

Climate-driven regime shifts in the biological communities of arctic lakes

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Communicated by David W. Schindler, University of Alberta, Edmonton, Canada, January 21, 2005 (received for review October 14, 2004)

Fifty-five paleolimnological records from lakes in the circumpolar Arctic reveal widespread species changes and ecological reorganizations in algae and invertebrate communities since approximately *anno Domini* 1850. The remoteness of these sites, coupled with the ecological characteristics of taxa involved, indicate that changes are primarily driven by climate warming through lengthening of the summer growing season and related limnological changes. The widespread distribution and similar character of these changes indicate that the opportunity to study arctic ecosystems unaffected by human influences may have disappeared.

climate change | paleolimnology | Anthropocene | warming | indicators

Polar amplification of anthropogenic warming is consistently predicted by general circulation models, largely because of positive feedback mechanisms involving cryospheric processes (1). This heightened climatic sensitivity is supported by recent accelerations of glacier retreat (2), sea-ice thinning (3), and permafrost degradation (4). Although the instrumental record of temperature across the Arctic is incomplete and generally of short duration, warming appears to be concentrated in the decades between approximately *anno Domini* 1915–1940 and approximately *anno Domini* 1965–2000 (5). However, proxy data indicate that much of the Arctic began to warm considerably earlier, in the mid-19th century (6). Such generalized trends, however, are neither spatially nor temporally uniform (7), because of regional differences in continentality, ocean heat transport, glacier and sea ice distribution, topography, and vegetation. For example, whereas much of Beringia and central Siberia have warmed $>0.5^{\circ}\text{C}$ in the last 50 years, there has been little change or even cooling (7) in parts of the North Atlantic sector. Nonetheless, all subregions of the Arctic are considered highly ecologically sensitive, implying that anthropogenic warming will test ecosystem resilience and potentially induce dramatic shifts in community composition.

In the absence of long-term climatic and environmental monitoring data, proxy data from the sediments of lakes and ponds, which are ubiquitous features of most arctic landscapes, can be used to provide a long-term perspective of environmental change (8, 9). Siliceous algal remains, specifically the valves of diatoms (Bacillariophyceae) and the stomatocysts and scales of chrysophytes (Chrysophyceae and Synurophyceae), as well as chitinous invertebrate remains (Chironomidae, Diptera and Cladocera, Crustacea), are the primary paleoindicators in lake sediments that provide reliable records of changes in water quality, habitat, and catchment processes (10). Here, we synthesize a large number of paleolimnological records from arctic lakes and ponds, providing a circumpolar assessment of recent ecological changes. These data show that

striking and often unprecedented ecological changes have occurred within the last ≈ 150 years, following several millennia of relatively stable communities.

High-latitude lakes are extremely responsive to climate change, because even slight warming results in decreased ice cover and, hence, longer growing seasons for algae and other organisms (9, 11). Lake ice has a profound significance in these ecosystems, where the coldest sites may retain ice cover throughout the summer, with only a shallow moat of open water forming for weeks each year. Decreased ice cover is linked to higher primary production and taxonomic shifts in both algae and invertebrates as new habitats become increasingly available and nutrients and other limnological variables change (9). In many cases, biological responses are accelerated when lakes and ponds pass through climate-related thresholds associated with snow and ice cover (9), habitat availability (12), and thermal stratification (13, 14). Each of these interrelated thresholds is ultimately linked with length of the ice-free season, itself directly modulated by climate. Snow and ice appear to exert increasingly dominant roles with latitude, whereas the onset and duration of thermal stratification becomes more important in subarctic lakes (13, 14). As thresholds are exceeded, aquatic community composition turnover is predicted to be high and pronounced, and regime shifts (15, 16) toward new ecological states may occur.

Methods

Sediments were obtained with gravity corers specifically designed to preserve the mud–water interface, and high-temporal resolution was attained by extrusion in continuous 0.25- to 1.0-cm increments (17). Geochronology is based primarily on ^{210}Pb dating and associated age–depth modeling (18). The biological indicators were processed and analyzed by using standard techniques for diatoms, chrysophytes, cladocerans, and chironomids (19, 20).

