

Assessing the efficacy of chironomid and diatom assemblages in tracking eutrophication in High Arctic sewage ponds

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Abstract Eutrophication is the most common water quality issue affecting freshwaters worldwide. Paleolimnological approaches have been used in temperate regions to track eutrophication over time, placing changes in historical context. Diatoms (Bacillariophyta) have a direct physiological response to changes in nutrients and are effective indicators of lake trophic status. Chironomids (Diptera) have also been used to track nutrient conditions; however, given that nutrients and oxygen are often tightly linked, it is difficult to disentangle which variable is driving shifts in assemblages. Here, we analyze chironomid and

diatom remains in sediments from sewage-impacted ponds in the High Arctic. These ponds have the unusual characteristics of elevated nutrient and oxygen concentrations, unlike those of typical eutrophic lakes where deepwater oxygen is often depleted. Our data show that while diatom assemblages responded to changing nutrients, no concomitant changes in chironomid assemblage composition were recorded. Furthermore, the dominance of oligotrophic, cold stenothermic chironomid taxa, and lack of so-called “eutrophic” species in the eutrophic sewage ponds suggests that oxygen, not nutrients, structures chironomid assemblages at these sites.

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Introduction

Sedimentary chironomid (Diptera) remains are often used in paleolimnological investigations of eutrophication because they respond to numerous production-related variables. As a result, chironomid-based inference models have been developed to infer concentrations of chlorophyll *a* (chl-*a*) (Brodersen & Lindegaard, 1999), total phosphorous (TP) (Brooks et al., 2001), and hypolimnetic oxygen (Quinlan et al., 1998). However, in temperate dimictic lakes, nutrients and deepwater oxygen concentrations are often tightly linked (because of interactions between primary

production and decomposition) and so, in most deep eutrophic lakes hypolimnetic oxygen is low. Monitoring and experimental evidence have documented the many physiological, morphological, and behavioral adaptations that allow some chironomid species to tolerate low oxygen conditions (Brodersen & Quinlan, 2006). However, there have been difficulties disentangling the respective roles of nutrients and oxygen (under eutrophic conditions especially) in structuring chironomid assemblages because chironomids also respond to the increased food availability and changing habitat structure that may occur with increased nutrient levels.

One way in which to ascertain whether chironomids are responding primarily to nutrients or oxygen is by studying sites where oxygen and nutrient concentrations are not closely associated with one another. Although rare, such limnological conditions were documented in a series of High Arctic ponds near Cape Vera on Devon Island, Nunavut (Blais et al., 2005). The Cape Vera ponds are eutrophic due to their proximity to a large colony of seabirds that releases nutrient-rich wastes to the surrounding catchment. However, in contrast to most eutrophic temperate lakes, the oxygen levels in the ponds remain high due to their shallow nature ($Z_{\max} < 2$ m) and 24 h of daylight during the growing season (i.e., no periods of respiration without concurrent photosynthesis). Because of the varying distances of each pond to the nesting colony, there exists a gradient of high-to-low nutrient concentrations extending away from the colony (Keatley et al., 2009). Although the impacted ponds of Cape Vera are highly eutrophic (Keatley et al., 2009), the chironomid species recorded in both surface sediments (Michelutti et al., 2011) and sediment cores (Stewart et al., 2013) of these ponds contain mainly cold stenothermic taxa that are typical of oligotrophic waters. Furthermore, sediments from the eutrophic ponds recorded remarkably similar species to those of a nearby oligotrophic control site outside the area affected by the seabird colony (Stewart et al., 2013). The similarity of chironomid community composition along a large nutrient gradient suggested that oxygen, which was elevated in all study sites, played a more important role than nutrients in governing chironomid assemblages.

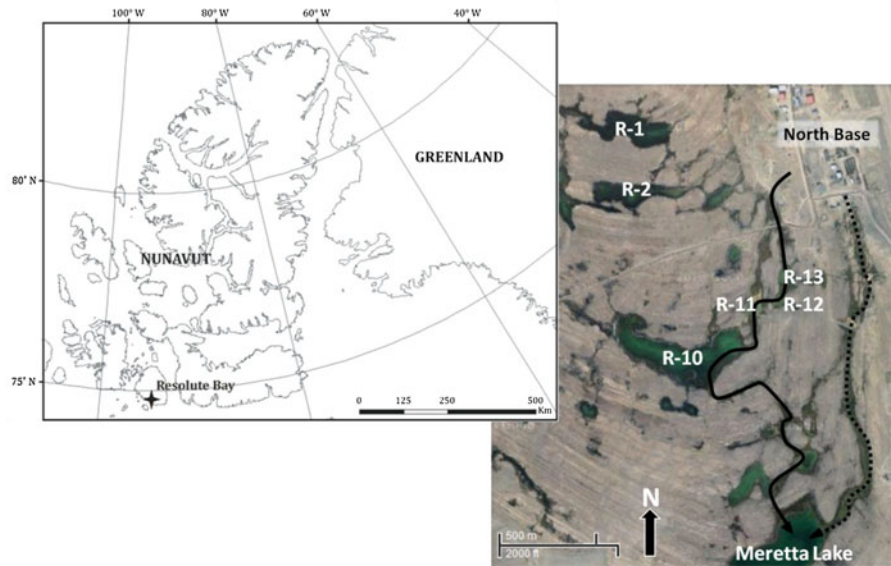
The Cape Vera study (Stewart et al., 2013) challenged some widely held beliefs about the applicability of chironomids in eutrophication studies,

namely their suitability for quantitative inference models of TP. However, this was the only study completed to date that was able to explicitly evaluate the relative influences of nutrient levels versus oxygen concentrations on chironomid assemblages, as typically lakewater TP and deepwater oxygen levels are negatively correlated. The question remained whether another “natural laboratory,” such as the Cape Vera ponds, could be found to further investigate these important relationships.

Several sewage-affected ponds near Resolute Bay on Cornwallis Island (Nunavut, Canada; Fig. 1) provide the opportunity to evaluate and expand on the conclusions reached in the Cape Vera study as to whether chironomids are responding primarily to nutrients or oxygen with eutrophication. In contrast to Cape Vera where nutrient-rich seabird wastes have eutrophied the ponds since their inception several centuries ago, a series of shallow ponds near Resolute Bay have only recently been eutrophied as a result of human sewage inputs (Fig. 1; Schindler et al., 1974). Beginning in 1949, sewage from a newly constructed Department of Transport Base (i.e., airport facilities) was released onto the landscape via two small watercourses (one of which crossed several naturally existing ponds referred to as the “sewage ponds”) before ultimately ending up in a terminal lake (Meretta Lake; Fig. 1; Douglas & Smol, 2000). In 1979, effluent from one of the sewage outlets (i.e., utilidor) was dismantled because of a steady decline in the number of residents, and all inputs from the other utilidor to Meretta Lake stopped completely by 1998 (Fig. 1; Douglas & Smol, 2000). The Resolute Bay sewage ponds likely always contained elevated oxygen levels, for similar reasons to the seabird-affected Cape Vera ponds, namely that they are shallow and thus well-mixed, and have no periods of respiration without concurrent photosynthesis during the 24-h daylight in the summer months. Like the shallow Cape Vera ponds, the Resolute Bay sewage ponds freeze solid through to the sediments during the winter.

One of our main study questions is “How have the chironomid assemblages in the sewage ponds responded to eutrophication and recovery, all the while remaining in an oxic environment?” We answer this question by examining subfossil chironomid remains in sediment cores and in surface sediment samples recovered during a long-term monitoring program that we began in the 1990s. By tracking the

Fig. 1 Map showing the location of Resolute Bay on Cornwallis Island (marked with a *star*), with an inset of Meretta Lake, sewage ponds (R-10, R-11, R-12, and R-13), and control ponds (R-1 and R-2). The *solid line* shows the water course that raw sewage travelled through the sewage ponds to Meretta Lake from 1949 to 1979. The *dashed line* shows the second water course that carried sewage directly to Meretta Lake from 1949 to 1998. Modified from Google maps



biological response to eutrophication and recovery *within* each Resolute sewage pond, we reduce any variability that may arise from inter-pond comparisons, such as was done at Cape Vera (Stewart et al., 2013), where we used a natural nutrient gradient (i.e., distance of each pond from the nesting colony) to compare the changes in chironomid assemblage associated with varying degrees of eutrophication.

In addition to chironomids, we also examine subfossil diatom assemblages from the Resolute Bay sewage ponds. Because diatoms have a direct physiological dependence on nutrients (i.e., they uptake nutrients directly from the water column and respond to habitat changes), they are often used for tracking eutrophication (Hall & Smol, 2010). To date, only a few paleolimnological studies have used diatoms to track cultural eutrophication in the Arctic, including one from Meretta Lake, the terminal lake for the Department of Transport Base sewage inputs at Resolute Bay (Douglas & Smol, 2000). Previous studies have shown that diatoms in Arctic lakes and ponds often display a relatively subtle taxonomic shift in response to nutrient enrichment (Douglas & Smol, 2000), and even a delayed response (Michelutti et al., 2007a), compared to changes recorded in temperate regions. This muted response is believed to be related to the overriding influence of the cool climate and ice cover on aquatic biota in Arctic lakes and ponds (Douglas & Smol, 2000; Michelutti et al., 2007a; Smol

& Douglas 2007a). This relationship illustrates an important caveat of using any bioindicator: diatoms, like most aquatic biota, will respond to multiple, interacting environmental drivers, such as nutrients as well as climate, and thus the relative influences of each must be considered. Nonetheless, although the diatom response to eutrophication in the Arctic is not as marked as in temperate regions, the diatoms do change with nutrient additions, and there are documented differences in diatom assemblages between eutrophic and oligotrophic sites (Keatley et al., 2011) from the same region as our previous chironomid work (Michelutti et al., 2011; Stewart et al., 2013).

