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Evaluating the Response of Cladocera to Recent Environmental Changes in Lakes from the Central Canadian Arctic Treeline Region

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Abstract

Arctic and subarctic ecosystems have undergone considerable environmental changes in recent years as the result of climate warming. Fossil records of freshwater diatoms in lakes throughout the circumpolar Arctic, including the central Canadian Arctic treeline region, have revealed marked directional shifts in diatom assemblages in recent lake sediments. These algal changes have been linked to longer growing seasons, decreased duration of ice cover, and/or increased thermal stability. The effects of these recent environmental changes on higher trophic levels, such as the Cladocera, are still unclear. Using cladoceran remains preserved in the sediments of 50 lakes, which were previously examined for changes in diatoms, we show that significant changes in cladoceran species composition have occurred from pre-industrial times to the present. However, these changes are considerably muted compared to the more substantial changes observed in the diatom record. We found no consistent patterns of change in planktonic cladocerans (i.e. *Daphnia*, *Bosmina*) within our study lakes, and the response of the Cladocera to environmental changes does not appear to be strongly coupled to recent changes in diatom communities, thus further confirming that the previously observed diatom changes were related to bottom-up limnological controls. These results highlight the complex response of Arctic freshwater food webs to climate change, and the need for incorporating multi-trophic studies into climate change investigations.

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Introduction

Freshwater lakes and ponds are one of the most ubiquitous features of Arctic and subarctic landscapes, and represent environments that are highly susceptible to the effects of climate change. Global warming trends are expected to be amplified at higher latitudes (Serreze and Francis, 2006), and, because of the sensitivity of hydro-ecological processes (Rouse et al., 1997; Wrona et al., 2005), freshwater ecosystems in the north are predicted to be particularly vulnerable to climate stressors. Numerous studies have suggested that high-latitude freshwater ecosystems have undergone significant environmental changes since pre-industrial times, including increasing lake temperatures, increased fluxes of nutrients, reduced periods of ice cover, longer growing seasons, and substantial reorganization of aquatic food webs (e.g. Serreze et al., 2000; Wrona et al., 2005; Hinzman et al., 2005; Smol et al., 2005; Quinlan et al., 2005; Duguay et al., 2006; Schindler and Smol, 2006).

Several striking examples of the impacts of climatic warming on freshwater ecosystems in the Arctic have been provided by paleolimnological studies of diatom communities. Douglas et al. (1994), for example, recorded dramatic shifts in diatom assemblages over the last ~200 years in a set of small High Arctic ponds on Ellesmere Island, Canada, whereas relatively stable diatom assemblages were found to have persisted throughout the preceding millennia. Smol et al. (2005) documented a similar restructuring of diatom communities in post-industrial lake sediments throughout most regions of the circumpolar Arctic. In subarctic Finnish Lapland, diatom assemblages shifted from being primarily composed of benthic taxa to having high abundances of

planktonic taxa (Sorvari and Korhola, 1998; Rautio et al., 2000; Korhola et al., 2002; Sorvari et al., 2002.). Likewise, Rühland et al. (2003a) recorded similar shifts in a series of 50 lakes in the central Canadian Arctic treeline region, with a shift from benthic to planktonic taxa. These widespread shifts in Arctic diatom taxa have been attributed to a shorter duration of ice cover, an increase in the length of the growing season, and/or increased thermal stability resulting from climate warming (Smol et al., 2005).

The Cladocera (Crustacea: Branchiopoda) are an important component of many high-latitude lakes and ponds, and are considered to be key organisms in both pelagic environments (i.e. the Daphniidae and Bosminidae families) as well as benthic habitats (i.e. the Chydoridae family) (Frey, 1988). Because of their crucial role in aquatic food webs, and their abilities to respond rapidly to changing environmental conditions, cladocerans have long been recognized as important ecological and paleolimnological indicators (Korhola and Rautio, 2001; Jeppesen et al., 2001; Bennike et al., 2004). As the chitinous exoskeletons of these animals are well preserved in lake sediments, changes in the sediment record can be used to examine the past response of cladoceran communities to changing environmental conditions (Korhola and Rautio, 2001). The environmental conditions of northern lakes influence the distributions and abundances of cladocerans (e.g. Korhola 1999; Bos and Cumming, 2003; Jeppesen et al., 2003; Sweetman and Smol, 2006) and, as a result, taxa in Arctic and subarctic lakes should also be expected to be strongly affected by climate warming.