Detrended canonical correspondence analysis (DCCA) (21) was used to develop quantitative estimates of compositional turnover as beta-diversity, scaled in SD units (22). DCCA is the constrained form of detrended correspondence analysis (DCA) (23), an ordination technique with attractive mathematical properties (24) and ecological robustness (25). Compared with other ordination procedures, DCA (and DCCA) have the advantage of scaling sample

Abbreviation: DCCA, detrended canonical correspondence analysis.

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Table 1. Locations, proxies, and beta-diversity estimates since approximately *anno Domini* 1850 for the 55 paleolimnological records comprising our circumpolar (circ.) network

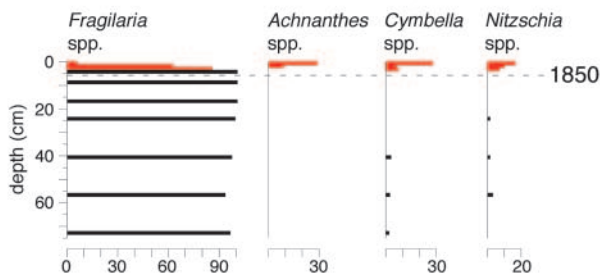
Region	Site name	Latitude	Longitude	Proxy	B.D. for circ. lakes, SD units	B.D. for circ. lake/ B.D. for ref. lakes
Ellesmere Island	Self Pond	82°27' N	62°02' W	Diatoms	1.35	1.38
	Sawtooth Lake	79°20' N	81°51' W	Diatoms	1.59	1.62
	Camp Pond	78°37' N	74°40' W	Diatoms	0.75	0.77
	Camp Pond	78°37' N	74°40' W	Chironomids	0.70	1.02
	Col Pond	78°36' N	74°40' W	Diatoms	2.84	2.90
	Col Pond	78°36' N	74°40' W	Chironomids	1.47	2.16
	Elison Lake	78°36' N	74°41' W	Diatoms	1.16	1.18
	Elison Lake	78°36' N	74°41' W	Chironomids	1.17	1.72
	Rock Basin	78°30' N	76°44' W	Diatoms	1.29	1.32
	Svalbard	Arresjøen	79°40' N	10°51' E	Diatoms	1.07
Birgervatnet		79°48' N	11°37' E	Diatoms	1.40	1.43
Scurvy Pond		79°44' N	12°18' E	Diatoms	0.89	0.91
Ossian Sarsfjellet		78°57' N	12°28' E	Chironomids	1.22	1.79
Ytertjørna		78°13' N	12°56' E	Chironomids	0.87	1.28
Ytertjørna		78°13' N	12°56' E	Diatoms	1.15	1.17
Tenndammen		78°06' N	15°02' E	Chironomids	0.66	0.97
Isachsen I-F		78°48' N	102°26' W	Diatoms	1.35	1.38
Ellef Ringnes Island	Isachsen I-O	78°46' N	103°46' W	Diatoms	1.21	1.23
	Melville Island	Melville MV-AT	75°19' N	111°25' W	Diatoms	1.21
Baffin Island	CF-11	70°28' N	68°40' W	Diatoms	1.20	1.22
	CF-10	70°26' N	69°07' W	Diatoms	0.87	0.89
Finnish Lapland	Lake 222	69°27' N	29°07' E	Diatoms	0.97	0.99
	Somas	69°16' N	21°31' E	Cladocera	0.41	n/a
	Stuoramohkki	69°14' N	21°04' E	Diatoms	1.07	1.09
	Toskaljärvi	69°11' N	21°27' E	Diatoms	1.15	1.17
	Masehjärvi	69°05' N	20°58' E	Diatoms	0.90	0.92
	Saanajärvi	69°05' N	20°52' E	Diatoms	1.19	1.21
	Saanajärvi	69°05' N	20°52' E	Cladocera	0.98	n/a
	Tsahkaljavri	69°01' N	20°55' E	Diatoms	1.23	1.26
	Sarvijärvi	68°06' N	24°06' E	Diatoms	0.89	0.91
	Tsuolbmajavri	68°41' N	22°03' E	Diatoms	0.83	0.85
	Vallijärvi	68°41' N	21°35' E	Cladocera	0.92	n/a
	Polar Urals	Vanuk-ty	68°00' N	62° 45' E	Diatoms	1.49
F8-4		67°53' N	59°40' E	Diatoms	1.18	1.20
Mitrofanovskoe		67°51' N	58°59' E	Diatoms	1.23	1.26
Mitrofanovskoe		67°51' N	58°59' E	Chironomids	1.08	1.59
Kola Peninsula	Chuna	67°57' N	32°29' E	Diatoms	1.08	1.10
	Northwest Territories	Slipper Lake	64°37' N	110°50' W	Diatoms	1.25
TK-20		64°09' N	107°49' W	Diatoms	1.09	1.11
Northern Québec	Airport Lake	62°10' N	75°39' W	Diatoms	0.96	0.98
	Tasikutaq	62°09' N	75°43' W	Diatoms	0.88	0.90
	Qaanganiittuq	62°07' N	75°36' W	Diatoms	0.88	0.90
	K2	58°44' N	65°56' W	Diatoms	1.12	1.14
	K2	58°44' N	65°56' W	Chironomids	0.88	1.29
	LR	58°19' N	65°38' W	Diatoms	1.01	1.03
	LM 1	58°17' N	65°40' W	Diatoms	0.83	0.85
	PC 1	57°34' N	65°31' W	Diatoms	0.90	0.92
	PC 2	57°28' N	65°21' W	Diatoms	1.05	1.07
	PC 3	57°36' N	65°24' W	Diatoms	0.74	0.76
	PC 4	58°30' N	65°45' W	Diatoms	0.84	0.86
	PC 5	58°43' N	65°57' W	Diatoms	0.70	0.71
Northern Labrador	Saglek 2	58°28' N	62°39' W	Diatoms	1.10	1.12
	Saglek 2	58°28' N	62°39' W	Chrysophytes	1.20	1.71
	Saglek 15	58°21' N	62°42' W	Diatoms	0.79	0.81
	Saglek 15	58°21' N	62°42' W	Chrysophytes	1.02	1.46