In this current study, the inclusion of both diatom and chironomid indicators allows us to compare the responses to eutrophication between primary producers (diatoms) and secondary consumers (chironomids). Our limnological monitoring program of the Resolute Bay sewage ponds spans from 1993 to 2011, making it one of the longest of its kind in the High Arctic. The sewage ponds, as well as nearby control ponds unaffected by sewage inputs, have been sampled for water chemistry, surface sediments, and rock scrapes (epilithon). In addition to the annual collections, sediment cores were recovered from the sewage ponds and nearby control sites, which provide a long-term record of chironomid and diatom changes over time. Our main objectives are to: (1) compare the responses to eutrophication and recovery of the

chironomids in the Resolute Bay sewage ponds with the responses of the diatoms; (2) compare the chironomid and diatom assemblages in sewage ponds to those in nearby control ponds that have never received human sewage inputs; and (3) assess the potential and efficacy of using chironomids and diatoms for understanding eutrophication and reconstructing production-related variables, while exploring the confounding effects of recent climate warming (Smol, 2010).

Materials and methods

Site description

Resolute Bay (74°41'11"N, 94°54'33"W), Nunavut, is on the southwestern coast of Cornwallis Island in the Canadian Arctic archipelago (Fig. 1). Resolute Bay and the surrounding area are classified as having a polar desert climate with a current mean annual temperature of -16.4°C and mean annual precipitation of 150 mm (Environment Canada, 2012). A weather station was built near Resolute Bay in 1948, and an air base (Department of Transportation, or "North Base") was constructed in 1949. North Base held a working population of ~ 150 people between 1949 and 1971, and the sewage from the base was disposed of directly onto the landscape through a series of utilidors or above ground pipes (photos in Douglas & Smol, 2000). Sewage flowed from each utilidor output along a north-to-south watercourse that spanned ~ 2 km until reaching the terminal site, Meretta Lake (Fig. 1). Our study sites include the four "sewage" ponds along one of the disposal pathways north of Meretta Lake.

The utilidor that released sewage through the pathway containing the four sewage ponds was dismantled in 1979, and all sewage inputs along this watercourse ceased at that time. A second utilidor remained in operation at another location until 1998; however, none of the sewage along this pathway would have entered into the four sewage ponds used in this study. The sewage ponds were informally named R-10, R-11, R-12, and R-13; with sewage outputs traveling from R-13, through R-12, then R-11, and finally R-10, before reaching Meretta Lake (Figs. 1, 2). In addition to the sewage ponds, two nearby control sites, informally named R-1 and R-2, that have never

received sewage inputs were included in the study (Figs. 1, 2).

The pH of the sewage ponds over our 18-year sampling period remained stable at $\text{pH} \sim 9$, whereas the control ponds maintained a pH of 8.5 over the same time period. Temperature in the Resolute Bay area has steadily increased from 1948, when meteorological measurements were first taken, until 2010 (Environment Canada, 2012). This 60-year-period shows a total increase in mean annual temperature from -17 to -16°C (Fig. 3). All ponds in this study are shallow and therefore reach relatively warm temperatures (e.g., 5 – 10°C) compared to deep ice-covered Arctic lakes during the short growing season (Figs. 4, 5).

Water chemistry

In 1993, 2002, 2006, 2009, and 2011, water samples for chemical analyses of the sewage ponds (R-10, R-11, R-12, and R-13) were taken following the identical procedures used by our lab in other High Arctic limnological work over the previous three decades (e.g., Antoniadou et al., 2003). In 1992, then each year from 1994 to 2009, and then again for 2011, water samples were collected for the control ponds (R-1 and R-2). Water was collected from ~ 10 cm below the surface, and was filtered on-site for chl-*a* and total filtered nitrogen (TN-f) according to standard methods provided by Environment Canada (1979). Water samples for total unfiltered phosphorus (TP-u), as well as the chl-*a* and TN-f filters, were analyzed at the National Laboratory for Environmental Testing (NLET) in Burlington, Ontario. Conductivity and pH measurements were obtained on-site using field meters.

Epilithic diatom sampling

Rock scrapes for diatom analyses were collected during the same approximate time interval each year (mid-July), which allows for meaningful comparisons over individual years. The sewage ponds were sampled in 1993, 2002, 2006, 2009, and 2011. These samples represent the only diatom data from R-10 and R-11, for which sediment cores could not be collected due to the rocky bottom substrate. In 1993, R-13 was considered too hazardous to sample due to the high concentration of sewage still present in the pond, and therefore the first sampling of this site did not occur

Fig. 2 Photographs of the ponds affected by sewage (R-10, R-11, R-12, and R-13), as well as control ponds (R-1 and R-2) near the Hamlet of Resolute Bay on Cornwallis Island, Nunavut. Photographs are courtesy of Christopher Grooms, Queen's University, Kingston, Canada

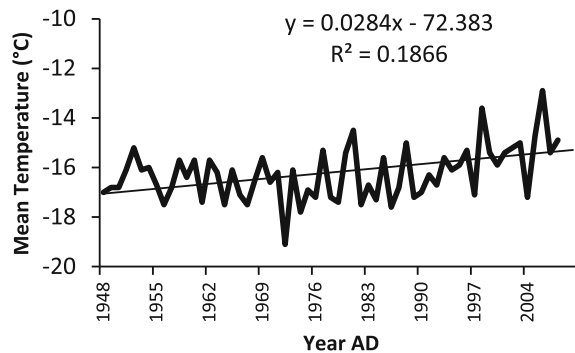
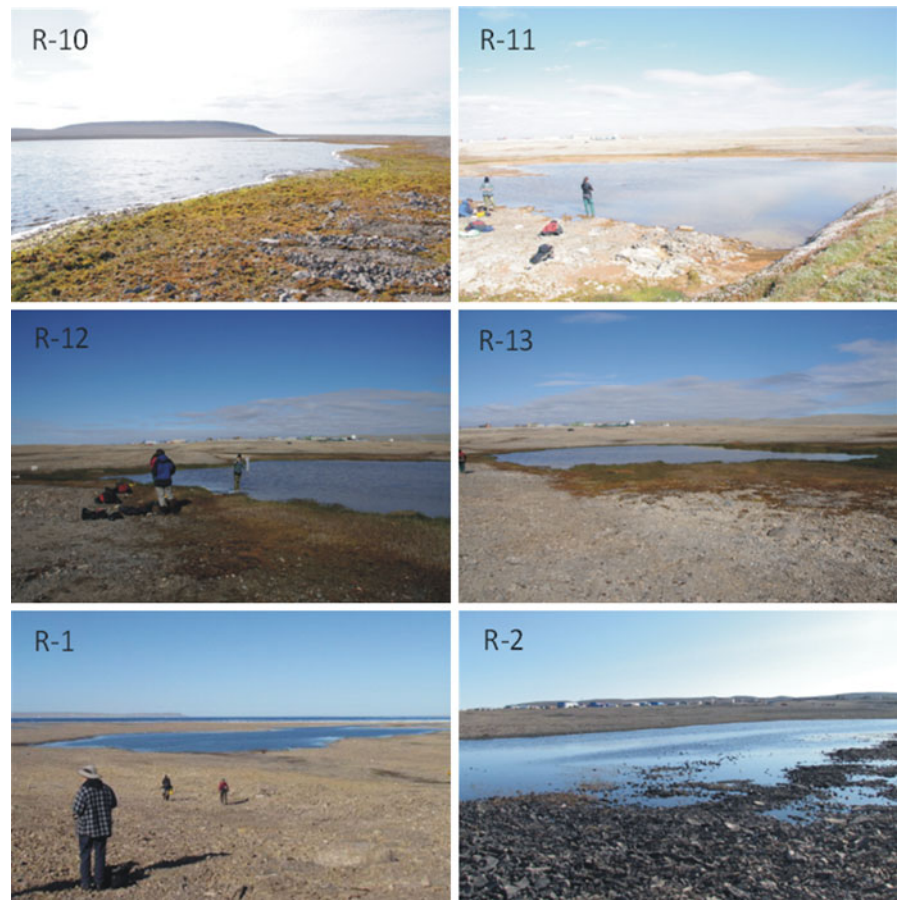


Fig. 3 Mean annual temperature for Resolute Bay, Nunavut, from 1948 to 2010. Data taken from Environment Canada (2012)

until 2006. The rock scrape samples were a composite of 4–5 rocks collected from different locations in the ponds, all of which were scraped with a small brush, rinsed into a plastic scintillation vial, and preserved with Lugol's solution.

Surface sediment and sediment core sampling

Using identical sampling methods each year, the uppermost ~ 1 cm of surface sediments of the sewage ponds was collected by hand in July of 1993, 2002, 2006, 2009, and 2011. In addition, sediment cores were retrieved using a 7.6-cm diameter Lexan[®] core tube. The sediment cores were sectioned on-site in 0.25-cm intervals (R-12 and R-13) or 1-cm intervals (R-1 and R-2) using a Glew (1988) extruder. The sediment cores from R-12 and R-13 were taken in July 2011 and those from R-1 and R-2 in July of 1992. Both chironomids and diatoms were analyzed from the same sediment core intervals. Sediment cores were dated using excess ²¹⁰Pb activities and developed into core chronologies using the constant-rate-of-supply (CRS) model (Appleby & Oldfield, 1978). The ²¹⁰Pb chronology was verified using ¹³⁷Cs, which indicates the ca. 1963 peak of aboveground nuclear weapons testing. The ²¹⁰Pb activities are presented in Appendix