Compared to the well documented shifts in diatom communities (e.g. Rühland et al., 2003a; Smol et al., 2005), however, the responses of higher trophic levels, including cladocerans, to recent

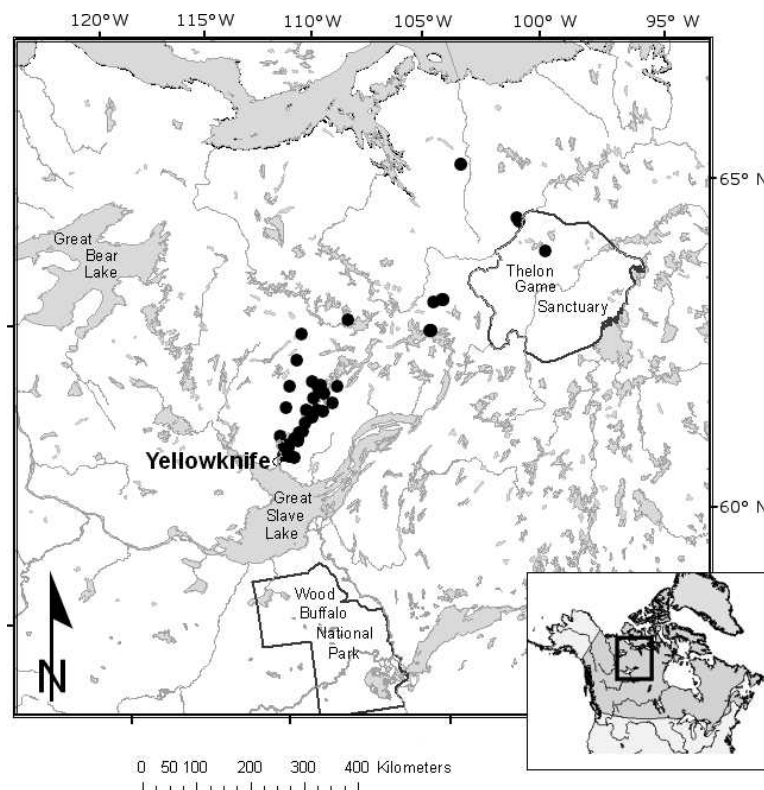


FIGURE 1. Locations of the 50 lakes across Arctic treeline. Study sites are indicated by black circles, with the exception of Slipper Lake, whose location is shown as a white circle.

environmental changes are not as well understood. In their review of the effects of climate change on Arctic and subarctic freshwater ecosystems, Rouse et al. (1997) predicted that, while increases in primary production will almost certainly be observed, the responses of higher trophic levels are likely much more variable. As food resources for planktonic grazers increase with higher levels of primary productivity in these ecosystems (e.g. Michelutti et al., 2005), the abundance of herbivorous cladocerans, such as *Daphnia*, might also be expected to increase. In some systems, this appears to be the case. For instance, in Lake Saanajärvi, located in northwestern Finnish Lapland, Rautio et al. (2000) and Korhola et al. (2002) found that increases in the planktonic cladoceran *Daphnia* were synchronous with the increases in planktonic diatom taxa described previously. O'Brien et al. (2005) also found that, following experimental fertilization of half of a partitioned lake in northern Alaska, *Daphnia longiremis* abundance was significantly higher in the treated half compared to the reference side. However, the response of food webs to climate warming is often difficult to predict (Petchey et al., 1999; Callaghan et al., 2004; Baulch et al., 2005). Climatic warming can potentially destabilize food webs, and responses of higher trophic levels may be much more complex and unpredictable than in algal communities (e.g. Beisner et al., 1997; Strecker et al., 2004). There is increasing evidence that in many temperate lakes, a decoupling of the algae-zooplankton relationship can occur (Winder and Schindler, 2004; Adrian et al., 2006). In Lake Washington, for example, Winder and Schindler (2004) documented a long-term decline in *Daphnia*, which they attributed to an increasing temporal mismatch with food resources, due to an earlier spring diatom bloom as the result of climate warming. Relatively few studies, however, have examined the impacts of climate change on Arctic freshwater food webs (e.g. Quinlan et al., 2005).

The objectives of our study were to evaluate the response of cladocerans to recent environmental changes in the central Canadian Arctic treeline region by comparing present-day and pre-industrial

cladoceran assemblages from a series of 50 lakes, and to compare the responses of the cladoceran communities to previously observed changes in diatom communities from the same lakes (Rühland et al., 2003a). Specifically, we were interested in knowing the following: (1) Have any changes occurred to the community composition or diversity of cladocerans between pre-industrial and present-day periods? (2) If so, was there a shift in abundances from benthic to planktonic cladoceran taxa similar to that observed in the diatom taxa? (3) Are changes in cladoceran and diatom assemblages contemporaneous? (4) Finally, do changes in grazing/predation regimes from cladocerans have a role in driving the response of diatom communities to recent climate warming? If the latter is the case, we would expect changes in cladoceran assemblages to closely correspond to the diatom changes across our 50 lake set.

Study Area

Sediments were analyzed from 50 lakes located in the central Canadian Arctic treeline region, between Yellowknife, Northwest Territories, and the northern boundary of the Thelon Game Sanctuary, Nunavut Territory (Fig. 1). The study lakes span a steep ecoclimatic gradient and are distributed across three major ecozones, from the boreal forest zone in the south, through the forest-tundra transitional zone, and into the Arctic tundra zone in the north (Rühland and Smol, 2002; Rühland et al., 2003a, 2003b).