Sites are arranged latitudinally by region. Beta-diversity (B.D.; species turnover) represents compositional changes within each biostratigraphic profile. Beta-diversity is also shown normalized to the average reference values (ref. lakes; for minimally impacted temperate lakes for the corresponding proxy).

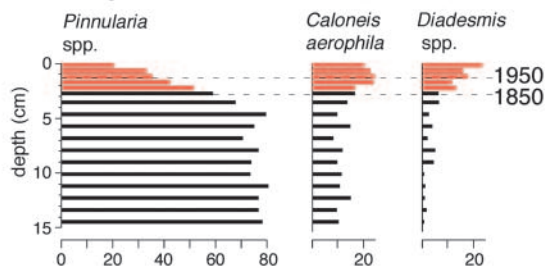
scores in SD or turnover units of beta-diversity. Differences in down-core DCCA sample scores provide an estimate of the amount of compositional change between samples along environmental or temporal gradients. Because the samples in each sequence are in a known temporal order, which is fundamental to the observed biostratigraphic patterns, we constrained the DCAs by using sample ages (based on ²¹⁰Pb dating and associated age-depth modeling) as the sole constraint in DCCA to estimate the total amount of

compositional change in each biostratigraphic record within the last ≈150 years (Table 1). In this way, all of the available stratigraphic data from the last ≈150 years of sediment accumulation were used to estimate the amount of species turnover. The greater the amount of species turnover in the last 150 years, the greater the increase in beta-diversity. All data sets were analyzed identically, by using square-root transformations of species-relative frequency data (to stabilize variances), no down-weighting of rare taxa, detrending by

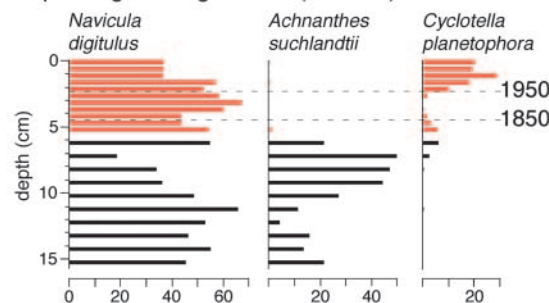
A Ellesmere Island - Col Pond (2.84 SD)



