 cal yr BP as the *C. rossii* complex increased, and *Cyclotella glomerata* (=*Discotella pseudostelligera* complex) was periodically important (>20%). In a lake in the southern Yukon (Chakraborty *et al.* 2010), the replacement of *Cyclotella ocellata* by *Cyclotella pseudostelligera* around 7000 cal yr BP is attributed to insolation-driven changes in thermal structure.

In the low arctic lakes of West Greenland, planktic diatoms in the genus *Cyclotella* replace pioneering benthic taxa in the early Holocene in coastal areas but in the late-Holocene period in lakes further inland, an area that was deglaciated much later (Perren *et al.* 2012). At the coastal site (SS49), the transition from benthic to planktic taxa could be a response to increased in-lake nutrient concentrations associated with weathering and soil development driven by Holocene climate warming, as well as to the development of a stratified water column. A possible role for greater in-lake nitrogen availability associated with the build of the ecosystem nitrogen pool is suggested by the close relationship between the abundance of *C. pseudostelligera* and %TN in the lake sediments (Figure 3). Sedimentary nitrogen is reactive and interpreting it directly in terms of nutrient availability has to be done with care. Likewise, it is not clear whether or not lake thermal structure influenced planktic diatom species composition; in any case, significant roles for nutrients and for stratification are not mutually exclusive. In the inland sites, the late-Holocene expansion of *Cyclotella* species cannot be attributed to warming, because it occurs at the onset of cooler and moister regional climate (Aebly and Fritz 2009); potential explanations include changes in nutrient loading either through direct climate impacts on water-column mixing or via indirect climate impacts on catchment-driven nutrient loading. At SS16, for example, the diatom and macrofossil records suggest a benthic-dominated lake in the early to mid Holocene (Heggen *et al.* 2010; Perren *et al.* 2012), possibly because nutrients were trapped or recycled in the littoral zone and were insufficient to support planktic diatoms. From ~4,000 cal year BP, with onset of Neoglacial cooling, however, diatom productivity increased dramatically, *Cyclotella* species expanded, macrophyte community structure changed with the reduced abundance of *Myriophyllum* and *Potamogeton* spp. (Fig 3), and shrub tundra started to contract (Heggen *et al.* 2010). The nitrogen content of glaciers is now known to be considerable (Hodson *et al.* 2008), and the extent to which N within the glacial system is transferred to local terrestrial and aquatic ecosystems remains unclear. None-the-less, at the time of *Cyclotella* expansion, eolian activity increased dramatically in inland areas proximal to the ice sheet (Willemse *et al.* 2003), with widespread loess deposition across the landscape, derived from glacial outwash. Dust can contain high concentrations of minerals and nutrients (Neff *et al.* 2008; Psenner 1999). Thus, increased nutrient (N) loading via dust may have enhanced lake productivity and fostered *Cyclotella* expansion. At another inland lake in West Greenland (SS2), *Cyclotella pseudostelligera* is present, albeit intermittently, from the mid-Holocene onward (Anderson *et al.* 2008), and a similar pattern occurs at Raffles Lake on east Greenland. Both may be associated with external nutrient input and Neoglacial cooling (Cremer *et al.* 2001).