Methods

Sediment cores were collected at approximately the deepest point of each of the lakes using a Glew gravity corer (Glew et al., 2001). The surface sediments (top 1.0 cm) and bottom sediments (bottom 1.0 cm) of each core were extruded using a vertical extruder (Glew, 1988). Additional details on water chemistry of the lakes, the modern distribution of diatoms and Cladocera, as

well as additional details about sediment core retrieval and sampling of these lakes were previously presented in Rühland and Smol (2002) and Rühland et al. (2003a, 2003b).

In order to evaluate the response of cladocerans to recent environmental change, we used a 'top-bottom' paleolimnological approach (Smol, 2008), identical to the approach used in the Rühland et al. (2003a) diatom study. This 'snap-shot' approach involves comparing subfossil assemblages from the surface lake sediments, which represent present-day conditions, to assemblages deposited in downcore lake sediments representing pre-impact conditions (ca. 1850). The goal of the comparisons made between these two discrete points in time (i.e. top vs. bottom) is to assess whether environmental conditions during the pre-industrial era are substantially different than present. These data can then be used to evaluate the magnitude, direction, and nature of cladoceran assemblage changes over the last ca. 200 years on a regional scale.

In addition to the 50-lake regional top-bottom analyses, we examined the detailed changes in cladoceran communities from a sediment core from Slipper Lake (64°35'65"N, 110°50'07"W), a site also examined for changes in diatom communities by Rühland et al. (2003a; 2005). As there was insufficient sediment from the original Slipper Lake core used by Rühland et al. (2003a), we examined cladoceran remains from a second core that was used by Rühland and Smol (2005) to verify the trends in the primary core. Both sediment cores were collected at the deepest point in the lake in March 1997 and sectioned into 0.5 cm intervals.

Analysis of cladoceran remains from the sediments of each lake followed standard procedures, outlined in Korhola and Rautio (2001). Approximately 2–4 g wet weight of sediment from each sample was deflocculated in 150 mL of a 10% KOH solution at 80°C for 30 minutes, after which they were rinsed through a 37 µm sieve. For Slipper Lake, the 0.5 cm intervals were combined into 1.0 cm intervals because of the low abundance of cladoceran remains. Slipper Lake samples were separated into >90 µm and 37–90 µm subsamples to facilitate identification of remains. Material retained on the sieves was stored in distilled water and ethanol. Safranin-glycerine solution was added to stain the cladoceran remains. Slides were prepared by pipetting 50 µL aliquots onto slides, and mounting in glycerin jelly. Cladocera were identified at 100–400× magnification using a Leica DMRB compound microscope. For each taxon, the most abundant remains (i.e. head shield, carapace, postabdomen) were used to calculate the number of individuals within a sample. A minimum of 50 individuals were counted per sample. Three lakes (TK-13, TK-21, and TK-40) contained insufficient numbers of Cladocera, and were excluded from subsequent analyses.

Changes in the cladoceran communities between top and bottom samples were quantified using detrended correspondence analysis (DCA). DCA is an unconstrained ordination technique, and has the advantage that the sample scores are scaled in standard deviation (SD), or units of species turnover (β -diversity) (Smol et al., 2005; Birks, 2007). Prior to analysis, all species relative abundance data were square-root transformed to stabilize variances. Bonferroni-adjusted paired *t*-tests were used to compare both axis 1 and axis 2 sample scores between the two time periods. Changes in the sample scores between top and bottom sediment samples were calculated following Quinlan et al. (2003). Briefly, the axis 1 sample score for the pre-industrial assemblage from each lake was subtracted from the axis 1 sample score of the present-day assemblage to calculate a net change in DCA sample scores along that axis. This calculation was also performed for axis 2 ordination scores. Differences in α -diversity between present-day and pre-industrial cladoceran communities were also compared, using Hill's N2 as a measure of α -diversity.

Bonferroni-adjusted paired *t*-tests were used to compare differences in diversity between time intervals. All ordinations and Hill's N2 calculations were carried out using CANOCO v. 4.5 (ter Braak and Šmilauer, 2002); *t*-tests were calculated using SYSTAT v. 9 (SPSS, 1998).

In order to assess how changes in cladoceran communities matched previously observed changes in diatom communities within the same lakes (Rühland et al., 2003a), the degree of dissimilarity between top and bottom samples was calculated using a Bray-Curtis dissimilarity coefficient (Clarke et al., 2006). Cladoceran Bray-Curtis dissimilarity coefficients were compared to the matching Bray-Curtis values for the diatom assemblages. In addition, we compared the relative abundance of the dominant planktonic diatom taxa (*Cyclotella*) to changes in pelagic Cladocera species, using simple Pearson correlations with Bonferroni-adjusted *p*-values for multiple comparisons. Correlations were calculated using SYSTAT v. 9 (SPSS, 1998).