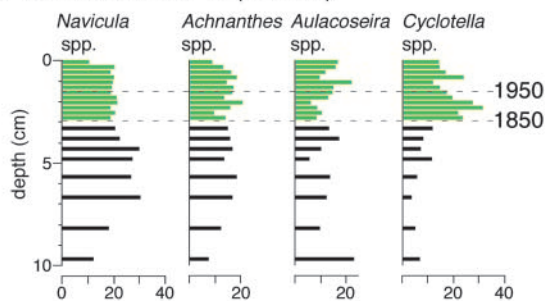
B Ellef Ringnes Island - Isachsen F (1.35 SD)



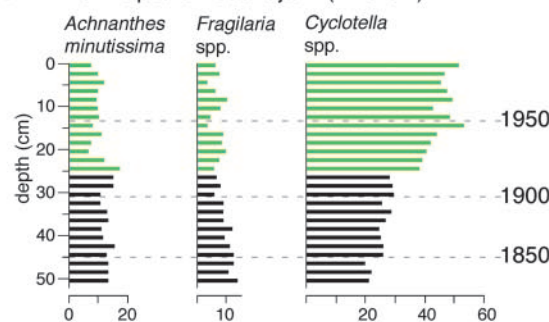
F Spitsbergen - Birgervatnet (1.40 SD)



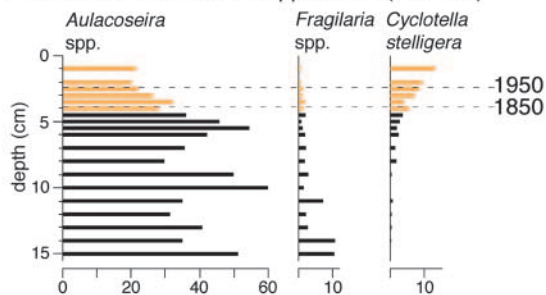
C Baffin Island - CF 11 (1.20 SD)



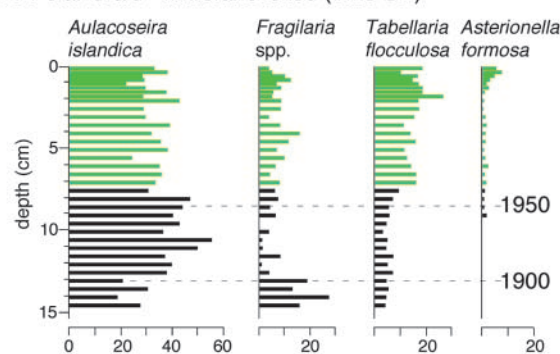
G Finnish Lapland - Saanajärvi (1.19 SD)



D Northwest Territories - Slipper Lake (1.25 SD)



H Polar Urals - Mitrofanovskoe (1.23 SD)



E Northern Quebec - PC4 (0.84 SD)

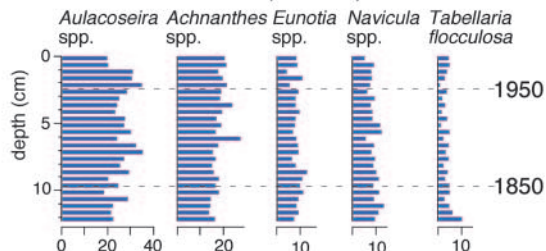


Fig. 1. Representative diatom profiles from the circumpolar Arctic showing the character and timing of recent assemblage shifts. Site locations (A–H) are shown on the map. Chronologies are based primarily on constant rate of supply modeling of excess sediment ^{210}Pb activities (10). Beta-diversity values (in SD units) (Table 1) are shown in bold next to each site's name. Colored intervals demarcate major assemblage changes and are coded according to beta-diversity as in Fig. 2: blue, 0–1.0 SD; green, 1.0–1.24 SD; orange, 1.24–1.5 SD; red, >1.5 SD. All data are expressed as relative frequency percentages of individual or collated diatom taxa based on counts of >400 valves per sample.

segments, and nonlinear rescaling. We included biostratigraphic records that had an adequate geochronology and a sediment sequence spanning at least ≈ 150 years. All DCCA analyses were conducted by using CANOCO 4.0 or CANOCO 4.5 (26).