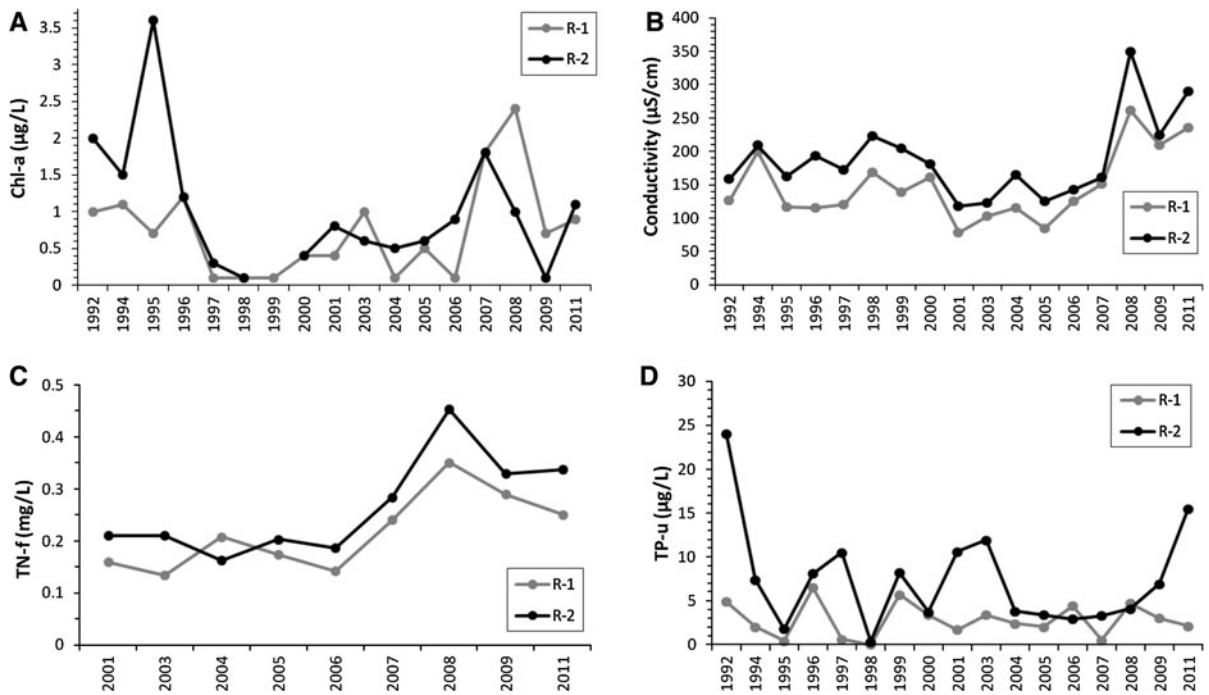


Fig. 4 Limnological variables over time for the control ponds, R-1 in gray and R-2 in black. **A** Chlorophyll-*a* (Chl-*a*) in µg/l (note: no value was available for R-2 in 1999), **B** specific conductivity in µS/cm, **C** total filtered nitrogen (TN) in mg/l, and **D** TP-u in µg/l

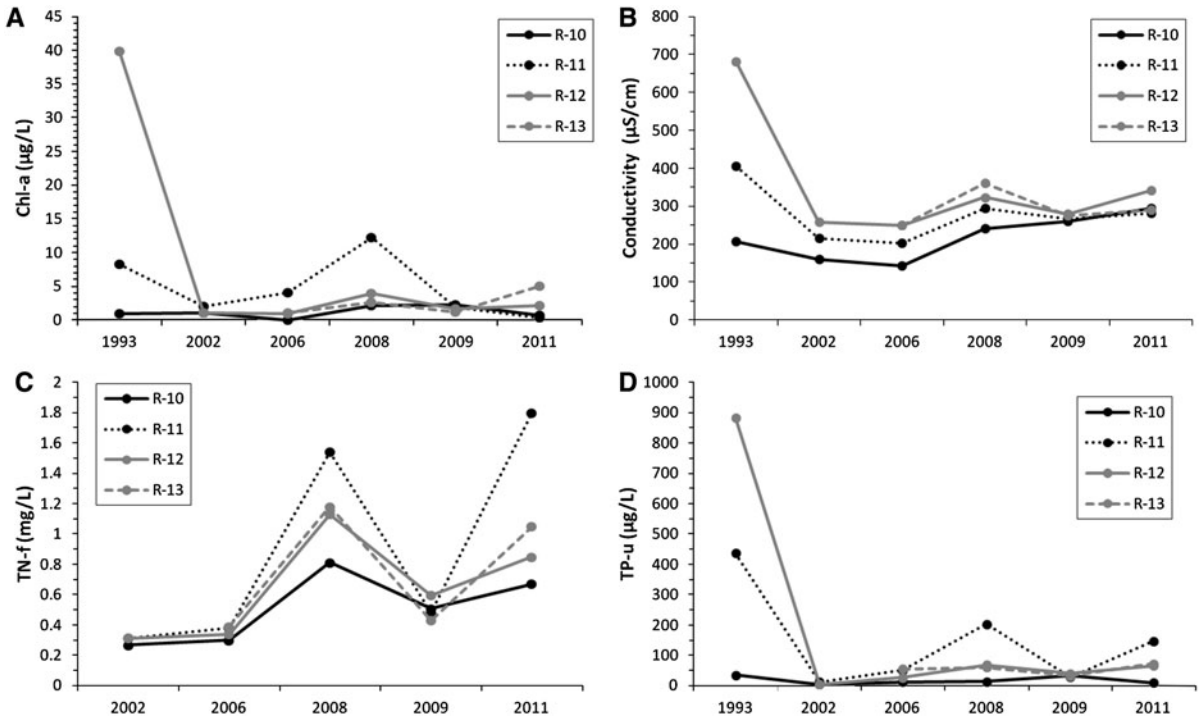


Fig. 5 Limnological variables over time for the sewage ponds, R-10 (solid black line), R-11 (dashed black line), R-12 (solid gray line), and R-13 (dashed gray line). **A** Chl-*a* in µg/l, **B** specific conductivity in µS/cm, **C** total filtered nitrogen (TN) in mg/l, and **D** TP-u in µg/l

1—Supplementary materials. The control pond, R-1, had insufficient ^{210}Pb activities, and so accurate dates could not be generated—a problem that is common in High Arctic environments (Wolfe et al., 2004).

Diatom processing and assessment

Diatoms slides were prepared for the sediment cores from ponds R-1, R-2, R-12, and R-13 and from the epilithon samples from ponds R-10, R-11, R-12, and R-13 using the procedures of Battarbee et al. (2001). Siliceous diatom valves were identified and enumerated using a Leica DMR HC light microscope. A minimum of 400 diatom valves were identified to the species level for each sample, primarily following the taxonomy of Antoniadou et al. (2008). Stratigraphies were drawn using C2 Data Analysis Program version 1.7.2 and edited with CorelDRAW Graphics Suite 12.

Chironomid head capsule collection and assessment

The collection of chironomid head capsules followed standard paleolimnological procedures outlined in Walker (2001). Identification to the lowest taxonomic level possible was achieved using a Leica DMR HC light microscope set to brightfield illumination at $100\times$ – $400\times$ magnification and primarily following the taxonomic guide of Brooks et al. (2007). A minimum of 50 whole head capsules were identified for each interval (when possible), as it is the statistically relevant minimum count required for making inferences about chironomid assemblages (Quinlan & Smol, 2001a). Minimum head capsule counts were not achieved for all samples (discussed below), but are reported nonetheless as they still provide important ecological information about the assemblage.

Chironomid head capsules were collected from the surface sediments of R-10, R-11, R-12, and R-13 (between the years of 1993 and 2011; data provided as supplementary material in Appendix 2—Supplementary materials). Stratigraphies for the chironomid assemblages from the sediment cores of R-12 and R-13 (collected in July 2011) as well as R-1 and R-2 (collected in July 1992) were created using C2 Data Analysis Program version 1.7.2 and edited with CorelDRAW Graphics Suite 12.

Statistical analysis

Diatoms from the sediment cores were assessed by indirect ordination using a detrended correspondence analysis (DCA) to compare the assemblages of the sewage ponds (R-12 and R-13) with those of the control ponds (R-1 and R-2). A similar analysis was performed for chironomids from R-12, R-13, and R-2 using a principle component analysis (PCA). The chironomid samples from R-1 could not be included in this analysis because counts were too low to yield reliable relative abundance estimates (Quinlan & Smol, 2001a). In addition, an individual PCA was run for each sediment core (R-12, R-13, R-1, and R-2) for both diatoms and chironomids revealing the main direction of variation in fossil assemblages over time (plotted as “PCA axis 1” on the right-hand side of each stratigraphy). All species data were $\log(x + 1)$ transformed, and all analyses were completed using CANOCO 5.

Results

Water chemistry

The TP-u values in the control ponds have remained low over the past two decades with values ranging from below detection limits ($<0.2 \mu\text{g/l}$) to $6.5 \mu\text{g/l}$ in R-1 and from 0.4 to $24 \mu\text{g/l}$ in R-2 (Fig. 4). This is in marked contrast to the sewage ponds that, following the time of sewage inputs, recorded values ranging from 35 to $883 \mu\text{g/l}$ (Fig. 5). TP-u values in the sewage ponds decreased dramatically early in our monitoring program. For example over a ~ 10 -year-period between 1993 and 2002, TP-u values dropped from 883.5 to $4.1 \mu\text{g/l}$ in R-12, from 435 to $12.4 \mu\text{g/l}$ in R-11, and from 35 to $4.7 \mu\text{g/l}$ in R-10. R-13 was not sampled (due to health concerns from the high concentration of sewage in the pond) until 2006, and so no record of a dramatic decrease in measured nutrients can be documented, although recovery could be surmised from simple visible changes in the pond.

Values of TN-f were similarly greatly elevated in the sewage ponds compared to the control ponds, as is clearly demonstrated by the ranges of measured values (Figs. 4, 5). TN-f values in the sewage ponds ranged from 0.268 to 1.18 mg/l (Fig. 5), whereas the range of TN-f values in the control ponds spanned from 0.159

to 0.453 mg/l over the ~20-year period of water chemistry sampling (Fig. 4). The TN-f values of the control ponds show an increase of approximately 0.1 mg/l over the past few years of sampling, and approximately a 0.6 mg/l increase in the sewage ponds.

The values for chl-*a* in the sewage ponds were elevated compared to the values in the control ponds. For example, in 1993 the chl-*a* in R-11 was 8.3 and 39.9 µg/l in R-12 (Fig. 5), whereas in the two control ponds it was 1 µg/l in R-1 and 2 µg/l in R-2 in 1992 (Fig. 4). The chl-*a* values in R-1 and R-2 remained relatively stable until 2011, although the values in R-11 and R-12 decreased to 0.3 and 2.1 µg/l, respectively, over the same time.

The specific conductivity for the two control ponds was similar in value, ranging from 78 to 261 µS/cm in R-1 and 118 to 349 µS/cm in R-2 (Fig. 4). In both control ponds, conductivity increased between 2008 and 2011. R-10 is the largest sewage pond that is furthest from the sewage output, and showed a very similar pattern in conductivity to the control ponds (Fig. 5). However, the conductivity in the sewage ponds R-11 and R-12 was higher than in the control ponds and showed a pattern of decline from 1993 to 2006 (Fig. 5). In R-11 the conductivity was 405 µS/cm in 1993 and declined to 215 µS/cm by 2006, staying relatively stable near 200 µS/cm. R-12 had a conductivity of 680 µS/cm in 1993 which decreased to 249 µS/cm by 2006. R-13 showed no discernible pattern in conductivity, likely because it was not sampled until 2006, though its values from 2006 and onwards were similar to those of R-11 and R-12 (Fig. 5). In all sewage ponds, there is a slight increase in conductivity from 2006 to 2011 (Fig. 5).