For the continuous sediment core data from Slipper Lake, a detrended canonical correspondence analysis (DCCA) was used to calculate a quantitative estimate of compositional turnover (β -diversity) following the procedures used by Birks (2007). An estimate of the total amount of compositional change for the last ~150 years was obtained by constraining the DCCA by using the ²¹⁰Pb-based sample ages as the sole constraint. Significance was measured using Monte Carlo permutations (999 permutations). For this analysis, species data were square-root transformed, there was no down-weighting of rare taxa in the ordination, detrending was by segments, and scaling was nonlinear. DCCA was performed using CANOCO v. 4.5 (ter Braak and Šmilauer, 2002).

Results

Most cladoceran taxa in our study lakes did not demonstrate a uniform pattern of change from the pre-industrial to the present-day assemblages (Fig. 2). This is in contrast to the diatom communities in the same lakes that showed a large and consistent increase in the planktonic species *Cyclotella stelligera*, and a corresponding decline in benthic *Fragilaria* taxa (Fig. 3; Rühland et al., 2003a). The cladoceran assemblages show no corresponding increase in planktonic species, notwithstanding a few lakes that showed changes in the dominant planktonic taxa (i.e. Bosminidae, Daphniidae). Despite no consistent increases or decreases in cladocerans across the study area, relatively subtle shifts were apparent. For example, the benthic cladoceran *Pleuroxus trigonellus*, which was only found in lake sediments from boreal forest lakes, decreased in abundance in modern sediments compared to pre-industrial periods (negative values in Fig. 2), whereas a second benthic chydorid taxon (*Camptocercus* spp.) increased in relative abundance in several lakes across the study region (positive values in Fig. 2). However, most taxa in our lakes did not show a synchronous shift in their relative abundance from pre-industrial assemblages to modern sediments.

The detailed paleolimnological record from the Slipper Lake sediment core is consistent with the regional top-bottom survey. Throughout the sediment record, the cladoceran assemblage remains relatively stable, and the pelagic cladocerans (*Daphnia*, *Bosmina*) present in the sediment record show no apparent change in their abundance (Fig. 3). This is in contrast with the large directional changes occurring in the diatom record (Fig. 3). Beginning at about 5 cm (A.D. ~1800), there is a shift in the diatom taxa, with pelagic *Cyclotella stelligera* becoming more