Results and Discussion

A subset of representative profiles from a series of 42 dated diatom stratigraphies (Table 1) is presented in Fig. 1. These sites range from small polar ponds to thermally stratified subarctic lakes and encompass a broad spectrum of water chemistry and lake morphology. From our northernmost sites in the Canadian High Arctic (Fig. 1A and B), we observed abrupt shifts toward diatom taxa characteristic of littoral habitats and mossy substrates, consistent with longer growing seasons and habitat expansions under warming conditions (12). Deeper lakes from Baffin Island (Fig. 1C), Svalbard (Fig. 1F), northern Fennoscandia (Fig. 1G), the western subarctic region of North America (Fig. 1D), and on Ellesmere Island (27), record pronounced increases in planktonic diatoms belonging mainly to the genus *Cyclotella*. These changes occur at the expense of benthic genera, including *Fragilaria* and *Achnanthes*, as well as tychoplanktonic (i.e., occurring in benthic and planktonic habitats) *Aulacoseira* species. The recent success of *Cyclotella* is linked to reduced ice cover and/or enhanced thermal stratification (13, 14). Small, benthic *Fragilaria* taxa, on the other hand, are often associated with cold conditions and extensive ice cover in arctic and alpine regions (9, 28). Regional trends from an additional 50 lakes in central subarctic Canada, where the greatest climate warming in North America has been documented (14), confirm that recent shifts in diatom life strategy from benthic to planktonic (e.g.,

Fragilaria to *Cyclotella*) are widespread. In sites that lack *Cyclotella*, other planktonic taxa, such as *Tabellaria* and *Asterionella*, show increases (Fig. 1H). In contrast, for regions where instrumental climate records indicate little to no warming (7, 29), diatom profiles show little change (Fig. 1E). Thus, across much of the Arctic and other cold, nutrient-poor regions, both shallow isothermal ponds and deeper lakes record 19th to 20th century taxonomic shifts consistent with expected responses of diatoms to climate warming (9, 12–14, 28). In contrast, no directional changes in diatom assemblages are observed in regions where temperature increases are not observed, including Labrador and northern Québec (30–32), although instrumental records for this region have often only been collected since ≈ 1940 .

Evidence that changes in diatom communities are representative of ecosystem-scale processes can be garnered from analyses of additional paleolimnological indicators. Zoological remains provide strong support that limnological responses to recent climate change have been transmitted to higher trophic levels. Chironomid (Diptera) head capsules in cores also analyzed for diatoms (12) reveal marked and synchronous increases in both concentrations and assemblage diversity (Table 1). For example, at Elison Lake (Ellesmere Island), *Corynoneura/Thienemanniella* have increasingly dominated chironomid communities in recent sediments, likely because these taxa are specialized for scraping algae attached to lake substrates, which have increased with recent warming (12). On Svalbard, cores from two lakes also record marked shifts in chironomid assemblages over the last ≈ 100 years, reflecting increased lake productivity and other limnological responses to recent warming (33, 34). Cladoceran microfossils in cores from Finnish