Diatom assemblages

Epilithic rock scrapes

The epilithic assemblages in the four sewage ponds were dominated by eutrophic indicators including high relative abundances of *Nitzschia perminuta*, *Nitzschia alpina*, and *Fistulifera saprophila* (Fig. 6). The dominance of these three taxa has gradually declined since 1993 in R-10, R-11, and R-12, and *Cymbella cleve-eulerai* and *Achnanthydium minutissimum* have increased in abundance. A nutrient gradient is apparent among the four sewage ponds, with decreasing dominance of the nutrient-tolerant taxa

(e.g., *N. perminuta*, *N. alpina*, and *F. saprophila*) in the ponds further from the utilidor outfall (e.g., R-10; Figs. 1, 6).

Sediment cores

The diatom assemblages in the sewage pond sediment cores (R-12 and R-13, Fig. 7A, B) were characterized by high relative abundances of *N. perminuta* and *N. alpina*. In R-12 at 4 cm depth, two taxa, *Cyclotella striata* and *Cyclotella meneghiniana*, appear alongside *Stephanodiscus minutulus*, all of which subsequently disappear circa 1970 (Fig. 7A). This finding is reflected in the PCA axis 1 scores which show a sharp increase and decrease during the same time (Fig. 7A). In contrast, the diatom assemblage in R-13 remained relatively stable over time, though a change in the PCA axis 1 scores likely reflect the subtle decreases in *Nitzschia* taxa and the appearance of *Cymbella cleve-eulerai* by the late 1990s (Fig. 7B). The two control ponds (R-1 and R-2) recorded markedly different assemblages compared to the sewage ponds, with dominant species including *A. minutissimum* and several *Cymbella sensu lato* taxa (Fig. 7C, D). This is further supported by the fact that sewage pond sediment intervals group separately from the control pond intervals in the DCA biplot (Fig. 9B, C).

Chironomid assemblages

Surface sediments

Low chironomid abundances were recorded in the surface sediment collections of all ponds, and therefore relative abundance data may be misleading for these samples (Quinlan & Smol, 2001a). However, species presence–absence data are provided for each pond for every year that sediments were collected (Appendix 2—Supplementary materials). As no sediment cores were taken from R-10 and R-11, these surface sediment data are the only samples of chironomid assemblages in these ponds. Examination of the surface samples showed that undifferentiated *Tanytarsini* species were found most, followed by *Tanytarsus gracilentus*-type. Other common chironomids included *Corynoneura arctica*-type, *Hydrobaenus/Oliveridia*, *Metriocnemus hygropetricus*-type, *Psectrocladius* group, *Chironomus plumosus*-type, and

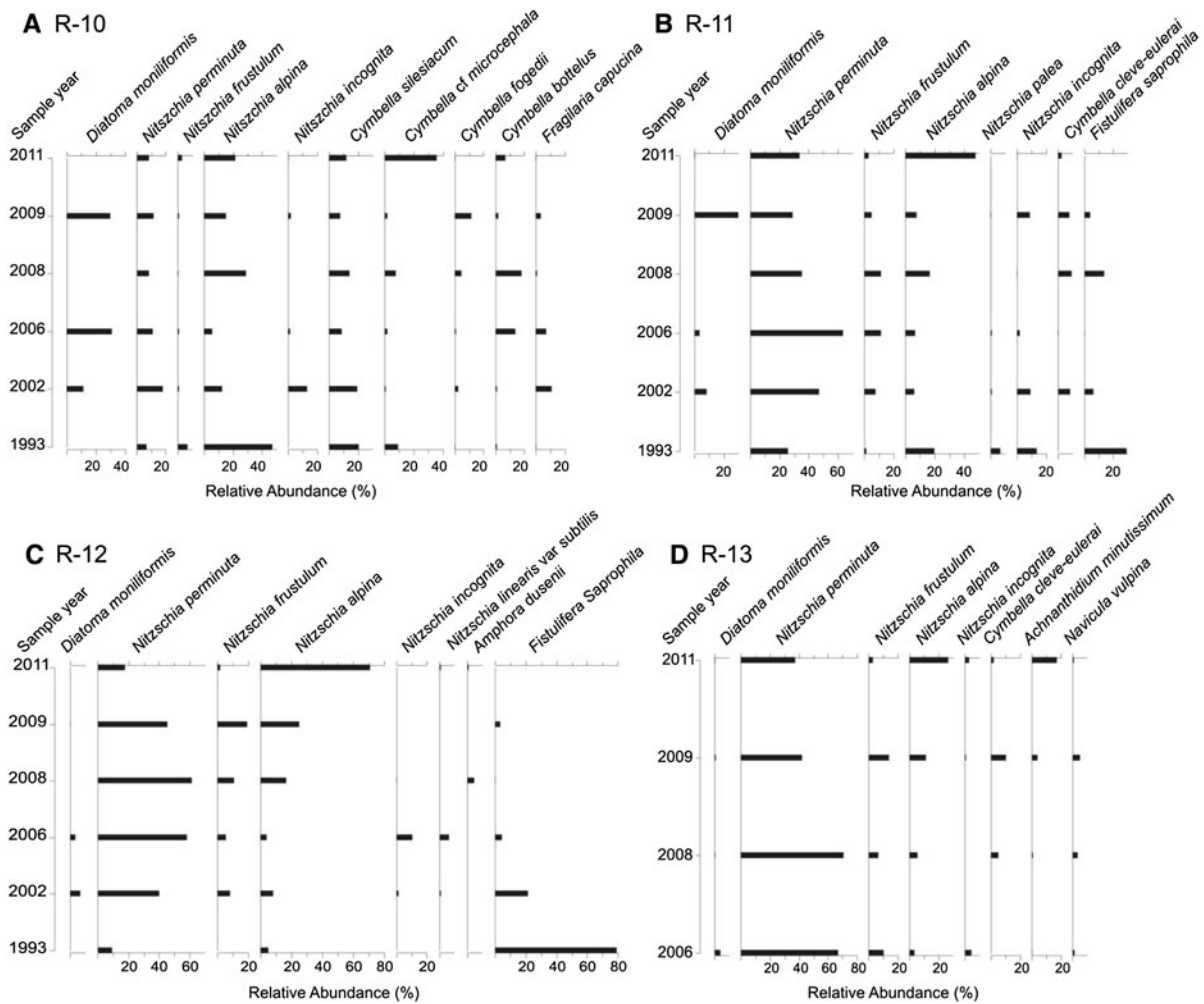


Fig. 6 The epilithic diatom assemblages for all sewage ponds **A** R-10, **B** R-11, **C** R-12, and **D** R-13 for several sampling years between 1993 and 2011

Procladius. Chironomid head capsules were notably more abundant in the two ponds closest to the sewage outfall, R-12 and R-13, compared to the two ponds furthest from the sewage outfall, R-10 and R-11.

Sediment cores

Both sewage ponds (R-12 and R-13) have similar chironomid assemblages, with the most common taxa being undifferentiated Tanytarsini species, followed by *T. gracilentus*-type, as well as *C. arctica*-type, *Hydrobaenus/Oliveridia*, *M. hygropetricus*-type, and *Psectrocladius* group (Fig. 8A, B). Trace abundances of *C. plumosus*-type and *Procladius* were present in

both R-12 and R-13. No major changes in chironomid assemblage are apparent over the time of sewage inputs (1949–1979), although by the late 1980s *C. arctica*-type appears and continues to increase in relative abundance to the present, as reflected by increases in the PCA axis 1 scores from negative to positive values (Fig. 8A, B). Head capsule abundance increases from the bottom of the core and remains constant at ~200–300 head capsules per gram dry sediment by approximately the 1970s for both R-12 and R-13, with slight decreases beginning in the early 2000s.

The chironomid assemblages recorded in the oligotrophic control ponds (R-1 and R-2) are similar