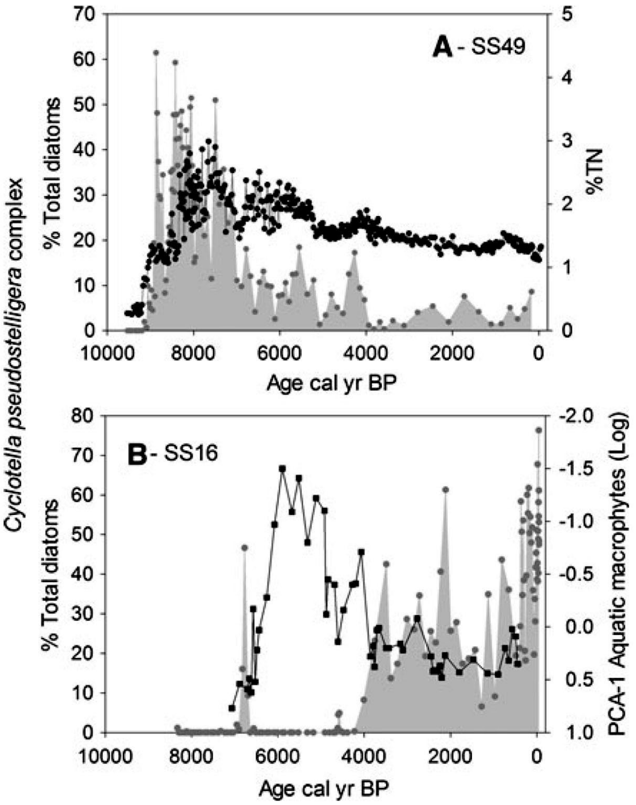

Figure 3. Core trajectories for two lakes in West Greenland: **a)** the relationship between total nitrogen content and *Cyclotella* relative abundance in a coastal lake (SS49) (original data from Perren *et al.* 2012); **b)** the inverse relationship between changing ecological structure of the macrophyte community as PCA axis 1 (which reflects the changing abundance of *Myriophyllum* and *Potamogeton* spp) and *Cyclotella* percentage in an inland lake (SS16) (original data from Perren *et al.* 2012; Heggen *et al.* 2010). *Cyclotella* is the *grey shade* in both plots.

An expansion of *Cyclotella* species also has been observed in multiple arctic and alpine lake records spanning the last century or so and has been variably attributed to the impacts of warming on lake mixing depth and to enhanced atmospheric nitrogen deposition. For example, Rühland *et al.* (2008) rejected nutrient dynamics as a mechanism for the widespread recent increase in small *Cyclotella* species in arctic and alpine lakes. However, Saros *et al.* (2012), using a combination of experimental and paleolimnological approaches, suggest that a dynamic interplay of light, thermal stratification, and nitrogen availability affect *Cyclotella* dominance in several alpine lakes in North America. Small *Cyclotella* assemblages are an important component of many lakes located close to the ice margin in Greenland today (Perren *et al.* 2009), a climatically cool area but with considerable loess deposition associated with strong katabatic winds. As we review above, paleolimnological evidence suggests that in many systems *Cyclotella* assemblages have been present for centuries, sometimes supported by a combination of external nutrient supply and mixing regimes. This long-term perspective suggests that both catchment mediated processes, such as DOM export and changing catchment-driven nutrient loading, as well as direct climate impacts on thermal and hydrological budgets may affect *Cyclotella* abundance over a range of timescales.

Strong climate-driven influences on lacustrine ecosystems

Changes in nutrient delivery to lakes associated with early ecosystem succession play a dominant role in most lakes in glaciated terranes, but the subsequent trajectory of ecosystem change in temperate latitudes seems to vary dependent on climate, elevation, and catchment geology. In alpine regions with moderate to high base status and where paludification is uncommon, climate may play a more substantive role in limnological change. In the Alps, for example, the date of the onset of isothermal mixing in the autumn is correlated with changes in diatom assemblage composition in a contemporary calibration data set, and a transfer function derived from these data has been successfully applied to reconstruct past climate variation from lacustrine diatom assemblages (Schmidt *et al.* 2004). In another hardwater lake on the Swiss Plateau, the development of a forested landscape in the early Holocene fostered meromixis and the stable dominance of a *Cyclotella* flora into the mid-Holocene (Lotter 2001). Yet within this interval were periods when enhanced water column mixing or changes in lake level were the primary influence on higher frequency changes in species composition. Similarly, in many alpine lakes in western North America, changes in the strength and duration of water-column mixing are the primary control on lacustrine nutrient concentrations and on diatom species assemblages (Chakraborty *et al.* 2010, Gavin *et al.* 2011; Whitlock *et al.* 2012).