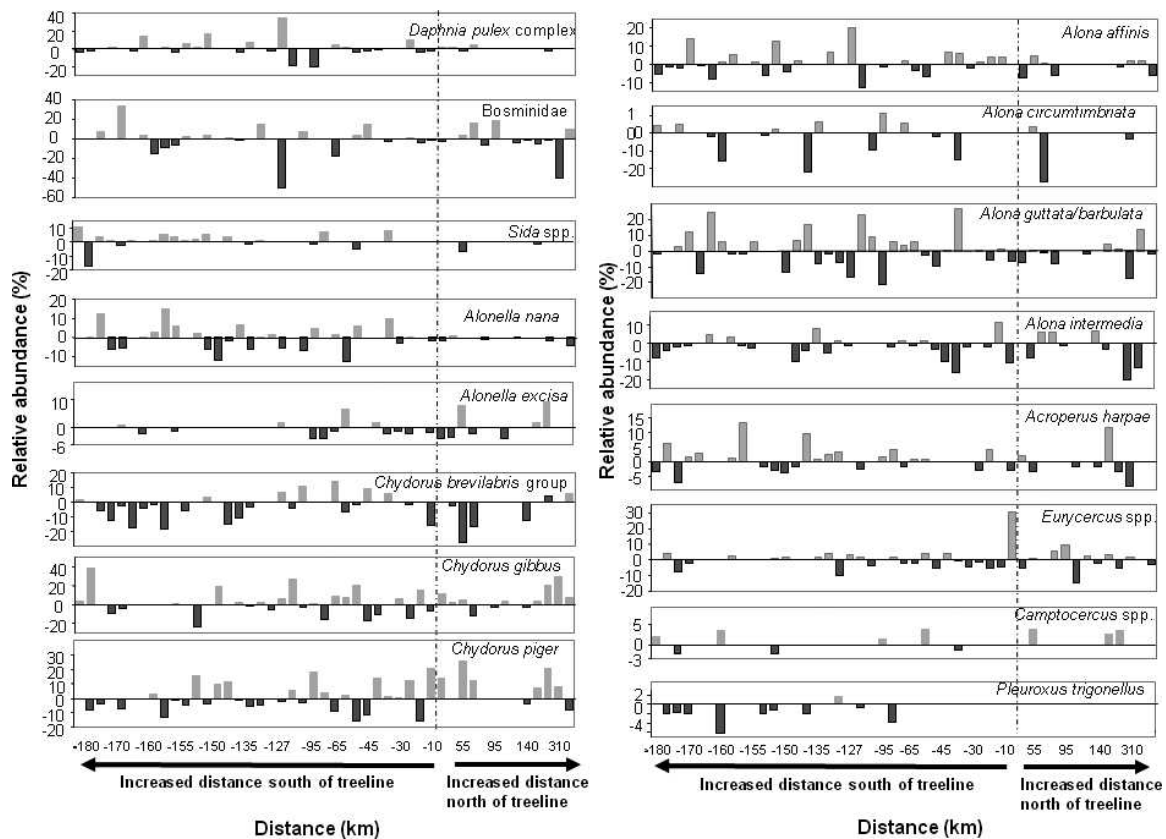


FIGURE 2. The percentage of change of the main cladoceran species from pre-industrial to modern lake sediments in the 47 central Canadian Arctic treeline lakes that contained sufficient numbers of fossil Cladocera for analysis. Lakes are arranged in order of the distance of each lake from current treeline. Distance to treeline (km) follows the delineation by Rühland et al. (2003a) and is based on percentage tree cover, derived from field observations, topographical maps, aerial photographs, and maps derived from satellite imagery. Positive distances along the x-axis indicate lakes north of treeline, and negative distances indicate lakes south of treeline. Positive values on the y-axis indicate an increase in the relative abundance (%) from pre-industrial to present-day lake sediments, while negative values on the y-axis indicates a decrease in the relative abundance (%) from pre-industrial to present-day lake sediments.

abundant and *Aulacoseira* and *Fragilaria* spp. decreasing in abundance towards present day.

Although there is no clear directional change in individual cladoceran taxa across our regional lake set, there is a significant

change in β -diversity (species turnover) (Fig. 4). Both DCA axis 1 and 2 sample scores were significantly different between present-day and pre-industrial times (DCA axis 1, paired t -test, $p < 0.0001$, $t = 4.470$; DCA axis 2, paired t -test, $p < 0.0001$, $t = 5.519$), indicating a

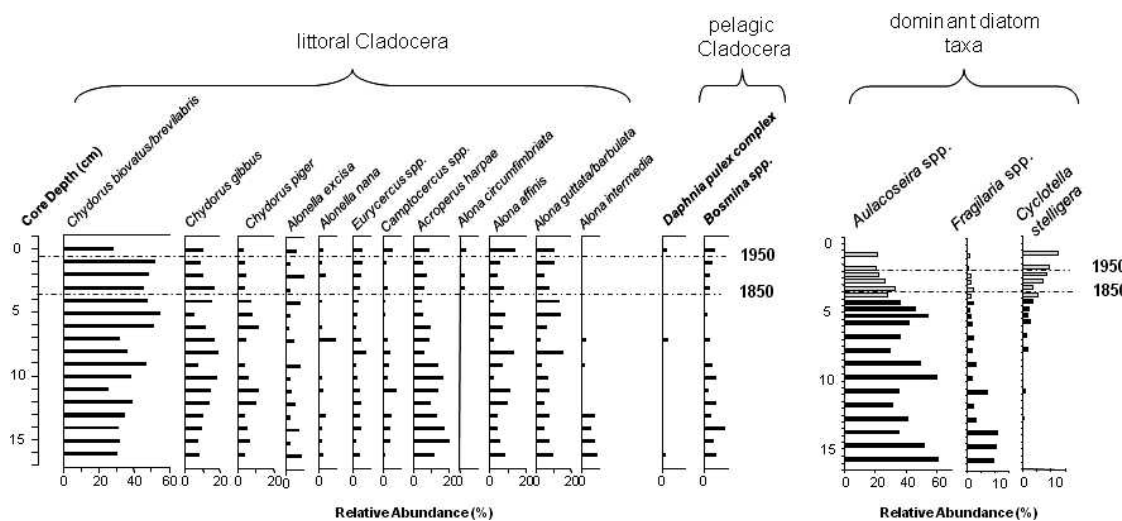


FIGURE 3. Relative abundances of littoral cladocerans, pelagic cladocerans, and dominant diatom taxa in Slipper Lake, Northwest Territories. The two *Chydorus* species, *C. biovatus* and *C. brevilabris*, were grouped together, as the remains of these taxa were difficult to distinguish from each other, as were the *Alona* species, *A. guttata* and *A. barbulata*. Diatom data are summarized from Rühland et al. (2003a) and Rühland and Smol (2005).