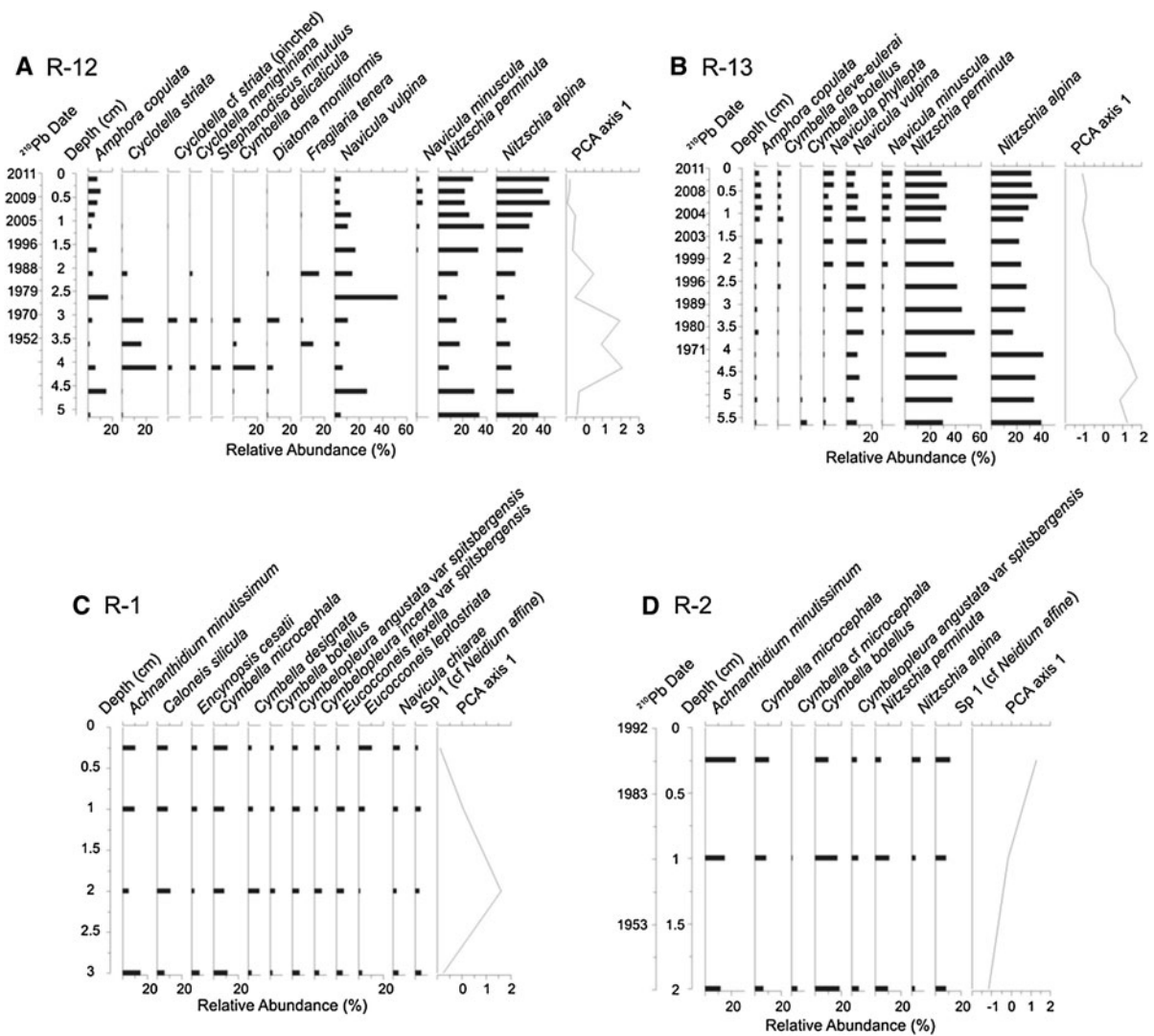


Fig. 7 The diatom species assemblage changes of the dominant taxa from the sediment cores for sewage ponds R-12 (A) and R-13 (B), as well as for the control ponds R-1 (C) and R-2 (D), presented as percent relative abundance (%). ²¹⁰Pb dates in years AD are given to the left of the R-12, R-13, and R-2

stratigraphies. Sediments from R-1 had insufficient ²¹⁰Pb activities to generate dates (see Appendix 1—Supplementary materials). PCA sample scores from axis 1 are plotted on the right-hand side of each stratigraphy (PCA axis 1)

in terms of the species present to those in the eutrophic sewage ponds (R-12 and R-13, Fig. 8). Undifferentiated Tanytarsini species, *C. arctica*-type, *Hydrobaenus/Oliveridia*, *M. hygroptericus*-type, and *Psectrocladius* group dominate, with low abundances of *C. plumosus*-type and *Procladius* (Fig. 8C, D). The most notable difference between the control and sewage ponds is not in the taxa that make up the assemblages, rather that the relative abundance of *C. plumosus*-type is slightly greater in the sewage ponds, which typically had 30–40

times greater concentrations of head capsules per gram dry weight compared to the control ponds (Fig. 8). In R-2, a notable increase in head capsules per gram dry sediment (HC/g DM) occurs near the surface of the core (Fig. 8D). According to the PCA, the sewage ponds sediment intervals separate from the control pond intervals based primarily on differences in the relative abundances of *T. gracilentus*-type, though this must be interpreted with caution because counts from the control ponds were low (Fig. 9A).

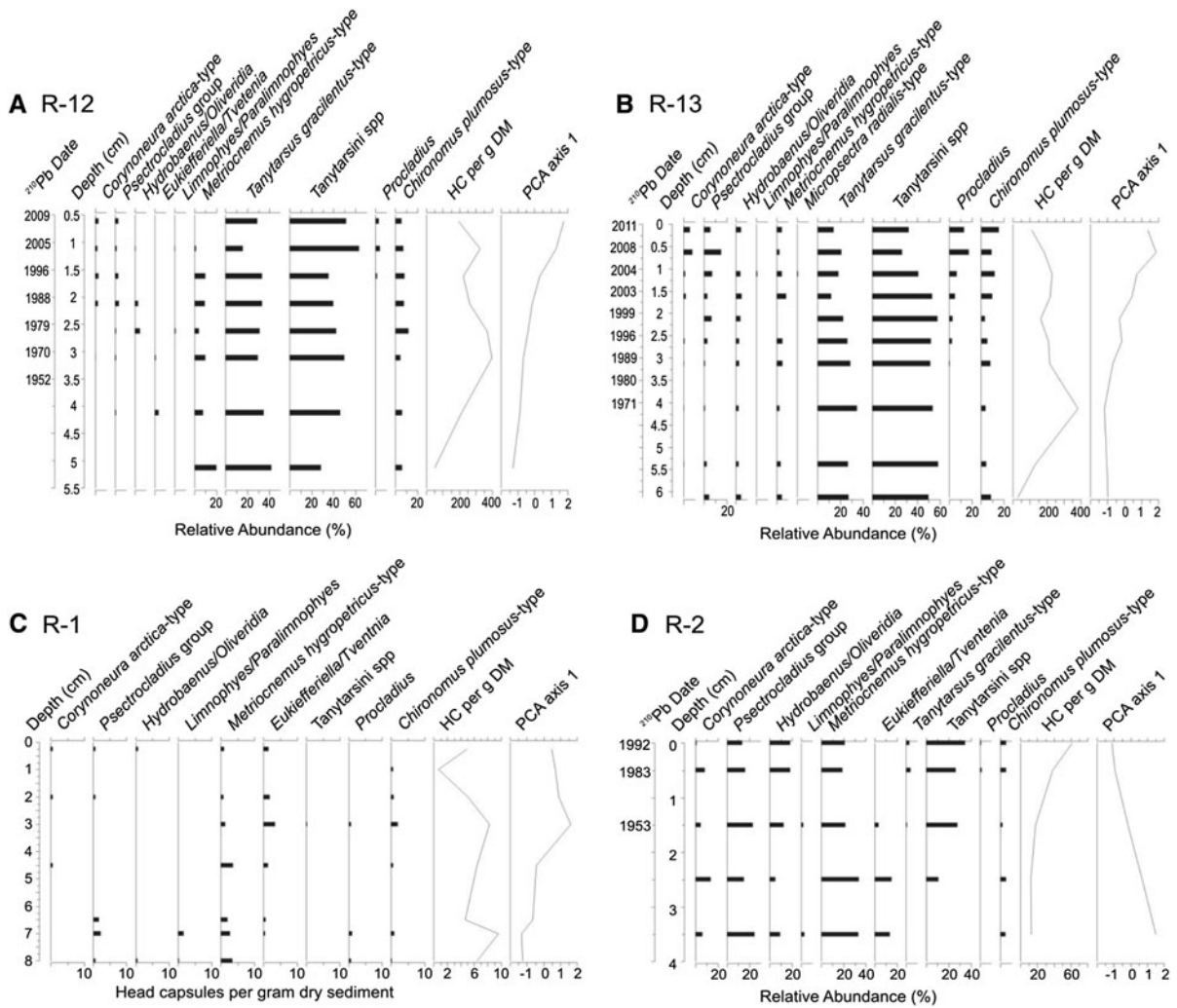


Fig. 8 The chironomid assemblage changes of the dominant taxa from the sewage pond core R-12 (A) and R-13 (B), as well as for the control pond R-2 (D), presented as relative abundance (%). Data for the other control pond R-1 (C) are presented as number of head capsules per gram of dry sediment (HC/g DM) due to the paucity of remains. For all ponds, the number of head capsules per gram of dry sediment is shown on the *rightmost*

side of each stratigraphy (HC per g DM). ²¹⁰Pb dates in years AD are given to the *left* of the R-12, R-13, and R-2 stratigraphies. Sediments from R-1 had insufficient ²¹⁰Pb activities to generate dates (see Appendix 1—Supplementary materials). PCA sample scores from axis 1 are plotted on the *right-hand side* of each stratigraphy (PCA axis 1)

Discussion

Limnological responses to changing sewage inputs

Our limnological monitoring program of the sewage ponds began in 1992, which is 13 years after the cessation of direct sewage inputs to the ponds [a history of the sewage inputs is discussed in Douglas & Smol (2000)]. Our data show changing production-related variables in the sewage pond waters over time

(Fig. 5). For example, in R-11, R-12, and R-13, TP-u, chl-*a*, and conductivity decreased drastically from the 1993 sampling year to 2006, the next year data were collected (Fig. 5). This trend is not apparent in R-10, which is the farthest from the sewage outlet and has a much larger catchment, which may be releasing nutrients from previous years’ accumulation (Fig. 5). Because the water chemistry measurements begin 13 years after sewage inputs stopped, we do not record eutrophication maxima in the ponds nor representative

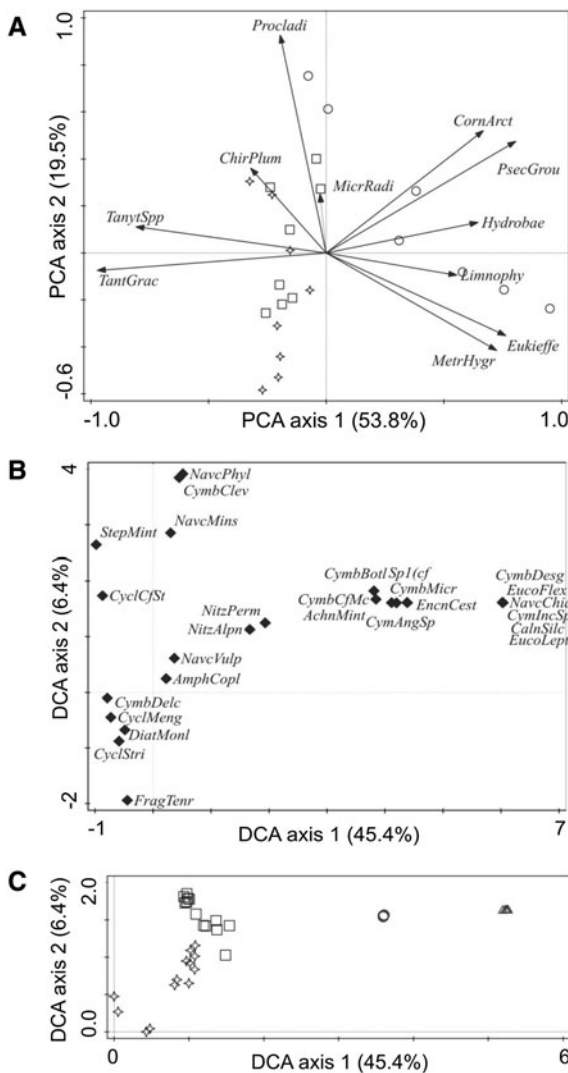


Fig. 9 **A** Principle component analysis biplot showing sediment core intervals (*points*) and chironomid species (*arrows*) for ponds R-2 (*circle*), R-12 (*star*), and R-13 (*square*). R-1 was not included in the analysis due to low counts of head capsules. DCA plot showing diatom species distribution (**B**) and sediment core intervals (**C**) from ponds R-1 (*triangle*), R-2, R-12, and R-13 (represented using the same *symbols* as above). Species abbreviations are given in Appendix 3—Supplementary materials

temporal trends of chemical recovery (including the rate or trajectory). However, the studies done of the terminal sewage basin, Meretta Lake, have more complete temporal records of recovery from eutrophication showing a slow continuous recovery from 1998 to the present (Douglas & Smol, 2000; Michelutti et al., 2002; Antoniadis et al., 2011).