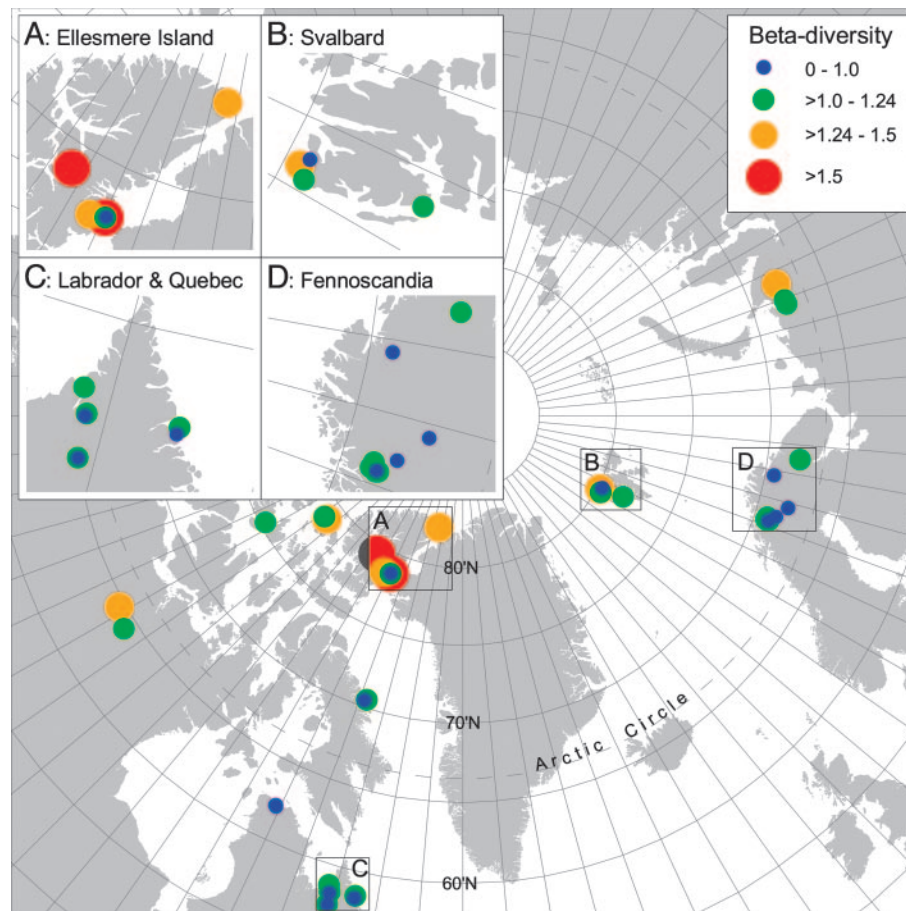


Fig. 2. Mapped increases in beta-diversity in the last ≈ 150 years (expressed in SD units as estimated by detrended canonical correspondence analysis) for the 42 diatom proxy records listed in Table 1.

Lapland reveal recent changes toward communities dominated by planktonic species, another expected response to climate warming (35, 36). The biostratigraphic shifts that we have documented cannot be explained by recent colonization events driven by non-climatic factors because the taxa that have undergone recent expansions were present, albeit in low relative and absolute numbers, in sediments long predating the major biostratigraphic changes. This early presence verifies that the biological changes themselves are not the result of newly colonized taxa; rather, they represent ecological responses to environmental change. Collectively, these results show that large-scale ecological reorganizations, or regime shifts, have occurred in many arctic lakes and that these changes are witnessed at several trophic levels across broad taxonomic groups.

To simplify the presentation of trends in 55 biostratigraphic profiles, we illustrate (Fig. 2 and Table 1) estimates of total species turnover as beta-diversity, scaled in SD units and obtained from DCCA (21). Hence, each of these values summarizes compositional change within the entire biostratigraphic series available since ≈ 1850 .

From these analyses, ranges of beta-diversity are 0.70–2.84 SD for the 42 diatom profiles, 0.66–1.47 SD for the eight chironomid profiles, 0.41–0.98 SD for the three cladoceran profiles, and 1.02–1.20 SD for the two chrysophyte stomatocyst profiles (Table 1). These values have been mapped to examine spatial variability of the results (Fig. 2) and were plotted zonally (Fig. 3). A critical question in interpreting these results is how circumpolar lakes compare objectively with temperate lakes that lack point-source disturbances (i.e., reference lakes). With this objective, we estimated beta-diversity by using identical protocols for 14 diatom records from nonarctic, relatively unimpacted (i.e., not affected by local watershed-scale disturbances) lakes in Canada, Scotland, and Ireland (H.J.B.B., unpublished data) with the assumption that the compositional changes and, hence, the beta-diversity values in arctic sites should be greater than those in the locally unimpacted temperate sites because of amplification of climate warming in northern high-latitude regions. The beta-diversity values in these temperate lakes yielded a range of 0.72–1.39 SD (mean, 0.98 SD; median, 1.02 SD). Thus, diatom beta-diversities at >1 SD in circumpolar lakes indicate greater taxonomic change relative to a population of undisturbed temperate lakes. For comparison, diatom beta-diversities from 14 strongly acidified lakes in Norway, Sweden, and the United Kingdom (37) range from 1.48 to 2.27 SD [mean, 1.98 SD; median, 1.89 SD (H.J.B.B., unpublished data)]. We further estimated reference beta-diversities of 0.68 SD for chironomids and 0.70 SD for chrysophyte stomatocysts by using profiles from north temperate lakes in the Experimental Lakes Area, Ontario, Canada. (K. E. Duff and D. W. Schindler, personal communication). At present, we lack reference data for cladocerans.