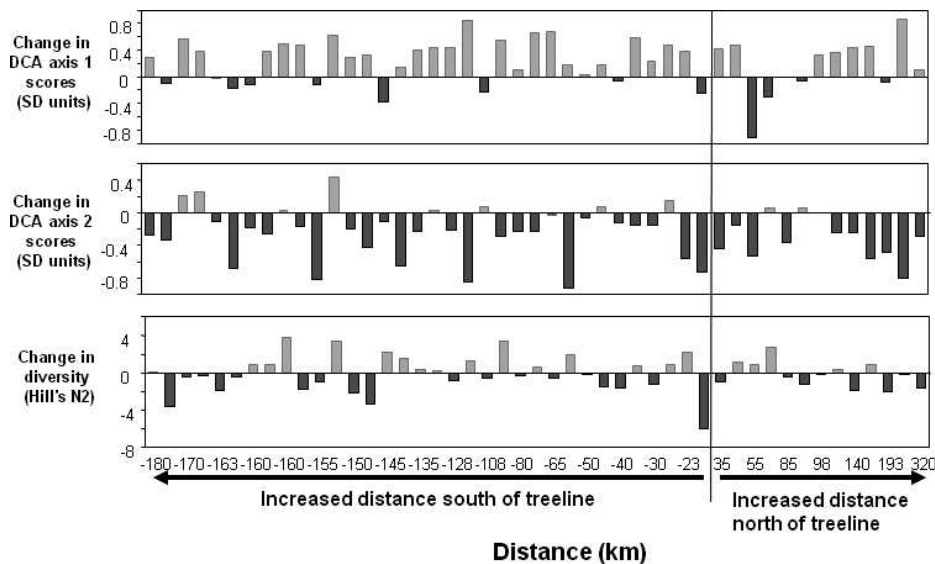


FIGURE 4. Changes between (top) DCA axis 1 sample scores; (center) DCA axis 2 sample scores, a measure of β -diversity; and (bottom) cladoceran species diversity (Hill's N2), a measure of α -diversity, between pre-industrial lake sediments and modern lake sediments in the 47 central Canadian Arctic treeline lakes. Lakes are arranged in order of the distance of each lake from current treeline.

directional shift in the overall composition of species assemblages. There was no significant change in α -diversity (Hill's N2) between pre-industrial and present-day cladoceran assemblages (Fig. 4; paired t -test, $p < 0.636$, $t = 0.477$). α -diversity refers to the diversity (i.e. species richness) within a particular area and is usually expressed as a measure of the number of species. Alternatively, β -diversity is a measure of the change in species diversity between areas, allowing a comparison between ecosystems or sites.

A comparison of the Bray-Curtis dissimilarity coefficients (DC) for diatom taxa (mean DC = 0.46) and cladocerans (mean DC = 0.33) suggests that the species composition of diatom assemblages are more dissimilar between pre-industrial and present-day periods than the cladoceran fauna (Fig. 5). This is not surprising, as the diatom assemblages show striking changes in their relative abundances (Rühland et al., 2003a).

A comparison of the modern distributions of *Cyclotella* and planktonic cladocerans reveals that the relative abundance of *Cyclotella* spp. in our 47-lake set is uncorrelated with *Daphnia* relative abundance ($r = 0.19$, $p = 0.188$), Bosminidae relative abundance ($r = 0.13$, $p = 0.377$), or total pelagic Cladocera ($r = 0.21$, $p = 0.159$). Both *Daphnia* and *Bosmina* remains occur at relatively low abundances throughout the Slipper Lake core, and neither pelagic taxa appear as dominant in the paleolimnological

record. The cladoceran fauna is comprised primarily of benthic chydorids and is relatively stable throughout the core (Fig. 3).

Discussion

The lowermost cladoceran assemblages from all of our study sites represent environmental conditions pre-dating ca. 1850 (pre-industrial times). Several of our study lakes have undergone detailed paleolimnological analyses that involved establishing a chronology based on ^{210}Pb dating techniques (including Slipper Lake). These sedimentary cores have consistently shown that background conditions (A.D. ~ 1850) occurred within the top 6 cm of the core, which is consistent with the typically low rates of sedimentation in Arctic lakes (Rühland et al., 2003a, 2003b). The mean core depth for all of the bottom sedimentary intervals from our lake set was 19.4 m (Table 1), suggesting that most, if not all, of our bottom intervals pre-date the onset of the industrial era.

Rühland et al. (2003a) found that increases in planktonic *Cyclotella* abundance were most pronounced in the deeper lakes (>6 m) within our study area. They suggested that, among other limnological changes, deeper lakes likely experienced increased water column stability as the warmer temperatures and longer growing season likely allowed longer and stronger periods of thermal stratification. One possible explanation why these deeper lakes did not show comparable increases in planktonic Cladocera is because of strong top-down predation pressure from fish or invertebrate predators. While data on the occurrence of potential predators in our study lakes were not available, it is likely that these deeper lakes sustained fish populations. In Arctic tundra lakes in Alaska, O'Brien et al. (2004) and Yurista and O'Brien (2001) found that deeper lakes tend to contain planktivorous fish populations, and in lakes with fish, large planktonic zooplankton species such as *Daphnia* were generally limited in their abundance. Lauridsen et al. (2001) also reported that in a survey of 56 lakes in Arctic Greenland, *Daphnia pulex* only occurred in lakes without fish.

Invertebrate predators may also have limited the response of *Daphnia*. O'Brien (2001) found that when the predatory copepod *Heterocope septentrionalis* was introduced into a pond that lacked both fish and invertebrate predators, *D. pulex* was eliminated from the pond within a year. Members of the *Daphnia pulex* complex (i.e. *D. middendorffiana* and *D. pulex*) may not be able to increase in abundance in the deeper lakes, despite increased algal food resources, due to suppression by predators.