Our water chemistry data also show strong evidence of a chemical gradient among sewage ponds, as higher values of production-related variables are recorded in ponds closest to the sewage output. This trend would likely be apparent in R-13, but we do not have data for R-13 before 2006 (as in fact the pond appeared to be so contaminated by sewage we chose not to sample it before 2006 for health concerns). As expected, there is no evidence of declining nutrients and primary production in the control ponds R-1 and R-2, and their concentrations are typical of other unaffected sites in the Arctic (Fig. 4; Douglas & Smol, 1994) and the rest of Cornwallis Island (Michelutti et al., 2007b). The only change in the water chemistry of the control ponds is the slight increase in conductivity and TN-f that both ponds experience by 2008, which is most likely linked to recent warming, as Resolute Bay has seen increases in mean annual temperature over the past 60 years (Fig. 3). Warming temperatures can be linked to greater evaporation during the ice-off period, and thereby concentrate ions in the water column (Smol et al., 2005; Smol & Douglas, 2007b). This trend is also apparent in the sewage ponds, as conductivity shows increases from 2006 to 2011, though it should be noted that these changes are more subtle than the early decreases linked to the cessation of sewage inputs (Fig. 5). Furthermore, TN-f has likewise increased recently in the sewage ponds, however, unlike most other water chemistry variables measured, TN-f was not recorded in our dataset until 2002, and thus our data do not show the elevated TN-f levels we would expect in the early 1990s.

Diatom response to eutrophication and recovery from the sediment cores

The diatom assemblages in the sediment cores from the two sewage ponds (R-13 and R-12) are dominated by *N. perminuta* and *N. alpina*. Although these two *Nitzschia* taxa are common to Arctic freshwaters (Antoniades et al., 2008), in high-latitude regions they typically only occur in large abundances in nutrient-rich, eutrophic lakes and ponds (e.g., Michelutti et al., 2007a; Keatley et al., 2011). The markedly different diatom assemblages between the sewage ponds and the nearby control ponds (Figs. 7, 9B, C) suggest that sewage inputs have altered the diatom assemblages in the affected ponds. This is in contrast to the fossil

chironomid data that show no changes in species present in these same impacted and control ponds (Fig. 8).

Though the response of the sewage pond diatoms to eutrophication is subtle, R-12 shows a likely response to sewage inputs around the 4-cm depth (before ~1952 according to our ^{210}Pb dates) as several taxa indicative of high conductivity (*Cyclotella striata* and *Cyclotella meneghiniana*) and high TP (*Stephanodiscus minutulus*) appear, and subsequently disappear circa 1970. This change is reflected in a PCA of the diatom assemblages in the R-12 core, as the sample score increases and decreases over the same time frame, indicating a notable assemblage change had occurred (Fig. 7A). The disappearance of these taxa approximately corresponds to the cessation of sewage inputs to the ponds in 1979 (Douglas & Smol, 2000), though not exactly due to the difficulty in obtaining precise dates. Our ^{210}Pb dates should be treated as approximate estimates of the timing of changes in our sediment cores, as ^{210}Pb activity in most Arctic sediments is often too low to give precise dates (Wolfe et al., 2004). The appearance and disappearance of diatom taxa indicative of high TP and high conductivity were not apparent in R-13 likely due to low resolution or dating issues, though both R-12 and R-13 record elevated abundances of *Nitzschia* taxa, which, as noted above, are typically only recorded at such high abundances in eutrophic systems in the High Arctic (e.g., Michelutti et al., 2007a; Keatley et al., 2011). The change in PCA axis 1 sample scores in R-13 by the late-1990s may reflect subtle decreases in the relative abundances of *Nitzschia* taxa.

Epilithic diatom response to continuing recovery

The epilithic rock samples provide an annual resolution of diatom assemblages (because winter ice effectively scrapes away the previous year's growth) for all the sewage ponds and illustrate how closely diatoms track even subtle changes along the nutrient gradient among the sewage ponds. Furthermore, the epilithic samples represent the only record of diatom assemblages available for Ponds R-10 and R-11. Pond R-13 is closest to the sewage outfall, and the epilithon are dominated by *Nitzschia* taxa, which at these high abundances typically indicate elevated nutrient levels (Fig. 6). In recent years, however, *Nitzschia* taxa have gradually declined and taxa characteristic of those

found in the control sites, including *Cymbella cleve-eulerai* and *Achnantheidium minutissimum*, have increased (Fig. 6D). This shift in diatom assemblages is consistent with improving water quality variables, such as TP-u (Fig. 5), and therefore continuing biological recovery from eutrophication is evident in the epilithic diatom samples.

Ponds R-12 and R-11 are the next two closest ponds to the sewage outfall. In 1993, the epilithon in both sites was dominated by *Fistulifera saprophila*. This taxon is known to reach high abundances in eutrophic and polluted waters (Spaulding & Edlund, 2009). Indeed, *F. saprophila* reached its highest abundances during the period when TP concentrations were also highest in our record (e.g., >400 $\mu\text{g/l}$). As TP concentrations decreased below hyper-eutrophic levels (Fig. 5), *N. perminta* and *N. alpina* increased in abundance at the expense of *F. saprophila* (Fig. 6B, C).

Pond R-10 is the site furthest from the sewage outfall. In 1993, the epilithon in Pond R-10 record an assemblage dominated by *Nitzschia* taxa (Fig. 6A). The absence of *F. saprophila* suggests that, not surprisingly due to its location, R-10 was less affected by nutrient inputs compared to ponds R-12 and R-11. In the early 1990s, the epilithon is dominated by *Cymbella*, *Fragilaria*, and *Nitzschia* taxa. This is in contrast to the more eutrophic sites where one or two diatom taxa dominated the assemblages. Indeed, the higher diatom diversity recorded in the post-sewage epilithon of Pond R-10 is similar to the control pond sediment cores (Figs. 6, 7).

Epilithic diatoms from the sewage ponds record assemblage changes that are consistent with declining nutrient concentrations and gradually improving water quality variables (Figs. 5, 6). Moreover, comparing epilithic diatom assemblages among the sewage ponds shows that assemblage composition reflects the nutrient gradient created by distance from the sewage outfall. This is in contrast to the chironomid assemblages that recorded largely similar species composition between sewage-affected and control ponds, as discussed in detail below.

Chironomid response to eutrophication and recovery

The chironomid taxa that dominated the sewage ponds included *Tanytarsus gracilentus*-type and undifferentiated *Tanytarsini* species, the former being common

in Arctic sediments (Brodersen et al., 2004), and the latter being a large group made up of many ecological types (Brooks et al., 2007). We therefore refrain from over-interpreting the Tantarsini group, as the group is too ecologically broad at this taxonomic resolution. Furthermore, there are cold-stenothermic taxa, which are commonly reported in oligotrophic waters, in both the sewage ponds as well as the control ponds (e.g., *C. arctica*-type, *Hydrobaenus/Oliveridia*, *M. hygropetricus*-type, and *Psectrocladius* group). In fact, the chironomid species present in the sewage ponds (R-12, R-13) were broadly similar to those recorded in the oligotrophic control ponds, as was the case for the seabird-eutrophied ponds and reference sites at Cape Vera (Stewart et al., 2013). Nonetheless, taxa typically considered eutrophic (e.g., *Chironomus plumosus*-type and *Procladius*) occurred at greater relative abundances in the sewage ponds, which also had much larger numbers of head capsules retrieved from the sediments, likely reflecting greater chironomid production as a result of greater food availability (Fig. 8). The similarities in species present between the sewage and control ponds demonstrate that nutrient concentrations are not directly affecting chironomid species assemblages. This is further corroborated by our observations that chironomid assemblages in the sewage ponds showed no directional compositional changes during the periods when the trophic status of the ponds changed the most, in contrast to the diatom assemblages. Conversely, the Cape Vera study ponds have nutrient concentrations that are consistently elevated over time because of the prolonged presence of the seabird colony, and thus both chironomids and diatom assemblages show no changes throughout the sediment record (Keatley et al., 2011; Stewart et al., 2013).

Chironomids feed on algal matter and detritus, and are thus undoubtedly indirectly affected by nutrients through their food source. Chironomids may respond to both increases in food quantity and quality. For example, chl-*a* concentrations in the sewage ponds are generally much higher than in the control sites (Figs. 4, 5), meaning food availability is greater, which then gives rise to the greater abundance of chironomids in the sewage ponds compared to the control ponds. Changes in the type of food available to the chironomids also may have occurred, as indicated by changes in diatom assemblages over time (in both epilithic and sediment core samples) in most of the

sewage ponds (Figs. 6, 7). Interestingly, the chironomid species assemblages in the sewage ponds show no directional assemblage shifts over periods of eutrophication, despite changes to both the availability and type of food source. This indicates that the primary control on species assemblage shifts for chironomids in these ponds is not nutrient concentrations.