Beta-diversity changes exceeding mean reference values have occurred in 28 of 44 arctic lakes for diatoms and chrysophytes and 7 of 8 lakes for chironomids (Table 1). Thus, striking community shifts have occurred during the last ≈ 150 years in the majority (67%) of investigated lakes, and these changes are expressed in both algal and invertebrate assemblages. Changes are especially pronounced in areas believed to have warmed the most (e.g., the Canadian High Arctic), whereas the smallest changes occurred in regions that have experienced very little or no recent warming (e.g., Labrador and northern Québec). For example, when beta-diversity from our circumpolar network is expressed relative to the reference value for the corresponding fossil group (Table 1), 81% of sites north of the treeline zone have increased more than the reference lakes, whereas 58% of subarctic sites have exceeded reference beta-diversity values. Trends in the latitudinal distribution of beta-diversity match the available instrumental climate record of recent warming (Fig. 3).

Local topographic, morphometric, and geologic factors also influence the nature and magnitude of limnological responses to

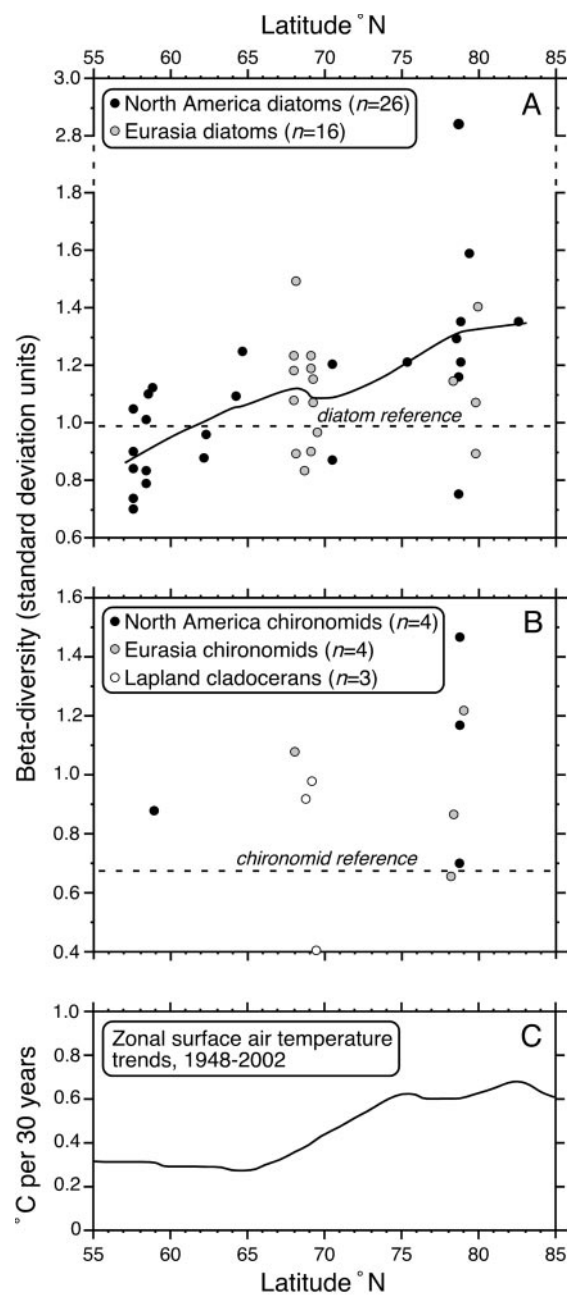


Fig. 3. Trends in beta-diversity of aquatic organisms and surface air temperature across northern latitudes. Latitudinal distribution of increases in beta-diversity values for diatom (A) and invertebrate (B) fossil groups. Horizontal dashed lines indicate mean values obtained from temperate reference lakes. The fitted line in A was obtained by using Loess smoothing with a span of 0.35. (C) Latitudinal warming trend based on zonally averaged monthly mean surface air temperatures from the National Centers for Environmental Prediction/National Center for Atmospheric Research reanalysis for the 1948–2002 interval (5), which clearly illustrates polar amplification of climate warming.

warming. For example, certain sites [e.g., some shallow ponds (12)] produce relatively low beta-diversity values, despite being situated in regions where adjacent sites have changed more markedly (Fig. 2 and Table 1). This finding results from the heightened sensitivities of some shallow ponds to even small climatic changes, which record species shifts both before and after approximately *anno Domini* 1850, and consequently lower beta-diversity estimates (Table 1). However, only the most recent assemblage changes are ecologically consistent with warming (12), which implies that our statistical

treatment provides conservative estimates of ecosystem changes attributable to warming.