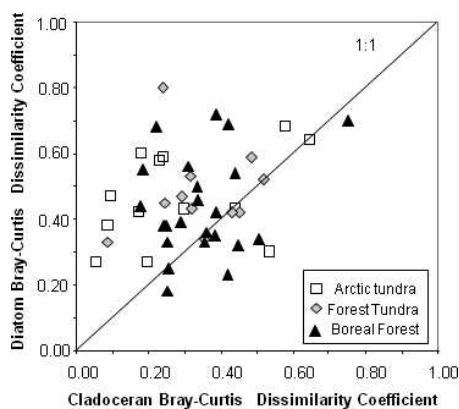


FIGURE 5. Scatter plot comparing Bray-Curtis dissimilarity coefficient values for diatoms and cladocerans for the 47 study lakes. The majority of lakes lie above the 1:1 line, indicating that diatom assemblages are more dissimilar than cladoceran assemblages between pre-industrial and modern lake sediments.

TABLE 1
Geographical and limnological data on the 50 study lakes.

Lake	Lat (N)	Long (W)	Area (ha.)	Depth (m)	Cond. ($\mu\text{S cm}^{-1}$)	DOC (mg L^{-1})	TP ($\mu\text{g L}^{-1}$)	Zone	Core Length (cm)
SL	64°37.00'	110°51.00'	19.0	14.0	33.8	5.0	9.3	AT	18.5
TK-6	66°41.31'	104°55.86'	5.3	4.5	17.0	1.7	4.2	AT	15.0
TK-7	66°41.23'	104°55.89'	1.8	9.5	12.3	1.3	8.4	AT	14.0
TK-9	64°53.36'	102°45.07'	35.7	5.5	36.3	2.7	13.4	AT	10.0
TK-10	65°29.40'	103°22.01'	36.6	3.0	14.8	3.0	5.3	AT	12.0
TK-11	65°33.62'	103°23.26'	6.3	3.5	9.7	2.4	5.6	AT	13.0
TK-13	64°36.15'	107°26.23'	2.6	3.1	16.1	2.3	5.9	AT	13.0
TK-14	64°35.90'	107°05.93'	2.8	4.9	9.2	1.7	4.3	AT	15.0
TK-15	64°35.74'	107°05.49'	0.1	3.0	9.4	1.3	4.6	AT	9.0
TK-16	64°35.60'	107°05.30'	4.2	6.0	7.3	1.3	4.2	AT	25.0
TK-17	64°35.69'	107°05.01'	10.3	5.9	9.3	1.7	2.7	AT	23.0
TK-18	64°09.39'	107°49.48'	10.6	7.3	8.7	3.3	31.3	AT	14.5
TK-19	64°09.39'	107°49.48'	8.4	0.8	9.7	5.3	28.1	AT	8.5
TK-20	64°09.00'	107°49.00'	9.7	8.8	8.7	2.3	6.2	AT	15.0
TK-21	64°09.00'	107°49.00'	9.7	1.0	17.1	10.3	28.3	AT	10.5
TK-29	63°25.25'	112°39.81'	18.0	10.1	14.6	138.0	4.2	FT	21.0
TK-30	63°33.70'	112°21.21'	10.7	1.5	15.0	30.4	28.5	FT	12.0
TK-31	63°37.03'	112°17.77'	3.5	5.0	13.4	27.3	9.2	FT	15.0
TK-32	63°29.05'	112°12.63'	5.9	1.5	13.7	17.5	24.5	FT	16.5
TK-50	63°18.48'	111°58.27'	4.3	1.8	26.2	13.4	4.5	FT	21.5
TK-51	63°32.91'	111°42.34'	8.8	1.8	18.4	11.0	9.4	FT	8.0
TK-52	63°35.61'	112°25.12'	9.0	1.9	18.1	14.0	6.0	FT	10.5
TK-53	63°42.54'	112°34.40'	4.6	19.0	19.8	13.4	4.2	FT	17.0
TK-54	64°30.68'	112°41.47'	9.9	3.4	12.3	5.8	3.1	FT	34.0
TK-55	64°06.01'	113°01.54'	9.8	2.6	20.6	10.4	5.3	FT	17.0
TK-56	63°41.42'	113°26.68'	13.2	6.0	25.2	11.4	7.8	FT	22.5
TK-22	62°42.03'	113°59.19'	8.8	2.8	62.0	12.8	16.2	BF	24.0
TK-23	62°43.73'	113°49.53'	6.9	2.0	24.2	15.2	7.9	BF	26.0
TK-24	62°54.20'	113°13.15'	16.8	8.0	102.2	24.3	11.0	BF	22.0
TK-26	62°54.14'	113°23.22'	20.9	16.0	56.9	6.2	6.9	BF	22.0
TK-27	62°49.23'	113°33.75'	10.1	3.0	64.6	11.0	23.0	BF	25.0
TK-28	63°15.31'	113°00.22'	8.8	6.1	74.8	165.0	10.8	BF	17.0
TK-33	63°12.97'	112°36.05'	6.1	10.0	2.5	116.0	6.1	BF	24.0
TK-34	63°07.64'	112°47.67'	3.6	5.0	25.9	15.0	12.1	BF	28.0
TK-35	63°02.72'	113°06.46'	4.3	7.0	44.1	332.0	15.6	BF	22.0
TK-36	62°45.75'	113°28.63'	4.2	1.5	39.1	80.1	23.3	BF	22.0
TK-38	62°33.59'	114°01.34'	17.4	2.1	64.4	26.5	8.7	BF	24.0
TK-39	62°32.89'	113°57.13'	14.4	1.0	271.1	69.9	48.6	BF	28.5
TK-40	62°32.87'	113°56.09'	7.9	2.2	238.9	30.2	11.2	BF	21.5
TK-41	62°34.09'	114°01.74'	4.3	0.5	149.5	51.6	13.0	BF	16.5
TK-42	62°32.75'	113°53.40'	8.4	0.9	138.5	44.8	34.8	BF	23.0
TK-43	62°31.49'	113°50.20'	7.3	7.3	42.8	13.4	3.7	BF	23.5
TK-44	62°31.49'	113°50.20'	2.9	1.4	134.0	26.2	5.7	BF	21.5
TK-45	62°31.01'	113°46.76'	8.0	6.5	228.9	24.8	8.7	BF	22.7
TK-46	62°30.44'	113°39.91'	2.6	0.7	405.1	61.1	10.9	BF	10.5
TK-47	62°40.69'	113°51.03'	4.6	2.5	32.8	17.4	8.5	BF	28.0
TK-48	62°48.27'	113°26.12'	18.5	1.5	100.2	24.6	22.1	BF	31.5
TK-49	63°10.99'	112°22.83'	12.2	3.7	97.4	9.6	5.5	BF	28.5
TK-57	63°20.21'	113°42.30'	3.0	4.6	27.6	16.4	6.0	BF	14.0
TK-58	62°53.37'	114°04.24'	2.6	3.2	76.9	26.2	10.8	BF	32.5
Mean			9.3	4.7	58.4	31.2	12.0		19.4