In other studies, changes in lake trophic status have been linked to shifts in chironomid assemblages. In temperate regions, eutrophic lakes often record an abundance of *Chironomus* species, whereas oligotrophic lakes are typically characterized by *Tanytarsus* species (Thienemann, 1920, 1954; Brundin, 1949, 1956). Thus, chironomids have been used quantitatively to infer changes in production-related variables including TP (Brooks et al., 2001) and chl-*a* (Brodersen & Lindegaard, 1999). Chironomids respond indirectly to nutrient increases through increased food availability, changes in habitat structure, and hypolimnetic oxygen depletion, and so species shifts will occur with changing nutrient concentrations (Brodersen & Quinlan, 2006). However, our data indicate that chironomid assemblages are not responding directly to changes in TP or other nutrients, but rather appear to be more strongly governed by elevated oxygen concentrations caused by constant production of oxygen by algae with access to 24 h of sunlight during the Arctic summer and wind mixing of the shallow water column ($Z_{\max} < 1$ m). The only apparent response of chironomids to nutrients in our sewage ponds is the higher abundances of individuals that occur with greater food availability, as was also the case in the seabird-impacted sites of Cape Vera (Stewart et al., 2013).

Physiological and behavioral evidence shows that chironomid species respond to changes in oxygen concentrations through various mechanisms including the concentration of hemoglobin in the hemolymph (Czeczuga, 1960; Weber, 1980), the ability to switch to anaerobic metabolism (Hamburger et al., 1995), efficient osmotic and ionic regulation under anaerobiosis (Scholz & Zerbst-Boroffka, 1998), the ventilation of tube dwellings (Int Panis et al., 1995), and large body size (Heinis et al., 1994). Accordingly, chironomids have been effectively used to infer past changes in hypolimnetic oxygen under eutrophication because of their strong relationships with oxygen depletion (Quinlan et al., 1998; Quinlan & Smol, 2001b). Our data on these eutrophic but well-oxygenated ponds

indicate that dominant chironomid taxa do not change with eutrophication if oxygen concentrations remain elevated.

Temperature is another factor that controls chironomid assemblage composition, as it governs the metabolic rate of chironomids (Eggermont & Heiri, 2012). In deep, cold, and eutrophic Meretta Lake (the terminal lake for North Base sewage disposal in Resolute), the cold climate prevented the proliferation of chironomids until the late 1970s, when anthropogenic climate warming reduced ice cover enough to allow the persistence of chironomids (Antoniades et al., 2011). This trend is not apparent in our small sewage ponds nor is it apparent in our control ponds, as these ponds are so shallow that they thaw and warm relatively early in the growing season, and certainly much earlier than Meretta Lake (Douglas & Smol, 2000). Though the cold climate does not prevent chironomid production in the sewage ponds like it did in Meretta Lake, the effects of temperature on chironomids are evident in both the sewage and control ponds. By the late 1980s, in both R-12 and R-13, *C. arctica*-type appears and increases in abundance until the present, as do several other taxa, and is reflected in the changes of the PCA sample scores from negative to positive values (Fig. 8A, B). This is similar to the changes documented in the oligotrophic ponds of Cape Herschel, Ellesmere Island, where increases in *Corynoneura* taxa, as well as increases in chironomid diversity, were attributed to the effects of recent climate warming (Quinlan et al., 2005). A marked directional shift in chironomid assemblage in our previous study of seabird-impacted ponds of Cape Vera can also likely be attributed to recent climate warming because of similar chironomid changes in sites ~200 km apart, as well as the nature of the species involved (Stewart et al., 2013). Furthermore, R-2, one of the oligotrophic control ponds, has recorded increasing abundances of head capsule concentrations in recent years, suggesting that greater ice-off periods have extended the growing season, allowing for greater numbers of chironomids. The evidence of recent climate warming in the Resolute Bay ponds adds to the growing body of scientific literature documenting the effects of anthropogenic climate change in the circumpolar region (Smol et al., 2005; Smol & Douglas, 2007a, b).

Our Resolute Bay pond findings are consistent with our previous studies of chironomid assemblages in

seabird-affected ponds at Cape Vera on Devon Island in the Canadian Arctic (Michelutti et al., 2011; Stewart et al., 2013). By using the shallow eutrophic ponds of Cape Vera, we showed, using a surface sediment approach, that so-called “oligotrophic” assemblages dominated eutrophic ponds, likely because of high oxygen levels. This was confirmed using detailed sediment core analysis, showing that chironomid assemblages were always characterized by so-called “oligotrophic” taxa in ponds that have clearly always been eutrophic, as the seabird colony has existed for the duration of the sediment record (Stewart et al., 2013). Moving from naturally eutrophic seabird-impacted ponds to the culturally eutrophied ponds of Resolute, we show that the Cape Vera study was not an isolated phenomenon. The dominance of the so-called “oligotrophic” chironomid assemblages in the well-oxygenated sewage ponds demonstrates that nutrient levels do not directly affect chironomid assemblages.

Evidence of recent climate warming

The influence of recent climate warming on the physical and biological limnology of the study ponds also seems apparent. Mean annual temperature records gathered by Environment Canada (2012) show an increase in the local temperature of Resolute Bay for approximately the past 20 years (Fig. 3), which is consistent with recent warming in other regions of the Arctic (Smol et al., 2005). In our study, the water chemistry and the chironomid data suggest that this recent temperature increase has had an effect on the chemical and biological properties of these ponds.

In both the control ponds (R-1 and R-2) and sewage ponds (R-10, R-11, R-12, and R-13), specific conductivity and TN-f have increased in our monitoring data, which is likely due to recent warming that has caused increased evaporation rates, leading to the concentration of ions and nutrients in the water column. The phenomenon of increased solute concentrations due to evaporation, and even unprecedented drying of ponds, has been recently documented at Cape Herschel, Ellesmere Island (Smol & Douglas, 2007b). Contrasting our findings with those from nearby Char Lake, which is large and deep, illustrate that the small size of our study ponds makes them especially susceptible to increased evaporation due to warming, as larger lakes tend to have delayed responses to warming given their

larger thermal inertia (Michelutti et al., 2003). Finally, the increase in conductivity and TN-f in our ponds is opposite to what was expected of the water chemistry in the sewage ponds, as we would have hypothesized continuing recovery from eutrophication. Our water chemistry monitoring clearly shows the confounding effects of recent warming, and furthermore illustrates the need to consider multiple stressors simultaneously.

The chironomids of the sewage and control ponds are responding to recent temperature increases in that head capsules per gram dry sediment (an indication of overall chironomid production) has tripled in the topmost centimeter of R-2 (Fig. 8). This phenomenon has been observed in the control site of Cape Vera as well, and was attributed to recent warming allowing for a longer growing season, and therefore greater chironomid production (Stewart et al., 2013). Furthermore, the increase of *Corynoneura* in the recent sediments of both sewage ponds is similar to the increases observed at Cape Herschel, which was also attributed to recent climate warming (Quinlan et al., 2005). The appearance of *Corynoneura* in the sediment cores of the sewage ponds coincides with the increases in conductivity and TN-f that also suggest the effects of recent climate warming.

The recent subtle changes in both water chemistry and chironomid assemblage observed in the Resolute ponds cannot be attributed to human-mediated eutrophication, as the changes occur in both the control ponds as well as the sewage ponds, and taxonomic changes have no linkage to previously claimed nutrient preferences. We therefore conclude that the study ponds at Resolute Bay are responding to recent warming in a similar fashion to what has been documented elsewhere in the Arctic (Smol et al., 2005; Smol & Douglas, 2007a, b).

Conclusions

Our Resolute pond dataset is a rare example of a long-term limnological monitoring program from the High Arctic that allows us to track and assess chemical and biological recovery from eutrophication. We used modern samples (water chemistry, surface sediments, and rock scrapes) from several years, as well as sediment cores, to track the changes in diatom and chironomid assemblages through time. The water chemistry data track chemical recovery from declining

sewage inputs, and also record a nutrient gradient reflecting distance from the sewage outfall. The epilithic diatom assemblages closely tracked nutrient subsidies from sewage inputs and subsequent recovery over time. Furthermore, differences in diatom assemblages are evident between control- and sewage-affected sites, as well as along a nutrient gradient in the sewage ponds, which are consistent with the known nutrient requirements of many of these taxa. In contrast, chironomid assemblages from sediment cores collected from the sewage ponds did not reflect the eutrophic nature of the ponds nor did the assemblages change with decreasing nutrient concentrations. Rather, chironomid assemblages from sewage ponds resembled those of nearby control ponds, being dominated by chironomid taxa typically referred to as “oligotrophic.” Finally, chironomid assemblages showed evidence of the effects of recent climate warming in both the control ponds and sewage ponds, as has been documented elsewhere in circumpolar regions.

The lack of major differences in the chironomid assemblage composition between sewage ponds and control ponds indicates that nutrients are not directly affecting chironomid species, as they do diatoms. Whereas diatom assemblage composition has been shown to be an effective tool for quantitatively inferring total phosphorus (reviewed in Hall & Smol, 2010), chironomids have no direct physiological connection to nutrient concentrations. Instead, chironomids have complex responses to eutrophication as reflected through interacting factors such as oxygen concentration, habitat structure, and food availability. Our findings show that chironomid survival and reproduction are more directly controlled by oxygen concentrations and temperature, which in turn may have strong relationships with nutrients.