Nonclimatic anthropogenic impacts cannot explain these patterns (12–14). Unlike most temperate regions, land use is generally absent at high latitudes, and, when land is used (e.g., reindeer and caribou herding), it is not sufficiently intensive to induce significant limnological responses (13, 32). Polar regions are affected by stratospheric ozone destruction and by deposition of persistent organic pollutants and other anthropogenic compounds (acids, nutrients, and metals). However, these phenomena are largely restricted to the latter half of the 20th century, thus postdating the observed initiation of algal and faunal changes by several decades. Furthermore, even high persistent organic pollutant concentrations have little apparent effect on diatom and chrysophyte assemblages in northern Labrador (31). Our records are inconsistent with atmospheric acidification or nutrient inputs, which are typically accompanied by losses of diatoms, such as *Cyclotella* (14, 37), and not their pronounced expansion (Fig. 1). Indeed, diatom-inferred reconstructions of pH (13, 34) and dissolved inorganic carbon (38) reveal no changes in water chemistry associated with recent assemblage shifts in Finland, Svalbard, and subarctic Canada. Instead, concurrent changes in algal and zoological indicators are expressed by taxa that are ecologically consistent with predicted limnological responses to climatic warming. Moreover, the timing of these changes, as early as the mid-19th century in some sites (Fig. 1), corresponds well to independent climate proxies, including varved sediments and tree rings (6). The general trend of increasing beta-diversity values with latitude (Fig. 3) suggests that polar amplification of climate warming (1, 5) is mirrored by the magnitude of compositional change in aquatic communities, a result that highlights the ecological sensitivity of arctic lakes and ponds to climate change. Furthermore, these latitudinal trends would unlikely be expressed if factors other than climate were at their root, because the latitudinal gradient is also one of remoteness and, hence, distance from nonclimatic, anthropogenic influences.

Several additional paleolimnological records support the notion of recent climate-induced regime shifts in arctic lakes, but these data were not included in our compilation because they were either too short in duration or were not dated with our screening criteria.

Examples include recent changes in chrysophyte populations from Ellesmere and Baffin islands (39) and diatom community shifts in lakes on Cornwallis (40) and Devon (41) islands and in other arctic regions (42–44). Finally, we note that the several records of temperature-sensitive abiotic proxies, notably lamina thickness in varved sediments (45, 46), are in complete agreement with our compiled biological data.

Our data show that many arctic freshwater ecosystems have experienced dramatic and unidirectional regime shifts within the last ≈ 150 years. For those sites where longer paleoecological records are available, recent changes in species composition appear unprecedented in the context of the last several centuries (13, 34) or even millennia (12, 14). In circumpolar lakes and ponds across latitudinal and longitudinal gradients exceeding 30° and 174° , respectively, and encompassing biomes ranging from subarctic treeline to high arctic tundra, large-scale ecosystem reorganizations have been triggered by climate warming. As ecological thresholds have been surpassed, regime shifts toward new ecological states have occurred. In shallow lakes, these shifts are characterized by taxonomically diverse and increasingly productive aquatic ecosystems, with more complex community and trophic structures. In deeper lakes, plankton development has been enhanced. These new ecological states are fingerprints of the Anthropocene, the most recent geological epoch characterized by human domination of several key global biogeochemical cycles and attendant climatic implications (47). Our paleolimnological data thus provide distinctive biostratigraphic signatures of the Holocene–Anthropocene transition for the most climatically sensitive subregions of the Arctic. As the widespread expression of this boundary becomes increasingly recognized, so too must the realization that even the world's most remote northern ecosystems have already been affected by human activities.

We thank Cathy Jenks for helping compile Table 1. This work was supported by the Natural Sciences and Engineering Research Council of Canada, the Earth System History Program from the National Science Foundation, the Polar Continental Shelf Project, the Natural Environmental Research Council, the Northern Scientific Training Program, Hydro Québec, the European Commission, the Academy of Finland, and the Research Council of Norway.

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