In sub-humid to semi-arid areas of the mid-latitudes (precipitation <~500 mm year^{-1}), even in mountainous terrane, climate is the dominant impact on lake ecosystem structure and function. Thus, changes in ecosystem state are most commonly associated with changes in effective moisture (precipitation minus evaporation) and its impacts on lake level and ionic concentration (Table 1) (Fritz *et al.* 2010). In parts of northwestern North America, for example, even the pioneering stages of lake development were under the strong influence of climate. High summer insolation in the late-Glacial period promoted rapid wastage of the continental ice sheets, and the lakes formed by the retreating ice often were dry or shallow and sometimes saline, because of high growing season temperature and evaporation (Fritz *et al.* 2000; Stone and Fritz 2006). In both forested and grassland sub-humid to semi-arid areas of the North American mid-continent, most fluctuations in diatom community structure are clearly driven by changes in lake depth and ionic concentration (Bennett *et al.* 2001; Fritz *et al.* 2010; Stone and Fritz 2006). Although both depth and ionic concentration may affect diatoms via their influence on nutrient availability (Saros and Fritz 2000), the changes in biogeochemical cycling are a result of direct climate impacts on the lake environment rather than climate effects that are mediated through catchment processes.

Conclusions

Catchment processes are universally important in the first centuries to millennia of limnological development as the landscape stabilizes and as weathering and early soil development generate higher biogeochemical fluxes from the catchment to the lake. The increased nutrient flux drives increased algal production, and, in lakes where depth and climate are suitable for the development of plankton, shifts from benthicdominated to planktic floras occur.

Subsequently the relative roles of catchment processes in mediating limnological change are a function of catchment geology, elevation, vegetation, and climate setting (Figure 1). In most parts of the Arctic and in boreal regions, pH decline is the dominant trajectory of change. This is driven primary by catchment processes in base-poor terranes or in climate settings that favor the build-up of organic-rich soils and subsequent podzolization. However, in some parts of the Canadian Arctic, pH decline over time is apparently mediated by climate impacts on productivity and lake-atmosphere CO_2 exchange, because the accumulation of surface tills and subsequent soil development is limited. In some arctic and alpine regions with moderate concentrations of base cations, planktic assemblages, often dominated by *Cyclotella* species, ultimately develop and persist for millennia, supported by a combination of external nutrient supply and patterns of thermal stratification. Long-termacidification driven by changes in vegetation and soils also is common in temperate latitudes with cool humid climate and base-poor substrates. But in humid regions on soils with moderate to high base concentrations, changes in nutrients and light are the most common drivers of changes in diatom species composition, associated primarily with the strength and duration of water-column mixing and secondarily with catchment processes that affect DOC and nutrient export. Climate impacts on aquatic structure and function are most pronounced in semi-arid and arid regions where lakes undergo pronounced shifts in lakelevel and in ionic concentration.

All geographic areas where long-term changes in lacustrine ecosystem state have been reconstructed from multiple sites show considerable variation among sites (Figure 2). In some cases, such as Glacier Bay, Alaska, the differences are attributed to variability in the early plant species that colonized specific regions and their impact on catchment nitrogen cycling (Fritz *et al.* 2004). In sub-alpine areas of northern Sweden, differences in pattern of change are correlated with geologic differences, specifically the mineralogy of parent bedrock (Bigler *et al.* 2002). In an Arctic transect, the chemistry and hence biotic assemblages in the lakes in the semi-arid region adjacent to the Greenland ice sheet are influenced by alkalinity changes and eolian activity during dry intervals, whereas lakes in humid coastal areas do not have this influence (Perren *et al.* 2012). The role of catchment processes in producing regional heterogeneity in paleolimnological studies indicates the need for more widespread use of multiple sites (i.e. regionally replicated studies) when using lake sediment records for reconstructing past climate (Fritz 2008; Kaufman 2012). The prominent role of localscale processes in mediating the impact of climate on lacustrine biotic communities and lakewater chemistry serves to emphasize the critical role of ecosystem processes in affecting lake structure and function (cf Lantz *et al.* 2010). Lake sediments from temperate, boreal, and arctic landscapes affected by glaciation undoubtedly reflect climate (Figure 1), but a greater understanding of the catchment filter and in-lake processes will enhance attempts to extract the climate signal from paleolimnological records.

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