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References

- Antoniades, D., M. S. V. Douglas & J. P. Smol, 2003. Comparative physical and chemical limnology of two Canadian High Arctic regions: alert (Ellesmere Island, NU) and Mould Bay (Prince Patrick Island, NWT). *Archiv für Hydrobiologie* 158: 485–516.
- Antoniades, D., P. B. Hamilton, M. S. V. Douglas & J. P. Smol, 2008. Diatoms of North America: the freshwater floras of Prince Patrick, Ellef Ringnes, and Northern Ellesmere Islands from the Canadian Arctic Archipelago. *Iconographia Diatomologica*, 17. A.R.G. Gantner/Verlag, Ruggell, Liechtenstein.
- Antoniades, D., N. Michelutti, R. Quinlan, J. M. Blais, S. Boinilla, M. S. V. Douglas, R. Pienitz, J. P. Smol & W. F. Vincent, 2011. Cultural eutrophication, anoxia, and ecosystem recovery in Meretta Lake, High Arctic Canada. *Limnology and Oceanography* 56: 639–665.
- Appleby, P. G. & F. Oldfield, 1978. The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. *Catena* 5: 1–8.
- Battarbee, R. W., L. Carvalho, V. G. Jones, R. J. Flower, et al., 2001. Diatoms. In Last, W. M. & J. P. Smol (eds), *Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators*. Kluwer, Dordrecht: 155–202.
- Blais, J. M., L. E. Kimpe, D. McMahon, B. E. Keatley, M. L. Mallory, M. S. V. Douglas & J. P. Smol, 2005. Arctic seabirds transport marine-derived contaminants. *Science* 309: 445.
- Brodersen, K. P. & C. Lindegaard, 1999. Classification, assessment and trophic reconstruction of Danish lakes using chironomids. *Freshwater Biology* 42: 143–157.
- Brodersen, K. P. & R. Quinlan, 2006. Midges as palaeoindicators of lake productivity. *Quaternary Science Reviews* 25: 1995–2012.
- Brodersen, K. P., O. Pedersen, C. Lindegaard & K. Hamburger, 2004. Chironomids (Diptera) and oxy-regulatory capacity: an experimental approach to paleolimnological interpretation. *Limnology and Oceanography* 49: 1549–1559.
- Brooks, S. J., H. Bennion & J. B. Birks, 2001. Tracing lake trophic history with a chironomid total phosphorus inference model. *Freshwater Biology* 46: 513–533.
- Brooks, S. J., P. G. Langdon & O. Heiri, 2007. The Identification and Use of PalaeArctic Chironomidae Larvae in Palaeoecology. QRA Technical Guide No. 10. Quaternary Research Association, London.
- Brundin, L., 1949. Chironomiden und andere Bodentiere der südschwedischen urgebirgsseen. *Report/Institute of Fresh-Water Research Drottningholm* 30: 1–914.
- Brundin, L., 1956. Die bodenfaunistischen Seetypen un ihre Anwenbarkeit auf die Südhalbkugel. Zugleich eine Theorie der produktionsbiologischen Bedeutung der glazialen Erosion. *Report/Institute of Fresh-water Research Drottningholm* 37: 186–235.
- Czeczuga, B., 1960. Haemoglobin content of the larvae of *Tendipes fl. plumosus* L. from various levels of bed sediment. *Nature* 186: 484.
- Douglas, M. S. V. & J. P. Smol, 1994. Limnology of high arctic ponds (Cape Herschel, Ellesmere Island, N.W.T.). *Archiv für Hydrobiologie* 131: 401–434.
- Douglas, M. S. V. & J. P. Smol, 2000. Eutrophication and recovery in the High Arctic: Meretta Lake (Cornwallis Island, Nunavut, Canada) revisited. *Hydrobiologia* 431: 193–204.
- Eggermont, H. & O. Heiri, 2012. The chironomid–temperature relationship: expression in nature and palaeoenvironmental implications. *Biological Reviews* 87: 430–456.
- Environment Canada, 1979. *Analytical Methods Manual*. Water Quality Branch, Inland Water Directorate, Ottawa, ON.
- Environment Canada, 2012. Canadian Climate Normals 1971–2000 [Internet]. Accessed 2012 May 16. Available from http://www.climate.weatheroffice.gc.ca/climate_normals/results_e.html?stnID=1776&autofwd=1.
- Glew, J. R., 1988. A portable extruding device for close interval sectioning of unconsolidated core samples. *Journal of Paleolimnology* 1: 235–239.
- Hall, R. I. & J. P. Smol, 2010. Diatoms as indicators of lake eutrophication. In Smol, J. P. & E. F. Stoermer (eds), *The Diatoms: Applications for the Environmental and Earth Sciences*. Cambridge University Press, Cambridge: 122–151.
- Hamburger, K., P. C. Dall & C. Lindegaard, 1995. Energy metabolism of *Chironomus anthracinus* (Diptera, Chironomidae) under laboratory and field conditions. *Hydrobiologia* 297: 187–200.
- Heinis, F., J.-P. Sweerts & E. Loopie, 1994. Micro-environment of chironomids larvae in the littoral and profundal zones of Lake Maarsseveen I, The Netherlands. *Fundamental Applied Limnology* 124: 173–289.
- Int Panis, L., B. Godeeris & R. F. Verheyen, 1995. On the relationship between oxygen microstratification in a pond and the spatial distribution of the benthic chironomid fauna. In Cranston, P. (ed.), *Chironomids: From Genes to Ecosystems*. CSIRO Publications, Melbourne: 323–328.
- Keatley, B. E., M. S. V. Douglas, J. M. Blais, M. L. Mallory & J. P. Smol, 2009. Impacts of seabird-derived nutrients on water quality and diatom assemblages from Cape Vera, Devon Island, Canadian High Arctic. *Hydrobiologia* 61: 191–205.
- Keatley, B. E., J. M. Blais, M. S. V. Douglas, I. Gregory-Eaves, M. L. Mallory, N. Michelutti & J. P. Smol, 2011. Historical seabird population dynamics and their effects on Arctic pond ecosystems: a multi-proxy paleolimnological study from Cape Vera, Devon Island, Arctic Canada. *Fundamental Applied Limnology* 179: 51–66.
- Michelutti, N., M. S. V. Douglas & J. P. Smol, 2002. Tracking recent recovery from eutrophication in a High-Arctic lake (Meretta Lake, Cornwallis Island, Nunavut, Canada) using fossil diatom assemblages. *Journal of Paleolimnology* 28: 377–381.
- Michelutti, N., M. S. V. Douglas & J. P. Smol, 2003. Diatom response to recent climatic change in a high arctic lake (Char Lake, Cornwallis Island, Nunavut). *Global and Planetary Change* 38: 257–271.
- Michelutti, N., M. H. Hermanson, J. P. Smol, P. J. Dillon & M. S. V. Douglas, 2007a. Delayed response of diatom assemblages to sewage inputs in an Arctic lake. *Aquatic Science* 69: 523–533.
- Michelutti, N., M. S. V. Douglas & J. P. Smol, 2007b. Evaluating diatom community composition in the absence of marked limnological gradients in the High Arctic: a surface sediment calibration set from Cornwallis Island (Nunavut, Canada). *Polar Biology* 30: 1459–1473.

- Michelutti, N., M. L. Mallory, J. M. Blais, M. S. V. Douglas & J. P. Smol, 2011. Chironomid assemblages from seabird-affected high Arctic ponds. *Polar Biology* 34: 799–812.
- Quinlan, R. & J. P. Smol, 2001a. Setting minimum head capsule abundance and taxa deletion criteria in chironomid-based inference models. *Journal of Paleolimnology* 26: 327–342.
- Quinlan, R. & J. P. Smol, 2001b. Chironomid-based inference models for estimating end-of-summer hypolimnetic oxygen from south-central Ontario lakes. *Freshwater Biology* 46: 1529–1551.
- Quinlan, R., J. P. Smol & R. I. Hall, 1998. Quantitative inferences of past hypolimnetic anoxia in south-central Ontario lakes using fossil midges (Diptera: Chironomidae). *Canadian Journal of Fisheries and Aquatic Sciences* 55: 587–596.
- Quinlan, R., M. S. V. Douglas & J. P. Smol, 2005. Food web changes in arctic ecosystems related to climate warming. *Global Change Biology* 11: 1381–1386.
- Schindler, D. W., J. Kalff, H. E. Welch, G. J. Brunskill, H. Kling & N. Kritsch, 1974. Eutrophication in the High Arctic – Meretta Lake, Cornwallis Island (75° N Lat.). *Journal of Fisheries Research Board of Canada* 31: 647–662.
- Scholz, F. & I. Zerbst-Boroffka, 1998. Environmental hypoxia affects osmotic and ionic regulation in freshwater midge-larvae. *Journal of Insect Physiology* 44: 427–436.
- Smol, J. P., 2010. The power of the past: using sediments to track the effects of multiple stressors on lake ecosystems. *Freshwater Biology* 55(Suppl. 1): 43–59.
- Smol, J. P. & M. S. V. Douglas, 2007a. From controversy to consensus: making the case for recent climatic change in the Arctic using lake sediments. *Frontiers in Ecology and the Environment* 5: 466–474.
- Smol, J. P. & M. S. V. Douglas, 2007b. Crossing the final ecological threshold in high Arctic ponds. *Proceedings of the National Academy of Sciences* 104: 12395–12397.
- Smol, J. P., A. P. Wolfe, H. J. B. Birks, M. S. V. Douglas, V. J. Jones, A. Korhola, R. Pienitz, K. Rühland, S. Sorvari, D. Antoniades, S. J. Brooks, M. Fallu, M. Hughes, B. E. Keatley, T. E. Laing, N. Michelutti, L. Nazarova, N. Nyman, A. M. Paterson, B. Perren, R. Quinlan, M. Rautio, E. Saulnier-Talbot, S. Siitonen, N. Solovieva & J. Weckstrom, 2005. Climate driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences of the United States of America* 102: 4397–4402.
- Spaulding, S. & M. Edlund, 2009. *Fistulifera*. In: *Diatoms of the United States*. Retrieved 12 October 2012. Available from <http://westerndiatoms.colorado.edu/taxa/genus/Fistulifera>.
- Stewart, E. M., N. Michelutti, J. M. Blais, M. L. Mallory, M. S. V. Douglas & J. P. Smol, 2013. Contrasting the effects of climate, nutrient, and oxygen dynamics on subfossil chironomid assemblages: a paleolimnological experiment from eutrophic High Arctic ponds. *Journal of Paleolimnology* 49: 205–219.
- Thienemann, A., 1920. Untersuchungen über die Beziehungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der Fauna in norddeutschen Seen. *Archiv für Hydrobiologie* 12: 1–65.
- Thienemann, A., 1954. Chironomus. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. *Binnengewässer* 20: 1–834.
- Walker, I. R., 2001. Midges: Chironomidae and related *Diptera*. In Smol, J. P., H. J. B. Birks & W. M. Last (eds), *Tracking Environmental Change Using Lake Sediments, Vol. 4: Zoological Indicators*. Kluwer Academic Publishers, Dordrecht: 43–66.
- Weber, R. E., 1980. Functions of invertebrate haemoglobins with special reference to adaptations to environmental hypoxia. *American Zoologist* 20: 79–101.
- Wolfe, A. P., G. F. Miller, C. A. Olsen, S. L. Forman, P. T. Doran & S. U. Holmgren, 2004. Geochronology of high latitude lake sediments. In Pienitz, R., M. S. V. Douglas & J. P. Smol (eds), *Developments in Paleoenvironmental Research, Vol. 8: Long-Term Environmental Change in the Arctic and Antarctic lakes*. Springer, Dordrecht: 19–52.