* AT = Arctic tundra; FT = forest-tundra; BF = boreal forest

Cladocerans make up only a component of the zooplankton of lakes. Other zooplankton taxa, such as copepods or rotifers populations, may have increased their abundance and prevented a response in the planktonic Cladocera because of competitive exclusion (MacIsaac and Gilbert, 1989; Dzialowski and O'Brien, 2004).

The paleolimnological record indicates that diatoms have shown a large shift in favor of planktonic taxa. While the diatom

flora within the phytoplankton may have increased significantly, other algal groups may not have responded to recent environmental changes to the same degree (Prowse et al., 2006). In a study of food sources and feeding rates in shallow high-latitude lakes and ponds, Rautio and Vincent (2006) found that zooplankton and phytoplankton communities were not strongly coupled, and that 89–98% of the zooplankton resources consisted of detritus. Despite the apparent changes in planktonic

algae, cladocerans may not have shown a similar response because of a decoupling of the food web (i.e. Brönmark and Weisner, 1996).

Conclusions

Despite evidence for marked ecological shifts in the diatom communities within the past ~150 years, the cladoceran assemblages within our treeline lakes do not appear to have experienced comparable ecological changes. Rühland et al. (2003a) documented striking shifts in the fossil diatom records within these same lakes, with the relative abundances of planktonic diatom taxa increasing across our study region. Although we found that there was a significant unidirectional shift in the composition of cladoceran species between pre-industrial and modern periods within the same study lakes, we found no consistent pattern of change in the planktonic cladocerans (i.e. *Daphnia*, *Bosmina*). The lack of a strong coupling between these two trophic levels suggests that cladoceran and diatom communities may be responding independently to climate change signals within our lakes, and that top-down controls (i.e. grazing) do not appear to have a strong impact in controlling diatom communities within these lakes. If this is true, and given the relatively muted shift in cladoceran assemblage composition, it is probable that the cladoceran fauna in subarctic Canadian lakes may not have reached an equivalent environmental threshold which the diatom communities have apparently surpassed. Cladoceran communities may be relatively more resilient to the impacts of recent climate change. These results highlight the complex response of Arctic freshwater food webs to climate change. Understanding the responses of organisms at multiple trophic levels will be essential for a holistic understanding of the impacts of climate warming on freshwater ecosystems. Given that Arctic ecosystems are predicted to experience an additional 4–6°C warming over the next century, substantial reorganizations of freshwater food webs will undoubtedly continue to occur in the future, particularly if higher trophic levels surpass ecological thresholds.

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